O.R.P. Bininda-Emonds, G.L. Powell,
H.A. Jamniczky, A.M. Bauer & J. Theodor (eds.)

All Animals are Interesting

A Festschrift in Honour of Anthony P. Russell

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I. Introduction and reflections

All animals are interesting: an introduction to the volume

Heather A. Jamniczky[1]*, Aaron M. Bauer*[2]*, G. Lawrence Powell*[3]*, and*
Olaf R.P. Bininda-Emonds[4]

[1] Department of Cell Biology & Anatomy, University of Calgary, 3280 Hospital Drive NW, Calgary, Alberta T2N 4Z6, Canada; E-mail: hajamnic@ucalgary.ca
[2] Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA; E-mail: aaron.bauer@villanova.edu
[3] Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada; E-mail: lpowell@ucalgary.ca
[4] Institute for Biology and Environmental Sciences, Carl von Ossietzky University, Carl-von-Ossietzky-Str. 9–11, Postbox 2503, 26111 Oldenburg, Germany; E-mail: olaf.bininda@uni-oldenburg.de

This volume contains a series of contributions assembled to mark the occasion of Anthony P. Russell's retirement in 2013 from a distinguished career spanning more than 40 years in the biological sciences, nearly all of them spent at the University of Calgary. Contributors include current and former academic colleagues and collaborators, many of whom are former trainees that have benefitted greatly from Tony's wisdom and expertise over the years as they have forged their own research and teaching careers.

The *Festschrift* is edited by former trainees Aaron Bauer (Villanova University), Olaf Bininda-Emonds (Carl von Ossietzky University Oldenburg), Heather Jamniczky (University of Calgary), and Larry Powell (University of Calgary) along with colleague Jessica Theodor (University of Calgary). In an introductory chapter, Heather, Larry, and Aaron also provide some history and context for Tony's career as well as a grad's-eye view of his many contributions that span teaching, research, and academic service. Herb Rosenberg then contributes a light-hearted piece from the perspective of a long-time colleague and close friend.

The scientific contributions in this volume fall into two groupings that roughly correspond to two of the main research streams in Tony's lab. However, be-

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cause interdisciplinarity and synthesis have always been hallmarks of Tony's, these groupings are somewhat arbitrary. First, a suite of palaeontological contributions celebrates Tony's interest in evolution and the fossil record as well as serving to demonstrate both the taxonomic and geographic breadth of his approach. A former graduate student, Jim Gardner, together with long-time collaborator Don Brinkman (both Royal Tyrrell Museum of Palaeontology) begin the palaeontological contributions by introducing a new fossil frog from Alberta, which they name after a much more famous extant (?) relative and his discoverer. In the following chapter, Don describes a new fossil turtle from Saskatchewan, which he names in Tony's honour. Former post-doctoral fellow Don Henderson (Royal Tyrrell Museum of Palaeontology) follows this by describing a new specimen of the ichthyosaur *Macgowania janiceps* from British Columbia, which, although not a new species, is nevertheless remarkable for its highly complete and, even more unusually, three-dimensional skull, thereby filling many holes in our knowledge of this species. Finally, former graduate students Caleb Brown (Royal Tyrrell Museum of Palaeontology) and Michael Ryan (Cleveland Museum of Natural History), together with collaborator David Evans (University of Toronto), provide a comprehensive overview of the dinosaurian fauna of Canada, updating a list that Michael and Tony published over a decade ago in 2001.

The second, loose thematic grouping in this volume includes evolutionary, morphological and/or ecologically oriented contributions, celebrating Tony's commitment to both furthering our understanding of, and conservation of, a diversity of taxa. Former graduate student Hillary Maddin (Carleton University) begins this section by using microcomputed tomography to describe the lissamphibian braincase in detail before continuing to infer its evolutionary history as well as possible application toward unravelling the phylogeny of the group, if not non-amniote tetrapods in general. Following this, former graduate student Philip Bergmann (Clark University) surveys squamate reptiles for instances of convergent evolution of body shape in an explicit phylogenetic framework, using a comprehensive species-level phylogeny for the group that he recently published. Similarly, but on a smaller scale, Tim Higham (University of California at Riverside), a former undergraduate student, explores pedal specializations in desert-dwelling lizards, thereby making functional correlations between the perhaps surprising degree of diversity to be found on both the morphological and habitat sides of the form-function equation. Following this are two contributions examining the skull morphology of two gekkotan species in some detail. First, Juan Daza (Villanova University) and Aaron Bauer describe the cranial anatomy of the pygopodid lizard *Aprasia repens*. In so doing, they pay particular attention to those adaptations related to miniaturisation, burrowing, and ant-eating (myrmecophagy) in this species, drawing parallels with scolecophidian lizards. Thereafter, former trainee Pat Wise describes the many elements of the skull of the Leopard Gecko (*Eublepharis macularius*) using a combination of disarticulated skulls and microcomputed tomography to frame a cranial osteological reference work for this species. Bruce Young (A.T. Still University), another former trainee, then provides an extensive review of hearing in snakes, formulating explanations connecting the known physiological data with the unusual morphology of the snake ear in the broader phylogenetic context of squamate reptiles as a whole. Former student and postdoctoral fellow Matt Vickaryous (University of Guelph) and long-time colleague and friend Brian Hall (Dalhousie University) continue by re-examining the evolutionary history of the avian furcula as well as the history of the debate surrounding it. In so doing, they also highlight Tony's important contributions to this long-standing discussion, particularly his effort to refocus the debate on issues of homology. Leaving vertebrates for a chapter, Amanda Lowe (Saint Mary's University) and former undergraduate student Randy Lauff (Saint Francis Xavier University) together describe the habitat preferences of the carrion-beetle community in Nova Scotia and that of various species of *Nicrophorus* in particular. Their results highlight the importance of assessing the habitat in three dimensions (i.e., including a vertical component), something that remains comparatively rare in analogous studies. Finally, former graduate student Ranjith Weerawardhena (University of Kelaniya) highlights Tony's interest in conservation biology through his chapter summarizing the conservation status of the amphibian fauna of Sri Lanka.

Although the topic coverage in this *Festschrift* is not completely representative of Tony's incredibly diverse research interests (both taxonomically and with respect to research area), we nevertheless hope that this volume provides at least a glimpse of the breadth and scope of Tony's scientific and mentoring contributions, as well as the inspiration that he provided to us through these activities. Tony's legacy includes both a startlingly large amount of quality science as well as a strong group of former trainees who continue his tradition of scholarship in animal biology. We hope that this *Festschrift* stands as both a celebration of Tony's career as well as an impetus for future students to pursue broad and integrative inquiry in all fields of the biological sciences.

Tony Russell: a grad's-eye view

Heather A. Jamniczky[1], *G. Lawrence Powell*[2], *and Aaron M. Bauer*[3]

[1] Department of Cell Biology & Anatomy, University of Calgary, 3280 Hospital Drive NW, Calgary, Alberta T2N 4Z6, Canada; E-mail: hajamnic@ucalgary.ca
[2] Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 4N1, Canada; E-mail: lpowell@ucalgary.ca
[3] Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA; E-mail: aaron.bauer@villanova.edu

Introduction

This *Festschrift* mostly comprises contributions from those who obtained postgraduate degrees with Tony Russell as an advisor or from those who worked as postdocs with him. It seems appropriate, then, to begin the volume with a brief summary of Tony's career as a graduate and postdoctoral advisor. Tony was a complete academic, however, and we include a summary of his administrative and teaching contributions as well to highlight his extraordinary commitment to his work.

Academic career—the bare facts

Tony Russell obtained his BSc, with a focus on Botany and Zoology, from the University of Exeter in 1969. This was followed (with rather unnerving rapidity to those of us he later supervised) by a PhD in 1972 from Queen Elizabeth College, University of London for a dissertation entitled "The foot of gekkonid lizards (Reptilia: Gekkonidae): a study in functional and comparative anatomy" under the supervision of Brian Gardiner. The decades-long preoccupation with geckos and their feet that this work foreshadowed had to be temporarily shelved, at least so far as formal research was concerned, because Tony's first post-graduation academic job was a temporary posting as a Lecturer at the Roma (Lesotho) campus of the University of Botswana,

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Lesotho, and Swaziland in 1973. This was shortly followed in the summer of 1973 by an appointment as a Lecturer at the University of Calgary, the beginnings of which are remarked upon briefly by Herb Rosenberg (this volume), which marked the beginning of an undergraduate teaching career to which Tony devoted great effort in the ensuing years (see below). He did not remain at this level for very long; a promotion to the rank of Assistant Professor was attained in 1975, followed by that of Associate Professor in 1979, and full Professor in 1987. During this academic ascent, he occupied various University offices, served on too many graduate committees to list here, and maintained a vigorous engagement with various academic societies such as the Canadian Society of Zoologists. As a rule, however, his graduate students were only marginally aware of these many activities. Tony always excelled in compartmentalising his very busy life and we found that, as an academic advisor, his attention was always focussed on us (or so it seemed—a postgraduate program requires a degree of self-absorption from those engrossed in it, but postdocs also maintained this misapprehension). However, an account of Tony as a graduate advisor requires that we take all these aspects of his career into account.

Undergraduate teaching

Tony's undergraduate teaching over the years was mainly concerned with the anatomy, evolution, and systematics of the vertebrates. These are difficult and complex subjects, and he always expected hard work and discipline; the bar was set high, but he demonstrated a deep commitment to student success, radiating an infectious enthusiasm about his subject matter. Tony used inquiry-based learning, long before this became a buzzword—students were always encouraged to find their own ways to answers, particularly in the teaching lab. Although the sheer volume of biological knowledge that he could draw upon at a moment's notice could be rather intimidating to an undergraduate student (or a graduate one, or even a colleague, for that matter), Tony was always approachable and supportive to the querying student, while allowing them to find their own paths to correct answers, something that he demonstrated constantly in his regular appearances in the teaching labs. Course material was continuously revised to incorporate changes in the science and to accommodate reviews of necessary background material that might not have been covered in other courses. Tony's teaching was never compromised by his investment in other tasks. As far as his undergraduates could tell, his involvement with them was, apparently, all that the University kept him around for. This has not gone unremarked by them. He received the Students' Union Teaching Excellence Award, the nomination and awarding of which is determined by the efforts of an instructor's own undergraduate students, in 2008, 2012 and 2013. In addition, he received the Faculty of Science Teaching Excellence Award in 2001. Regardless of this, however, as far back as any of us can remember, he made a point of showing up at every convocation to see his undergraduates off and offer them his best wishes for their post-varsity lives.

Comparative vertebrate anatomy was Tony's main undergraduate teaching concern for over thirty years and he went to great lengths to provide his students with resources far in excess of those required for a basic understanding of the subject. The comparative anatomy teaching collection began as an assemblage of stuffed birds acquired by the late Dr. Tim Myres and was soon augmented in the 1970s by the acquisition of a series of native fish specimens from the Calgary Brewing and Malting Company collection. Tony's association with this nascent teaching collection under the *de facto* curatorship of Herb Rosenberg was marked by a fruitful relationship with the Calgary Zoo, resulting in the acquisition of many of the Zoo's mortalities for the teaching collection. Undergraduates in organismal vertebrate courses have thus long had access to skeletal preparations of such exotica as giraffe forelimbs and gorilla skulls. When the BioSciences Department decided to formally institute a Zoology Museum with Tony as its *de facto* curator in 1986, this only formalised the status of a collection which, under Herb and Tony, had been growing for years. The Zoology Museum encompasses not only a wide range of vertebrate teaching material, but also serves as a repository for a reference collection of Alberta vertebrate specimens.

Undergraduates frequently found places in Tony's research program and there was usually one or two working in the lab on studies under his direction, either over the summer or during the regular academic year. This early exposure to research frequently resulted in published papers, a great boost for anyone considering going on to graduate school. Many of these students did make this transition, either in Calgary under Tony's supervision or elsewhere, and some, such as Amanda Melin, Matt Vickaryous, Tim Higham, Heather Jamniczky, Philip Bergmann, and Olaf Bininda-Emonds, have since embarked upon successful academic careers of their own.

University service

In this aspect of his academic career, Tony, as always, led by example, voluntarily undertaking administrative tasks that, frequently, no one else seemed to want to do. As part of his belief in duty to his academic community, he performed (relatively) arduous tasks over the long term and, as always, with excellence, no matter what other commitments drew from his time. His stints as Department Head (always a rather perilous office) from July 1994 to July 1999 and, again, from July 2011 to July 2012 as a stand-in resulted in balanced budgets and a department streamlined against the inclement winds of financial restraint, as well as a faculty left content, accomplishments not easily attained.

Tony has also been active in service roles to the University community as a whole. In addition to his stints as Assistant Dean (Student Affairs) of the Faculty of Science (from 1985 to 1988) and Associate Dean of the Faculty of Science (from 1988 to 1991), he has served repeatedly on the General Faculties Council (being elected by the Council to serve on the Board of Governors of the University of Calgary from 2003 to 2009) and as a member of the University of Calgary Press Editorial Board.

His service commitments have not been restricted to the University of Calgary. Tony was appointed by the President of the University of Calgary as one of two representatives from the University to the Management Council of the Western Canadian Universities Marine Biology Society (from 1994 to 1999). Tony has been president of the Canadian Society of Zoologists, the International Society of Vertebrate Morphologists, and the University of Calgary chapter of Sigma Xi (twice). He is a Fellow of the Zoological Society of London and of the Linnean Society of London as well as being an active member of many more professional societies. He has organised three international scientific meetings and convened symposia at four others. He has served on the editorial boards of four journals, and acted as a referee for thirty-five.

Tony has also engaged actively with the non-academic community. He has been a frequent commentator on local and national radio about scientific issues in general and about his own research. In addition to making many outreach and enrichment visits to schools in Calgary, he has liaised extensively with the Calgary Science Network and is the originator of the Curriculum Enhancement Program for local elementary-school teachers, introducing senior biological sciences undergraduates into local schools to interact with both students and teachers.

In recognition of this busy and varied professional presence, Tony received the University of Calgary Distinguished Faculty Achievement Award in 2003. This is awarded by the University's Teaching and Learning Centre in recognition of the demonstration of excellence in "teaching, research, and service to the University, to their students, and to their discipline", but also denotes a faculty member who has inspired and challenged students to excel in their own undertakings.

All this activity had relatively little impact upon life in the Russell lab. Graduate students were generally unaware of Tony's, at times, rather hectic administrative and professional schedule, and certainly were not under the impression that all this other business was of greater import than their dealings with him. Again, Tony's ability to divide his energies among commitments enabled him to perform each at a high level.

Research and supervision

Now we come to an aspect of Tony's career to which we can speak with some authority and the one in which he had the greatest impact on our own lives and careers. As a graduate and postdoctoral advisor, Tony expected commitment and dedication from his students, repaying these by demonstrating absolute commitment and support, liberally mixed with a dry sense of humour. He has always fostered independence and research creativity. Grad students were expected to develop their own projects and side projects and 'experiments' were always encouraged. This is a contrast to the situation in many labs in which grad students either undertake research relevant to the advisor's own primary research interests or go elsewhere (subsequent sojourns to such labs have proved disconcerting to many of Tony's former students). The range of research topics in which he supported projects was extensive and innovation was always encouraged. He expected wide, deep, thoughtful reading, particularly of historical literature and obscure sources, both of which were likely to unexpectedly surface during advisor-student conversations in which Tony consistently demonstrated his ability to push students beyond where they thought they could go while preserving their readiness to try. All to the best: one was treated as a colleague from the start, which represents excellent training in actually becoming worthy of consideration as one, but a definite challenge for new trainees!

Graduate research in the Russell lab has always been robust and thorough, with an emphasis on quality. Research projects were followed through to their ends, resulting in many doorstopper theses and dissertations, the culminations of many agonising (for all concerned, no doubt) rounds of red-pen-infused drafts. A Russell grad was always supported through these travails, however, and these massive, detailed theses tended to yield multiple publications and formed foundations for further research. Indeed, more than one of us was supported through a post-graduation period to enable this writing to occur. And most of us got to this point: the graduation rate of Russell lab trainees was consistently high throughout his academic career and many went to make their own places in academia. It was only fitting then that Tony was given the 2003 Faculty of Grad Studies "Outstanding Achievement in Supervision" award for "Individuals who have actively promoted excellence in graduate education and research through excellence in supervision …".

Tony's approach to postdoctoral supervision was, appropriately, more hands-off, but equally steeped in his commitment to quality and thoroughness. Postdoctoral researchers in Tony's lab have included numerous University of Calgary grads who stayed on to pursue further work, including Bruce Young (a Herb Rosenberg student) and Betsy Nicholls, Heather Jamniczky, and Matt Vickaryous (all of whom received graduate degrees under Tony) as well as some imports: Jeff Thomason (PhD, University of Toronto), Aaron Bauer (PhD, University of California, Berkeley), Harold Bryant (PhD, University of Toronto), Xiao-Chun Wu (PhD, McGill University), Sean Modesto (PhD, University of Toronto), and Don Henderson (PhD, University of Bristol). Some of these were largely independent researchers hosted by Tony, whereas others more actively partnered with him on topics that were central to his core research themes. All benefitted not only from Tony's breadth and depth of knowledge, but from his thoughtful perspectives on higher education, the nature of scientific inquiry, and the role of the teacher-scholar in academia.

Russell lab research varied widely in topic and taxon, but all projects shared some unifying characteristics. The research undertaken has always been erected upon a phylogenetic framework and trainees were required to demonstrate a thorough understanding of patterns of relationship before proceeding further in their research. With the exception of the work on geckos, chelonians and anoles, it tended to restrict itself geographically to Alberta in subject matter, both today and in the deep past. Many projects involved fieldwork and most covered multiple disciplines. It was important to Tony to foster both depth and breadth in his trainees and so, although we make a superficial attempt to categorise this work below on the basis of broad questions of interest, we note that no thesis produced under Tony's supervision could ever be considered to be one-dimensional. Indeed, most work intentionally spanned several of the categories we describe.

Systematics and biogeography

"How do patterns of relationship inform our understanding of animals, their environment, and their evolution?"

Systematics has informed a great deal of the graduate research which was undertaken in the Russell Lab and remains a long-standing interest of Tony's. Graduate students were liable to find themselves suddenly discussing the subject with him, regardless of the starting point of the conversation, and all were encouraged to take a phylogenetic perspective in their projects. Some went further and explicitly investigated the interrelationships of modern groups as diverse as mustelids (Warren Fitch), phocid seals (Olaf Bininda-Emonds), and the gekkotan genus *Thecadactylus* (Philip Bergmann). Others incorporated both neontological and palaeontological data in their systematic projects, such as Heather Jamniczky and Jim Gardner (who both worked upon turtles). Exclusively palaeontological projects almost invariably involved the phylogenetics of the group under study, but Michael Ryan (ceratopsian dinosaurs), Robin Cuthbertson (ichthyosaurs), and Pat Druckenmiller (plesiosaurs) explicitly concentrated upon the systematics of their respective groups, describing new species and setting them in their phylogenetic contexts. The use of µCT methods allowed Hillary Maddin to revise the classification of the caecilians (Gymnophiona). At a finer level of resolution, Mark Thompson and Magdalene Leung investigated the phylogeographies of Long-Toed Salamanders (*Ambystoma macrodactylum*) and Greater Short-Horned Lizards (*Phrynosoma hernandesi*), respectively.

A large part of the gecko research that Tony carried out with postdoctoral fellow Aaron Bauer in the late 1980s was explicitly phylogenetic or taxonomic. This resulted in revisionary studies of many groups, especially those from Africa and Madagascar.

Morphology and development

> *"How do animals function in their native environment? What is the role of development in providing the raw materials for phenotypic diversity?"*

A wide spectrum of extant tetrapods have been the subjects of morphological and developmental studies by Russell lab graduates over the decades. Many of these fitted into Tony's long-term research projects, whereas others had more idiosyncratic foci, reflecting Tony's tendency to allow students to follow their own bents to select interesting research topics. This work always reflected Tony's model of combined attention to detail and consideration of context in biological research: seldom did anyone use only one technique or examine only one taxon in isolation. Rather, trainees were encouraged to employ a comparative approach, double- and triple-check observations, and cross-validate against both the literature and their own complementary investigations. The theses on gecko locomotor anatomy fall into the first category. The investigations of Sonia Delannoy and Megan Johnson into the setae that enable these lizards to escape the horizontal are expansions of a research program of Tony's that goes back to his own graduate days. David Rittenhouse looked at the vocal apparatus in a variety of geckos, painstakingly reconstructing three-dimensional models of larynges from sequences of histological sections. Locomotor adaptations of *Anolis* lizards that also enable vertical excursions were examined by Mindy Myers and Lisa McGregor.

The breast-shoulder apparatus of tetrapods has long been a subject of investigation in the Russell lab, beginning with Ron Quaife's investigation of the forelimb of the North American Badger (*Taxidea taxus*). Hollie Knoll took a detailed look at this complex in birds and Alex Tinius is currently completing a dissertation on the breast-shoulder apparatus in lizards. Locomotory adaptations in mammals were the subject of research by Colleen Pollock and Dale Eslinger (White-Tailed and Mule Deer, *Odocoileus virginianus* and *Odocoileus hemionus*, respectively) and Beverly Anderson (Vampire Bats, *Desmodus rotundus*). Richard Pereschitz examined the developmental osteology of the skull in Richardson's Ground Squirrels (*Spermophilus richardsonii*). As always, students were encouraged to also consider the animal in its environment, not as a specimen on a laboratory bench. Tony's encyclopaedic knowledge of vertebrates spanning a wide range of habitats was both intimidating and stimulating to many of us.

Ontogenetic processes were also the subject of Sheri Watson's thesis on larval development in the Long-Toed Salamander (*Ambystoma macrodactylum*), which resulted in a staging table for this species. The embryonic development of the skull in the Leopard Gecko (*Eublepharis macularius*) was painstakingly worked out by Pat Wise (see his chapter in this volume). Of continuing interest to Tony were the concepts of homology and key innovation, and many theses included a detailed treatment of development regardless of the larger focus of the work. Such concepts tend to be abstract and difficult to grasp for beginning graduate students and many of us were left scratching our heads, trying to answer a very simple sounding question posed by Tony during our weekly meetings.

Finally, biomechanics was a focus of postdoctoral research in the Russell lab, with Jeff Thomason pursuing work on the functional role of the mammalian secondary palate and Aaron Bauer examining the tensile strength of gecko skin.

Palaeontology and evolution

"How has animal form changed over time?
What are the implications of such changes for today's fauna?"

Tony was a firm proponent of studying extinct taxa as animals rather than as curious shapes in stone. While he encouraged students to consider stratigraphy in addition to patterns of relationship in extinct groups, he pioneered the use of the extant phylogenetic bracket with Harold Bryant to once again push us to understand context and evolutionary change.

The late Betsy Nicholls was an important figure in the development of a palaeontological research program in the Russell lab. Betsy had located, excavated, and prepared several large Cretaceous vertebrate fossils, such as the plesiosaur and the *Ornithomimus* specimen displayed in the hall outside the BioSciences departmental office, before returning to graduate school for her doctorate under Tony's supervision in the early 1980s. Her doctoral study of a Cretaceous marine reptile fauna entailed large numbers of bones of extinct marine monsters laid out upon most of the available flat surfaces in the lab at the time. Tony established collaborative relationships with staff members of the (then new and not yet royal) Royal Tyrrell Museum of Paleontology, including Phil Currie and Don Brinkman, around this time, leading to a long and mutually rewarding research relationship within which graduate students thrived and found projects. These types of collaborations, also evident in areas other than palaeontology, provided unique training environments and opportunities, and none of Tony's trainees lacked chances to meet leaders in the field and visit key venues in their respective research areas.

While graduate research on fossil marine reptiles (plesiosaurs, Patrick Druckenmiller; ichthyosaurs, Robin Cuthbertson) and fossil (Jim Gardner) and extant (Heather Jamniczky) turtles throve, Alberta's rich trove of Cretaceous dinosaurs could not be neglected. Projects involving feeding and locomotor anatomy in the large theropods (Eric Snively), the breast-shoulder apparatus in theropods (Sandra Jasinoski) and ancestral birds (Nick Longrich), anatomy and systematics of ceratopsians (Michael Ryan and Ben Borkovic), small ornithischian anatomy and systematics (Caleb Brown), and ankylosaur anatomy and systematics (Matt Vickaryous) combined modern techniques such as geometric morphometrics and finite-element analysis with more traditional techniques. Neontological data (such as Eric Snively's examination of neck musculature and feeding techniques in modern birds) informed palaeontological research whenever possible and graduate projects contributed to Tony's long-term research programs, such as the study of the evolution of the breast-shoulder apparatus in theropods and birds. Traces of the smaller fauna of Cretaceous Alberta were brought to light by Peng Jianghua in his palaeoecological study of microsite fossils. The breadth of the paleontological work in many ways illustrated Tony's ability to mesh apparently widely separated areas of research into a cohesive and productive research program. Once again, his interest in the details and significance of form was evident in the palaeontological arena and we continued to be impressed (and intimidated) by both his vast knowledge of phenotypic variation that spanned many millions of years and many different animal groups and his vision of how disparate parts of the vertebrate family tree fit together.

Most of Tony's postdocs have been palaeontologists. Their work with Tony has spanned groups as diverse as crocodyliforms (Xiao-Chun Wu) and carnivoran mammals (Harold Bryant) in addition to the groups mentioned above.

Ecology

"How do animals integrate into their environments?
How might this change over time?"

Morphology and evolution are best understood within an ecological context and this was an important theme in the Russell lab's research projects from an early date. Indeed, large amounts of time and effort were invested in ecological studies and much remains to be published from these projects. Tony was particularly interested in range-marginal and at-risk species and populations, and focusing on the amphibians and reptiles of Alberta enabled him to pursue this work. This fauna was relatively poorly known at the beginning of Tony's career at the University of Calgary. The literature on it consisted largely of anecdotal observations on various species and although its composition was known, true abundances and distributions of many of its components remained uncertain. Tony's first move to remedy this was to dispatch Larry Powell to southern Alberta to study the ecology of the Greater Short-Horned Lizard (*Phrynosoma hernandesi*) in 1979, a project that yielded a far better understanding of this species than heretofore and which formed the basis for further studies.

With Aaron Bauer, Tony set to work in the late 1980s to write a field guide to Alberta's amphibian and reptile species. This undertaking required field work, extensive literature reviews, exhaustive dredging of museum catalogues to define distributions, and the co-option of an artist and a photographer to produce portraits of all the species to be found within Alberta. The result was a handsome volume published by the University of Calgary Press in 1993, containing up-to-date range maps for each of Alberta's amphibian and reptile species, detailed species accounts summarising what was known of their habitats and habits, diagnostic keys, and beautifully detailed portraits and handsome photographs of each species, permitting easy and unambiguous identification. All this information was set explicitly into a context of boreal herpetology, outlining the challenges faced by amphibians and reptiles in the cold Alberta climate and the strategies by which they met them. As one reviewer said, a good test of a field guide is whether or not it makes you want to get out into the field and use it. Tony and Aaron's volume ranked highly on this criterion, with the subsequent spate of research on Alberta's herpetofauna necessitating a second edition in 2000. The first edition was a finalist in the Alberta Foundation for Environmental Excellence Emerald Award (1995) and also garnered the Alberta Book Publisher's Association Scholarly Title of the Year award. It should be noted that all proceeds from the sale of this volume were redirected to a scholarship fund for University of Calgary students.

Field projects on aspects of the ecologies of Alberta amphibians and reptiles in the 1990s began as collaborations with Alberta Fish and Wildlife. Theses such as Sheri Watson's on Long-Toed Salamander larval development, Janice James' on Greater Short-Horned Lizard thermal ecology, and Mark Thompson's and Magdalene Leung's on the phylogeographies of the Long-Toed Salamander and the Greater Short-Horned Lizard, respectively, were rooted in these collaborative projects. The Russell lab was also heavily involved in the production of provincial species status reports for the species that had been studied in depth and for others, and these kept graduate students employed through much of the 1990s.

Conservation considerations have always played a role in the ecological research carried out by members of the Russell lab on Alberta amphibians and reptiles. Efforts to preserve threatened amphibian and reptile populations are bound to be more fruitful if based upon a thorough understanding of the species' population biology and ecological requirements, and the research projects on such species as Long-Toed Salamanders were always designed to further such understanding. Ranjith Weerawardhena's thesis project, involving the impact of habitat alteration upon Sri Lanka's native anuran fauna (see his chapter in this volume), extended these goals abroad. In addition to this fundamental work, both Tony and some of his students have served as consultants to government agencies tasked with environmental protection when amphibians and reptiles were of concern.

Summing up

Tony has always favoured a collaborative and collegial approach to research with current students as well as with former students and postdocs who followed careers in academia, either working out earlier lines of inquiry or initiating new ones. This continued interest in his protégés' lives and careers goes further than simple academics, however. He could always invariably be relied upon for such things as letters of recommendation (always managing to be both honest and positive) or attendance at the wedding of former students, even in remote venues. Tony set a remarkable example (and standard) for all of us, both as academics and individuals, by always emphasising commitment, excellence, and thoughtful attention to detail no matter the size or nature of the task at hand. Tony's ability to synthesise information from many research areas, as exemplified by the breadth of projects executed under his direction, and his ability to motivate and inspire, as evident in the motley variety of trainees who have found their niches under his supervision, combined to produce both a unique academic environment and an influence that will be felt for many years to come, both within and beyond Canadian biological sciences. With this volume, we wish to collectively thank Tony for his support and guidance, and to celebrate his many achievements and contributions.

Acknowledgements

For reviewing this document and/or for sharing certain arcana with us, we would like to thank Robert Barclay, Warren Fitch, Herb Rosenberg, George Bourne, and Dick Walker. Any errors of fact of course remain ours. The authors have all, at various times, had Tony as an academic supervisor; we all wish him the best in his retirement, with our thanks for such great send-offs on our own careers.

No geckos were harmed in the composition of this review.

Graduate theses and dissertations completed under the supervision of A.P. Russell

MSc theses

Eslinger, D.H. (1976). Form, function and biological role in the locomotory apparatus of the genus *Odocoileus* in Alberta (Mammalia: Artiodactyla).

Quaife, L.R. (1978). Form and function of the North American Badger (*Taxidea taxus*) in relation to its fossorial way of life.

Powell, G.L. (1982). The Eastern Short-horned Lizard in Alberta: basic field ecology of northern marginal populations.

Fitch, W.D. (1986). Relationships between extant genera of the Mustelidae (Mammalia: Carnivora).

Anderson, B.A. (1990). The Vampire Bat (*Desmodus rotundus*): an extreme in evolutionary morphology?

Pollock, C.M. (1991). The relationship between body mass and the capacity for storage of elastic strain energy in mammalian limb tendons. (Co-supervised with Dr. Robert Shadwick)

Ryan, M.J. (1992). The taphonomy of a *Centrosaurus* (Reptilia: Ornithischia) bone bed (Campanian). Dinosaur Provincial Park, Alberta, Canada.

Gardner, J.D. (1992). Systematics of the soft-shelled turtles (Family Trionychidae) from the Judith River Formation (Campanian).

Pereschitz, R. (1994). Cranial anatomy and variation of Richardson's Ground Squirrel (*Spermophilus richardsonii*).

Bininda-Emonds, O.R.P. (1995). The phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae).

Rittenhouse, D.R. (1995). Laryngeal morphology of Afro-Madagascan gekkonine lizards (Gekkonidae: Reptilia).

James, J.D. (1997). Pre- and post-parturition thermoregulation in free-ranging female Eastern Short-Horned Lizards (*Phrynosoma douglasii brevirostre*) in southeastern Alberta.

Watson, S.M. (1997). Food level effects on metamorphic timing in the Long-Toed Salamander, *Ambystoma macrodactylum krausei*.

Myers, M.F. (1997). Morphometry of the limb skeleton in *Anolis garmani*: practical and theoretical implications.

McGregor, L.D. (2000). Locomotor morphology of *Anolis*: comparative investigations of the design and function of the subdigital adhesive system.

Snively, E. (2000). Functional morphology of the tyrannosaurid arctometatarsus.

Vickaryous, M. (2001). Skull morphology of the Ankylosauria.

Jasinoski, S. (2003). Evolutionary morphology of the theropod scapulocoracoid.

Bergmann, P. (2003). Systematics and biogeography of *Thecadactylus* (Squamata: Gekkonidae).

Thompson, M. (2003). Phylogeography of the Long-toed Salamander in the Pacific Northwest.

Delannoy, S. (2006). Evolutionary morphology of the setae of gekkotan lizards.

Johnson, M. (2008). Relationships between setal field and natural substratum microtopography in the genus *Rhoptropus* (Gekkota: Geckonidae) in Namibia, southern Africa.

Knoll, H. (2009). Comparative morphology of the neognath furcula and breast-shoulder apparatus: relationships to flight style and phylogeny.

Brown, C. (2010). *Thescelosaurus* (Dinosauria: Ornithischia) and related taxa from the late Cretaceous of Alberta and Saskatchewan.

Wise, P. (2010). *In ovo* development of the head skeleton of the Leopard Gecko (*Eublepharis macularius*).

Weerawardhena, R. (2010). Patterns of recolonization by tropical anurans following forest habitat alteration.

Hynes, S. (2012). Resource partitioning during caudal regeneration: assessing the impact of dietary intake on tail and body growth in the Leopard Gecko (*Eublepharis macularius*).

Leung, M. (2012). Phylogeography of the Greater Short-Horned Lizard (*Phrynosoma hernandesi*) in Alberta.

Borkovic, B. (2013). Investigating sexual dimorphism in ceratopsid horncores.

PhD dissertations

Nicholls, E.L. (1989). Marine vertebrates of the Pembina member of the Pierce shale (Campanian, Upper Cretaceous) of Manitoba and their significance to the biogeography of the Western Interior Seaway.

Peng, J. (1998). Palaeoecology of vertebrate assemblages from the Upper Cretaceous Judith River Group (Campanian) of southeastern Alberta, Canada.

Ryan, M. (2003). Taxonomy, systematics and evolution of centrosaurine ceratopsids of the Campanian Western Interior Basin of North America.

Snively, E. (2006). Functional morphology of cranial and cervical musculature of diapsids.

Druckenmiller, P. (2006). Systematics, paleobiology and biogeography of plesiosaurs.

Jamniczky, H. (2006). Systematics of extant and extinct turtles with special reference to cranial nerves and blood vessels.

Longrich, N. (2008). The flight of *Archaeopteryx lithographica*: implications for understanding the origins and evolution of avian flight.

Maddin, H. (2011). Phylogenetic implications of the morphology and development of the braincase of caecilian amphibians (Gymnophiona).

Cuthbertson, R. (2012). Early to middle Triassic ichthopterygians from the Sulphur Mountain formation of East-Central British Columbia: phylogenetic and evolutionary implications.

Observations of a next-door neighbour

Herb Rosenberg

Department of Biological Sciences, University of Calgary, Calgary, Alberta, T2N 1N4, Canada; E-mail: herb.rosenberg@ucalgary.ca

Introduction

I worked with Tony Russell from the day of his arrival in Calgary in 1973 until my retirement in 2005. Happily, our time together was such that for the past eight years (while Tony continued to work and I enjoyed retirement) our friendship has continued. We taught courses together, occupied offices in close proximity to one other (often just a few centimetres away), and exercised together in the Phys-Ed gym. My comments and observations are recorded to fill the gaps between the formal scientific papers printed in this well deserved *Festschrift*.

Early days

I picked up Tony and his wife Geraldine in 1973 at the Calgary International Airport in a well-worn vehicle. A steel stop sign reinforced the back floorboards that had rusted out after many a Calgary winter. That stop sign gave Geraldine and Tony pause. If a full-time member of the professoriate was driving such a heap, how was a mere demonstrator supposed to fare? Furthermore, when Tony learned that his predecessor had left to operate a lumberyard, he really became concerned.

Tony was hired sight unseen because the name of Professor Angus Bellairs appeared somewhere on his résumé. In fact, that was the only name I recognised on his documents. I had landed my job at the University of Calgary (the U of C) after obtaining a PhD under Carl Gans; we had used one of Bellairs'

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books in Dr Gans' herpetology course. If Tony knew Bellairs, that was good enough for me.

Tony replaced the lumberman as a demonstrator in the comparative vertebrate anatomy course that I taught. The role of demonstrator was established in the British educational system, was inherited by the Commonwealth countries, and has since almost gone the way of the dodo. A demonstrator was in charge of the graduate teaching assistants, prepared the course lab assignments, and ran the lab portion of the course. Slowly but surely, Tony was given greater responsibility in the course and eventually we each presented half the lectures. Tony pole-vaulted into the professorial stream by virtue of his outstanding academic accomplishments. When I retired, Tony gave all the lectures in this and another advanced vertebrate zoology course we had shared previously; I assumed that I was irreplaceable.

Teaching

We started with Romer's textbook "The Vertebrate Body" and Warren Walker's lab manual. Changes were made over the years and we were helped admirably by Warren Fitch, the osteology collection at the U of C, and many graduate teaching assistants. In the beginning, anatomical drawings were painstakingly created on the blackboard before students entered the lecture hall. By the time I retired, students could access textbook illustrations on websites and chalkboards were replaced by digital projectors.

Tony's lectures were very well organised and he took his responsibilities as a teacher very seriously. Students appreciated his candour and efforts to help them through the course. I will never forget our friendly bickering when selecting the student who would receive "The Golden Scalpel" for superior achievement in the comparative anatomy lab. Tony did much to enrich our courses in vertebrate zoology. He originated field trips to the Royal Tyrrell Museum of Palaeontology; many students had never been there even though this wonderful place is virtually in their backyard (by Canadian standards). He developed and presented tutorials designed to help students grasp the detailed curriculum of vertebrate anatomy. He regularly presented a hilarious "concluding remarks" lecture in the comparative anatomy course that poked fun at lecturers, students, and animals. It is no wonder that Tony recently received the Student's Union Award for Teaching Excellence for the third time in total and then for the second year running.

Research

I am convinced that Tony has an intimate knowledge of every muscle fiber, tendon, blood sinus, and integumentary specialisation in the digits of most species of gecko. The detailed illustrations that he prepared helped elucidate the locomotor adaptations that define some groups of these fascinating lizards. Tony has extensive experience working on a variety of functional morphological research projects in extant and fossil vertebrates with colleagues and his graduate students. He has published over 300 papers and book chapters as well as a book with Aaron Bauer of Villanova University on the (depauperate) herpetofauna of Alberta.

Tony has taken field trips to the Caribbean, Africa, and Australia. One trip that stands out was our drive from Ann Arbor, Michigan to Calgary in 1976. I had just finished a full sabbatical at the University of Michigan and it was time to drive home. Tony agreed to fly down to the Gans Lab on a one-way ticket to obtain experience with some of the equipment used in functional analyses, to meet with Ken Kardong (our mutual friend and colleague), and then to share the driving with me on our return to Calgary. All went well until Tony nearly blew up a powerful aircraft strobe light used to illuminate high-speed movies. We recovered from that shocking experience by perpetrating a prank of a haberdashical nature on Ken. Tony and I beat a hasty retreat out of Carl’s driveway in my yellow Barracuda (only a zoological model for us!) while listening to the newscast of the Israeli rescue at Entebbe; it was July 4, 1976. Memorable stops were made with a miraculous family in Madison, Wisconsin and Tony’s relatives in Winnipeg (complete with an unforgettable lava lamp).

Administration

Tony’s plate was filled to overflowing with teaching, research, graduate students, grant applications, committee work, and a young family. Yet, he felt it was only proper to serve the University in additional capacities. Thus, he served on many committees at all levels within the university framework. In addition, he chaired the Division of Animal Sciences, the Department of Biological Sciences (more than once), and was an Associate Dean in the Faculty of Science. Tony managed all these administrative duties while maintaining his teaching and research at an outstandingly high level.

His administrative activities were totally organised; Tony runs a very tight ship. One secret he let me in on: he would always manage to empty his "in basket" by the end of the day. Thus, all campus mail, snail mail, and e-mails (not to mention phone calls) were dealt with on a daily basis. That approach made for many long, but satisfyingly productive days. It is therefore fitting that Tony was awarded the "U Make a Difference Award" by the University of Calgary in 2012.

Conclusion

It was not all work, preserved sharks and cats, and grading those many exam papers by hand. I don't dare begin to count the coffee breaks and lunch time discussions dealing with (in no meaningful order): FIA (Formula 1 racing), soccer, obscure (to me) British and American rock 'n' roll groups, Monty Python skits, rhyming slang (as in "trouble and strife" or "apples and pears"), and zoological luminaries throughout the universe. The odd visit by Aaron Bauer also enhanced the atmosphere; no one was safe from the Russell-Bauer type specimen characterisations or the chalkboard rebuses.

Thank you, Tony, you certainly managed to broaden my perspective.

And now for something completely different …

II. Palaeontology

A new frog (Lissamphibia, Anura) from the Late Cretaceous of Alberta, Canada

James D. Gardner and Donald B. Brinkman

Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta, T0J 0Y0, Canada; E-mail: james.gardner@gov.ab.ca and don.brinkman@gov.ab.ca

Abstract

Non-marine sedimentary rocks in the North American Western Interior contain one of the richest and stratigraphically most nearly continuous records for anurans (frogs) during the Late Cretaceous (ca. 99.5–65.5 million years ago). Most of this record consists of isolated, three-dimensionally preserved bones recovered from vertebrate microfossil localities (i.e., accumulations of small-sized, fossilised bones, teeth, and scales). North American Late Cretaceous anurans are best known from the terminal Cretaceous (late Maastrichtian, ca. 68–65.5 million years ago) of Montana and Wyoming, USA. In this paper, we describe a geologically older (middle to late Campanian, ca. 77–76 million years ago) new anuran genus and species, *Hensonbatrachus kermiti*, on the basis of distinctive skull and appendicular bones, collected from nine localities in the Dinosaur Park Formation and the upper part of the Oldman Formation in southeastern Alberta, Canada. This new taxon exhibits a unique mix of features (e. g., moderate body size, pattern of external cranial ornament, form and inferred contacts of maxilla and squamosal, pattern of incrassations on the ventral surface of frontoparietal, and details of iliac acetabular region and shaft) that differentiate it from other anurans, especially those known from the North American Late Cretaceous. Because of its fragmentary nature and mix of conflicting character states, the higher-level relationships of *H. kermiti* are uncertain. *Hensonbatrachus kermiti* is interpreted as a generalised, ground-dwelling anuran that was part of a taxonomically diverse,

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but as yet poorly documented, anuran assemblage that existed during the middle to late Campanian in present day southeastern Alberta.

Introduction

The Belly River Group (*sensu* Eberth 2005) is a predominantly non-marine, sedimentary unit of Late Cretaceous age that crops out in southeastern Alberta and west-central Saskatchewan, Canada. More precisely, the unit is dated to the middle to late Campanian (ca. 80–75.7 million years ago; Eberth 2005, pers. comm. 2013) or equivalent to the Judithian North American Land Mammal Age (see Kielan-Jaworowska *et al.* 2004). The Belly River Group is richly fossiliferous and has yielded a wealth of plant, invertebrate, and vertebrate fossils that provide important insights into the diversity, evolutionary histories, and palaeoecology of organisms during the latter part of the Cretaceous in western North America (e. g., Currie & Koppelhus 2005 and papers therein). Dozens of vertebrate taxa are known from the Belly River Group, including fish, lissamphibians, turtles, crocodilians, lizards, choristoderes, dinosaurs, birds, and mammals (e. g., Fox 1976a; Eberth *et al.* 2001; Peng *et al.* 2001; Currie & Koppelhus 2005 and papers therein). Anurans (frogs) are a characteristic, but poorly understood, component of the Belly River Group vertebrate assemblage (Fox 1976a; Dodson 1983; Brinkman 1990; Eberth *et al.* 1990, 2001; Peng *et al.* 1995, 2001; Eberth & Brinkman 1997; Gardner 2000, 2005; Brinkman *et al.* 2004; Frampton 2006). As is typical for the Late Cretaceous record of anurans throughout North America (e. g., see Estes & Sanchíz 1982; Roček 2000; Holman 2003; Gardner 2008; Roček *et al.* 2010; Gardner & DeMar 2013), anuran fossils in the Belly River Group are limited to isolated bones (e. g., Brinkman 1990; Gardner 2000, 2005; Peng *et al.* 2001). On the basis of distinctive skull and postcranial bones, several anuran taxa have been informally recognised from the Belly River Group (Fox 1976a; Gardner 2000, 2005; Eberth *et al.* 2001; Gardner & DeMar 2013), but none of these has been formally named.

In this paper, we describe a new anuran genus and species for isolated bones (maxillae, premaxilla, squamosals, nasal, frontoparietals, ilia, and humerus) from nine localities in the upper two units of the Belly River Group (Oldman and Dinosaur Park Formations) in southeastern Alberta, Canada. We also provide the first substantial information about the geology, stratigraphic position, and history of the Irvine vertebrate microfossil locality, which not only is the holotype locality for the new anuran described in this paper, but also has been an important source since the mid 1960s for small-bodied, Campanian vertebrate fossils in Alberta (e. g., Fox 1976a, 1979a–c, 1980, 1981; Gao & Fox 1991, 1996, 1998; Wilson *et al.* 1992; Gardner 2000, 2003, 2005).

Material and methods

The new anuran taxon reported in this paper is known by isolated and, typically, incomplete bones that were recovered by surface collecting and screen washing of vertebrate microfossil localities (i.e., accumulations of small-sized, fossilised bones, teeth, and scales). Those specimens are housed in the following two institutional collections in Alberta, Canada: the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) in Edmonton and the Royal Tyrrell Museum of Palaeontology (TMP) in Drumheller. Comparisons were made by the first author with other published (e. g., Estes 1964, 1969; Sahni 1972; Fox 1976b; Estes & Sanchíz 1982; Gardner 2008; Roček *et al.* 2010) and unpublished collections of North American Late Cretaceous anuran fossils, with skeletal specimens of extant anurans, and with relevant publications. Osteological terms generally follow Roček (1981) for skull bones, Holman (2003) for humeri, and Gardner *et al.* (2010) for ilia. We also follow Trueb (1973) and Fox (1976b) in using the term "pars facialis" for the dorsally directed flange extending the length of the maxilla and located above the lingually directed, shelf-like lamina horizontalis (= pars palatinum of some authors) and the ventrally directed, often tooth-bearing crista dentalis (= pars dentalis of some authors). The following dental terms are used to denote tooth surfaces, directions, and orientations: "apical", towards crown; "distal", towards skull-jaw articulation; "mesial", towards inter-mandibular joint; "labial", towards outside (exterior) of mouth; and "lingual", towards inside (interior) of mouth. We also use the latter pair of terms to denote the corresponding surfaces on the premaxilla and maxilla, but, to be consistent with anatomical terms for structures on those bones, we use the terms "medial" and "lateral" for the premaxilla and "anterior" and "posterior" for the maxilla instead of, respectively, "mesial" and "distal". Linear measurements are straight-line values. Body-size estimates were based on comparisons with extant anuran skeletons and used equations presented by Esteban *et al.* (1995).

Geological setting

The Belly River Group is an eastwardly-thinning, non-marine to paralic clastic wedge that can be traced for more than 1000 km in outcrop and the subsurface from southeastern Alberta into west-central Saskatchewan and, as the "Judith River Formation", into north-central Montana (e. g., Eberth & Hamblin 1993, their Fig. 2). The Belly River Group was deposited during the middle and late Campanian across a broad alluvial and costal plain between the emergent Rocky Mountains to the west and the western margin of the Western Interior Seaway to the east. It is bracketed above (Bearpaw Formation) and below (Pakowki Formation) by marine shales (Fig. 1) deposited during westward transgressions of that seaway. Sediments of the Belly River Group consist largely of sand-, silt-, and mudstones, with minor coals and bentonites that were deposited in a mixture of alluvial, floodplain, fluvial, swamp, estuarine, and lagoonal environments under warm temperate to subtropical conditions (e. g., Eberth & Hamblin 1993; Eberth *et al.* 2001; Eberth 2005). In ascending order, the Belly River Group is subdivided into the following three units (Eberth & Hamblin 1993; Eberth 2005): the Foremost, Oldman, and Dinosaur Park Formations. As summarised in earlier publications (e. g., Eberth & Hamblin 1993; Eberth 2005), various names have been applied historically to the above-mentioned rock units (see Fig. 1); in this paper, we follow the most recent stratigraphic nomenclature proposed by Eberth (2005). For the new anuran reported in this paper, it is important to clarify the following: (1) the name "Oldman Formation" (*sensu* Russell & Landes 1940) as used in many reports before the late 1990s (e. g., Russell 1964; Fox 1976a, 1979a–c, 1980, 1981; Béland & Russell 1978; Gao & Fox 1991, 1996, 1998; Wilson *et al.* 1992) denotes the same package of rock now subdivided into the Oldman and Dinosaur Park Formations, and (2) the names "Judith River Formation" (*sensu* McLean 1971) and "Judith River Group" (*sensu* Eberth & Hamblin 1993) as used in some other reports (e. g., Brinkman 1990; Eberth 1990; Eberth & Hamblin 1993; Brinkman *et al.* 2004) are equivalent to the Belly River Group.

Anuran fossils are known from several dozen localities in all three formations of the Belly River Group in southeastern Alberta (e. g., Brinkman 1990; Peng *et al.* 2001; Brinkman *et al.* 2004; Gardner 2005; Gardner & DeMar 2013) as follows (Fig. 2): near the town of Irvine (upper part of Dinosaur Park Formation), in Dinosaur Provincial Park and the surrounding area (Dinosaur Park Formation and upper part of Oldman Formation), along the South

Saskatchewan River near Sandy Point (Oldman Formation) and farther upstream near Bow Island (Foremost Formation), in the Manyberries and Onefour areas (Dinosaur Park Formation), and along the eastern portion of the Milk River (Oldman and Foremost Formations). This report focuses on specimens from nine localities in the Oldman and Dinosaur Park Formations.

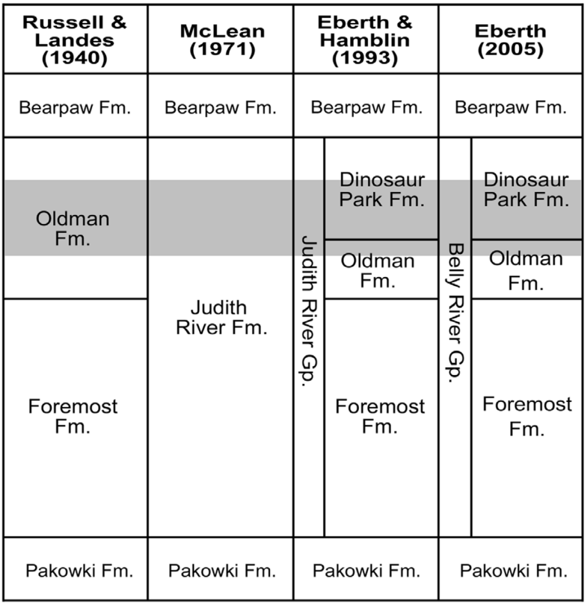


Figure 1:
Chart summarising history of names used for the Upper Cretaceous (middle–late Campanian or Judithian) Belly River Group and its constituent formations in southeastern Alberta, Canada. Vertical extents of formations in the Belly River Group are depicted proportional to one another; vertical extents for the Bearpaw and Pakowki formations are not. Shaded area represents approximate vertical extent of exposures containing localities that have yielded specimens of *Hensonbatrachus kermiti* new genus and species; see also stratigraphic correlation chart in Fig. 4. Chart adapted from Eberth (2005, his Fig. 3.2). Abbreviations: Fm., Formation and Gp., Group.

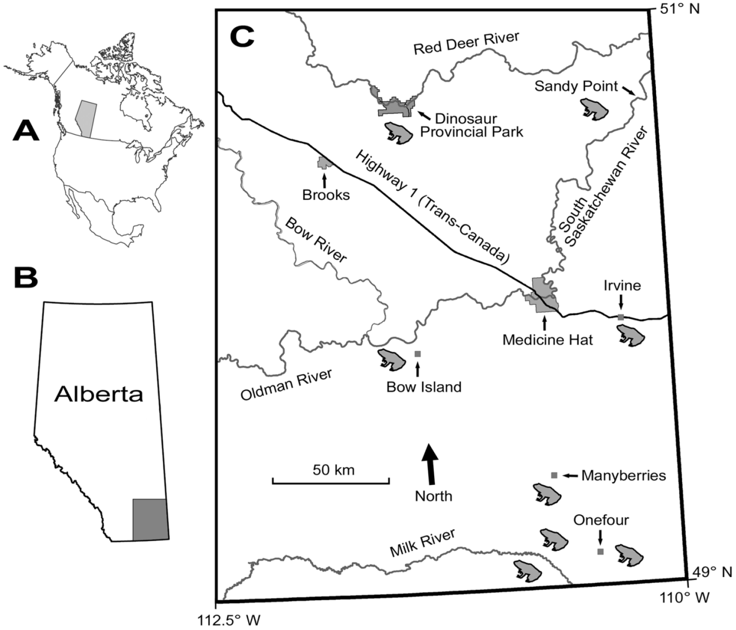


Figure 2:
Maps showing anuran fossil localities mentioned in the text within the Belly River Group (middle–late Campanian or Judithian) of southeastern Alberta, Canada. A, Outline map of North America with Alberta shaded. B, Outline map of Alberta with southeastern portion depicted in next map shaded. C, Map of southeastern Alberta depicting areas where anuran fossils (anuran icon) have been recovered from the Belly River Group. Specimens of *Hensonbatrachus kermiti* new genus and species are from the Dinosaur Provincial Park and Irvine areas (see maps in Fig. 3 and stratigraphic correlation chart in Fig. 4) and from near Sandy Point.

The Oldman Formation is a southwest-thickening unit that records the maximum regressional phase of the Western Interior Seaway during the Campanian (Eberth & Hamblin 1993; Eberth *et al.* 2001; Eberth 2005). The formation consists of light-coloured, mostly yellowish sandstones and sandy mudstones formed in low sinuosity and ephemeral palaeochannels and as adjacent levee, splay, and overbank deposits. The Oldman Formation is exclusively non-marine and is informally subdivided into three units, namely a lower and an upper mudstone-dominated unit and a middle sandstone-dominated unit.

Three localities in the Oldman Formation have each yielded one specimen of the new anuran reported in this paper. BB 100 and BB 103 are vertebrate microfossil bone beds within (BB 100) and about 5 km northeast of (BB 103) Dinosaur Provincial Park (Fig. 3A). Both localities occur in crevasse splay deposits and lie about 5 m below the top of the formation (Fig. 4; Eberth 1990, his Table 1 and Fig. 5), which would place them in the upper, mudstone-dominated unit. The third locality is recorded on the corresponding specimen label as being "5 miles upstream of Sandy Point" (Fig. 2). Based on that description and the local geology, this locality occurs within the Oldman Formation, but its position within the formation cannot be determined (D. Eberth pers. comm. 2013).

The overlying Dinosaur Park Formation is a northwest-thickening unit that records the beginning of the last major transgression of the Western Interior Seaway in southern Alberta (Eberth & Hamblin 1993; Eberth *et al.* 2001; Eberth 2005). The formation consists of darker coloured (grey, brown, and green) sands and muds deposited in alluvial, estuarine, and paralic environments. The Dinosaur Park Formation is informally subdivided into a lower, sandy zone dominated by alluvial palaeochannel deposits and an upper, muddy zone representing an overbank-dominated succession that culminates in the brackish Lethbridge Coal Zone at the top of the formation.

Most of the new anuran specimens come from four localities in the Dinosaur Park Formation. Three of these localities are within or near Dinosaur Provincial Park (Fig. 3A). BB 31 and BB 86 are within the Park and have each produced one specimen. Both localities lie at the base of the lower sandy zone within about 1 m of the lower boundary of the Dinosaur Park Formation, but occur in different depositional settings: BB 31 is in a crevasse splay deposit, whereas BB 86 is in an intraclast deposit (Fig. 4; Eberth 1990, his Table 1 and Fig. 5). Another four specimens come from the Steveville Railway Grade or BB 102. This locality occurs in an intraclast deposit and lies about midway through the vertical extent of the Dinosaur Park Formation close to the top of the sandy zone (Fig. 4; Eberth 1990, his Table 1 and Fig. 5). Although, at one time, this locality was within Dinosaur Provincial Park, it now lies about 1 km outside to the west because of changes in the Park's boundaries (compare Fig. 3A vs. Eberth 1990, his Fig. 1).

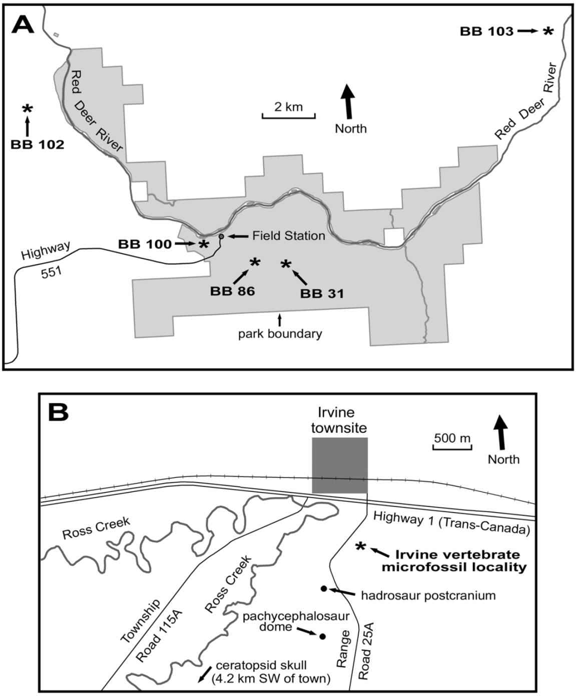


Figure 3:
Maps showing fossil localities for *Hensonbatrachus kermiti* new genus and species in the Dinosaur Provincial Park and Irvine areas of southeastern Alberta, Canada. A, Simplified map of Dinosaur Provincial Park (shaded) and surrounding area depicting locations of the five microfossil bone beds that have yielded referred specimens of *H. kermiti* new genus and species. B, Simplified map of the Irvine area, depicting the Irvine vertebrate microfossil locality (holotype locality for *H. kermiti* new genus and species) and locations of three dinosaur specimens (see text) collected from the same area; outline of the Irvine town site is depicted diagrammatically as a square. See Fig. 5 for photographs of the Irvine vertebrate microfossil locality. Maps are at different scales. Abbreviation: BB, microfossil bone beds (all TMP localities).

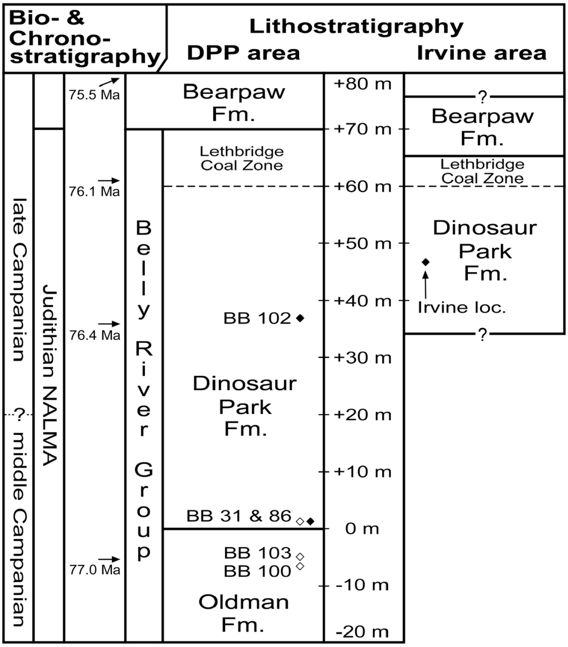


Figure 4:
Stratigraphic correlation chart depicting vertical extent of exposures of the Belly River Group in the Dinosaur Provincial Park and Irvine areas of southeastern Alberta, Canada, and the relative stratigraphic positions in the areas of localities that have yielded specimens of *Hensonbatrachus kermiti* new genus and species. The Dinosaur Provincial Park area exposes the entire 70-meter vertical extent of the Dinosaur Park Formation and the upper 20 m of the Oldman Formation, whereas only the upper portion of the Dinosaur Park Formation is exposed in the Irvine area. Correlations between the two areas are aligned using the lower boundary of the Lethbridge Coal Zone within the upper part of the Dinosaur Park Formation; note that the Lethbridge Coal Zone varies in thickness and absolute age across southern Alberta. Chart compiled from the following sources: placement of Judithian NALMA follows Kielan-Jaworowska *et al.* (2004); placement of the boundary between the middle and late Campanian and the lithostratigraphy for the Dinosaur Provincial Park area both follow Eberth (2005, his Fig. 3.1); absolute ages are from ash beds in the Dinosaur Provincial Park areas and were provided by D. Eberth (pers. comm. 2013); positions and depositional interpretations of microfossil bone beds in the Dinosaur Provincial Park area follow Eberth (1990, his Table 1 and Fig. 5); and the Irvine portion of the chart is based on measurements and observations taken by us in 1995 and 2008 and on unpublished information provided by D. Braman (pers. comm. 2013). Note that in the Dinosaur Provincial Park area, stratigraphic positions of microfossil bone beds were measured relative to the boundary between the Dinosaur Park and Oldman Formations (Eberth 1990, his Table 1 and *(continued overleaf)*

(continued from overleaf)

Fig. 5), whereas in the Irvine area, where that boundary is not preserved, the position of the Irvine vertebrate microfossil locality was measured by us from the base of the Lethbridge Coal Zone. Symbols: black diamonds, intraclast deposits; white diamonds, splay deposits; question mark, uncertain placement of the boundary between the middle and late Campanian (left side) and uncertain extents of the Bearpaw Formation (upper portion probably eroded away) and of the Dinosaur Park Formation (lower portion probably continues into subsurface) of exposures in the Irvine area (right side). Abbreviations: BB, microfossil bone beds (all TMP localities); DPP, Dinosaur Provincial Park; Fm., Formation; loc., locality; Ma, millions of years ago; and NALMA, North American Land Mammal Age.

About 125 km southeast of Dinosaur Provincial Park is the Irvine vertebrate microfossil locality (Fig. 2), which is the source for the holotype and most of the referred specimens of the new anuran. This locality is situated about 700 m south of the town of Irvine in a small patch of exposures of the Dinosaur Park Formation along the eastern side of the broad valley containing Ross Creek (Figs. 3B, 5). Fox (1976a, 1979a, b, 1981) recognised that the Irvine vertebrate microfossil locality was high in section by stating, for example, that the locality was in the “upper beds” (Fox 1976a: erratum for p. 6) or “uppermost parts” (Fox 1979a: 96) of what was then called the Oldman Formation (*sensu* Russell & Landes 1940). Based on measurements taken by us in July 1995, the Irvine vertebrate microfossil locality lies within the lower portion of the more mud-dominated, upper zone of the Dinosaur Park Formation and about 13 m below the base of the Lethbridge Coal Zone (Fig. 4). When compared to the Dinosaur Provincial Park area, the Irvine vertebrate microfossil locality is slightly higher in section than the Steveville Railway Grade (Fig. 4). However, these latter two localities might be closer in age because the top of the Dinosaur Park Formation dips and becomes younger towards the east (Eberth & Hamblin 1993). At the Irvine vertebrate microfossil locality, the fossiliferous layer is about 30 cm thick and occurs in a mudstone-pebble intraclast deposit (Fig. 5E–F) comparable to some of the vertebrate microfossil bone beds mentioned above and described by Eberth (1990) in the Dinosaur Provincial Park area. Nearby exposures of the upper part of the Dinosaur Park Formation to the south and southwest along Ross Creek also have yielded larger vertebrate fossils, including the following dinosaurs: a ceratopsid skull collected in 1958 (Canadian Museum of Nature specimen 41357; Holmes *et al.* 2001, their Figs. 2–6); a pachycephalosaurid skull dome collected in 1999 (TMP 1999.62.01; Sullivan 2003, his Fig. 2A–C); and an incomplete hadrosaurid postcranium collected in 2003 (TMP 2003.11.01; unpubl.).

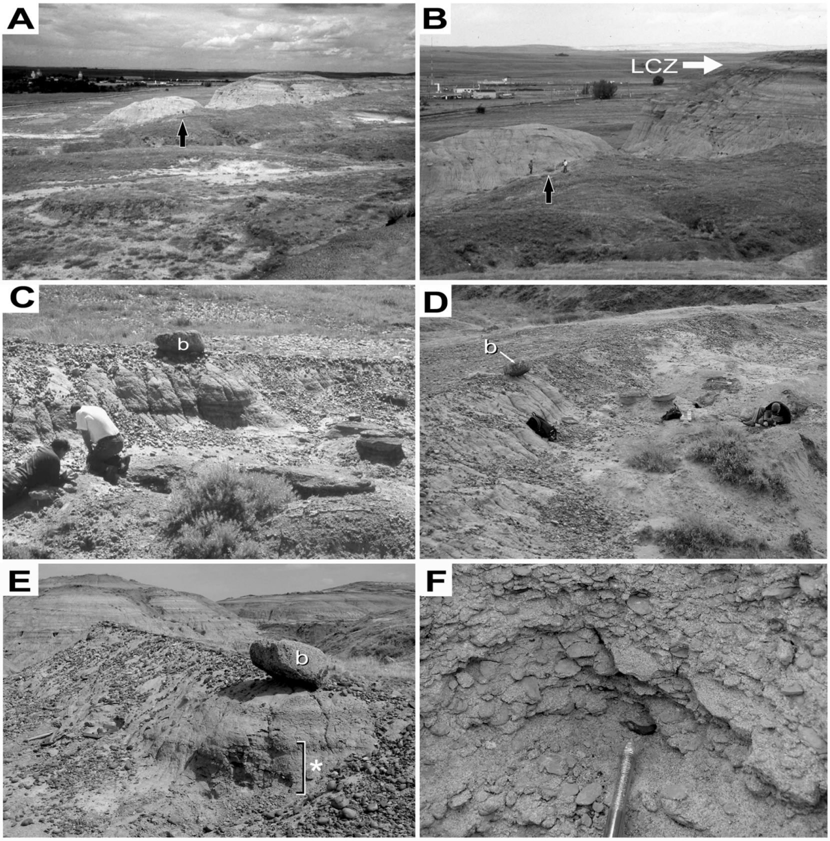


Figure 5:
Photographs of the Irvine vertebrate microfossil locality in the upper part of the Dinosaur Park Formation taken well after the interval (1967–1976) when the University of Alberta collected at that locality. A–C, Locality in July 1995. A, The small patch of badlands containing the Irvine locality (black arrow). Photograph taken from several hundred metres away and looking north, with Irvine town site visible in far distance at upper left. Note person (immediately above the arrow) for scale standing at the locality. B, Similar to previous photograph, but taken closer to the Irvine locality (black arrow). Buildings north of the Irvine locality are part of a farmyard between the locality and the Irvine town site. Note two people (above and to either side of the arrow) for scale standing at either end of the locality. Exposures to the northeast (right side of photograph) preserve the lower portion of the Lethbridge Coal Zone (LCZ and white arrow), which is a regional marker bed at the top of the Dinosaur Park Formation *(continued overleaf)*

(continued from overleaf) that was used to estimate the stratigraphic position of the Irvine locality. C, Closer view of the Irvine locality, looking northeast. The fossiliferous layer is below the boulder (b) in the upper middle of the photograph and that layer originally extended farther west; the bowl-shaped depression in the fore- and middle ground where people are surface collecting is the area where matrix was excavated for screen washing by University of Alberta crews. D–F, Locality in April 2008. D, Looking east along the wall of the quarry. Note how weathering and erosion has pushed the quarry wall back almost to the position of the same boulder (b) depicted in C. E, Closer view of quarry wall near the same boulder (b), looking north and slightly west. The asterisk marks the fossiliferous layer, which is about 30 cm thick along this portion of the quarry wall. F, Close up view of excavated quarry wall, showing unidentified bone *in situ* within intraclast pebbles.

As a historical aside, it is worth documenting that the fossiliferous nature of the Upper Cretaceous exposures near Irvine had been recognised since at least the mid 1880s. The earliest published record known to us is in an account by Panton (1884) of his travels the previous August from Winnipeg, Manitoba, into southern Alberta. In the section dealing with what he called the "Irvine Ravine", Panton (1884: 6) stated, "Here in the spring of this year [i.e., 1883] Mr. Lawson, of Medicine Hat Coal Mine, while prospecting for coal discovered the remains of what appeared to be an animal of reptilian nature." On the next page, Panton (1884: 7) reported finding fragmentary dinosaur bones in multiple locations when he visited "Irvine Ravine" in August of that same year; he was not, however, able to follow up on an intriguing verbal report "by a member of the Mounted Police [forerunner of today's Royal Canadian Mounted Police] that there is, about 15 miles up the ravine, the remains of a huge lizard-like creature in the rocks: that it has been known to the Indians for a long time, and by them held in superstitious awe under the name of the 'great lizard'". Later, during explorations for the Geological Survey of Canada in the same decade, T.C. Weston collected fish teeth and scales, *Champsosaurus* vertebrae, crocodilian teeth, and dinosaur bones near Irvine at "Ross coulée" and "Irvine coulée" in 1884 and 1888, respectively (Lambe 1902: 28–28, 46–47, and 53).

Discovery of the Irvine vertebrate microfossil locality did not occur until the early 1960s, when it was found by either the late Luke Lindoe, then the director of research and mining at Medicine Hat Brick and Tile, or by his son Allan Lindoe, then a high school student and who went on to become a long-time fossil preparator and technician at the UALVP (A. Lindoe pers. comm. 2013). Allan found the first fossil mammal teeth at the locality and, shortly after starting work at the University of Alberta, showed them to Professor

Richard C. Fox, who had recently been hired to develop a vertebrate palaeontology program at that institution (Scott *et al.* 2013). Field crews working under Professor Fox's direction extensively sacked and screen washed the locality each summer from 1967 to about 1976 (R. Fox pers. comm. 2002). Aside from two subsequent visits by crews from the TMP—the first in 1995 when the section was measured and about 250 kg of matrix were collected and the second in 2008 when a mammal jaw was collected—the locality has not been worked further. The current landowner has forbidden access to the property so no additional work at the Irvine vertebrate microfossil locality is possible for the foreseeable future. Fortunately, thousands of small bones, teeth, and scales are available from the locality. Although a comprehensive faunal study of the Irvine vertebrate microfossil locality has not been attempted, it is evident from publications dealing with specimens and taxa from there (e. g., Fox 1976a, 1979a–c, 1980, 1981; Naylor 1979, 1981; Gao & Fox 1991, 1996, 1998; Wilson *et al.* 1992; Meng & Fox 1995; Gardner 2000, 2003, 2005) and from our examination of collections that it is one of the best localities for small-bodied Judithian vertebrates in terms of the number and quality of specimens and the diversity of taxa it preserves. As an example of its significance, the Irvine vertebrate microfossil locality is the holotype locality for 11 vertebrate species (Table 1).

The final two localities (UALVP localities BGN-2 and RCF-1) have each yielded an ilium, but their geographic and stratigraphic positions are uncertain. These specimens were picked from small samples of uncatalogued vertebrate microfossils housed in a drawer labelled "Oldman Formation, Alberta" at the UALVP. Aside from labels stating that the BGN-2 and RCF-1 samples were collected in 1979 and 1974, respectively, all we can say about those localities is that they are from either the Oldman or Dinosaur Park Formations somewhere in Alberta, most likely one of the areas worked by UALVP crews during the mid to late 1970s (e. g., near Manyberries or Onefour, in the Steveville/Dinosaur Provincial Park or Irvine areas, or along the South Saskatchewan River).

Table 1:
The 11 fossil vertebrate species named (as of June 2014) for holotypes from the Irvine vertebrate microfossil locality.

Amphibia (*n* = 2):	
	Habrosaurus prodilatus Gardner 2003
	Hensonbatrachus kermiti new genus and species
Reptilia (*n* = 6):	
	Sphenosiagon simplex Gao & Fox 1991
	Glyptogenys ornata Gao & Fox 1991
	Gerontoseps irvinensis Gao & Fox 1991
	Leptochamops thrinax Gao & Fox 1991
	Orthrioscincus mixtus Gao & Fox 1996
	Odaxosaurus priscus Gao & Fox 1996
Mammalia (*n* = 3):	
	Turgidodon russelli (Fox 1979a)[1]
	Leptalestes prokrejcii (Fox 1979b)[2]
	Paranyctoides sternbergi Fox 1979c

[1] Originally named *Alphadon russelli* by Fox (1979a); the species subsequently was transferred to *Turgidodon* by Johanson (1996).

[2] Originally named *Pediomys prokrejcii* by Fox (1979b); the species subsequently was transferred to *Leptalestes* by Davis (2007).

Systematic palaeontology

Subclass Lissamphibia Haeckel 1866

Order Salientia Laurenti 1768

Crown-order Anura Rafinesque 1815

Family Indeterminate

Hensonbatrachus kermiti new genus and species

(Figs. 6–9)

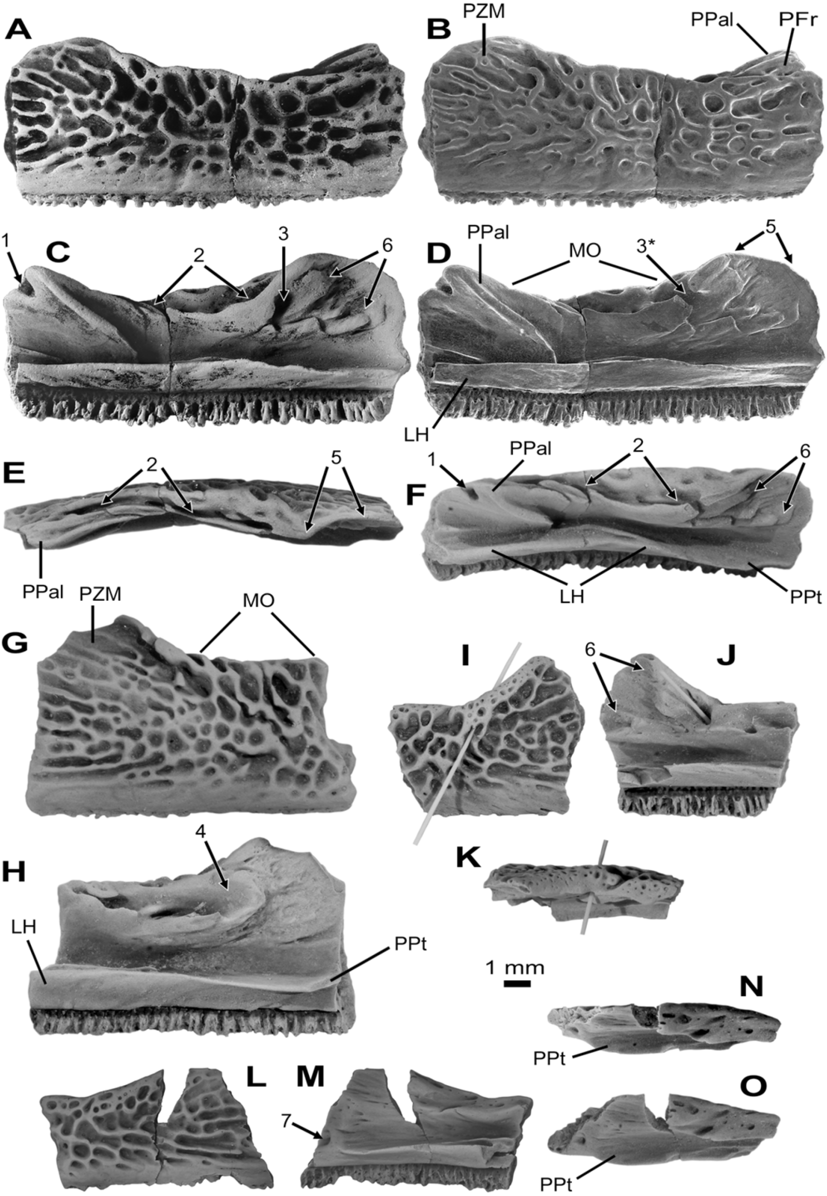
Synonyms: “Genus and Species Unnamed B” (Gardner 2000: 547–549, his Fig. 12-5). “Gen. et sp. indet. #2” (Eberth *et al.* 2001: 58). “New gen. and sp. B” (Gardner 2005, his Tables 10-1 and 10-2 and Fig. 10-1K). “Anura indet” (Roček *et al.* 2012, their fig. 3I). “Anura gen. et sp. nov. 2” (Gardner & DeMar 2013, their Fig. 2k, Table 4, and Appendix 4).

Etymology: Genus name combines “Henson”, in honour of puppeteer Jim Henson for creating one of the most memorable anuran characters in popular culture, namely Kermit the Frog, + “*batrachus*”, Greek for frog, a common suffix for anuran generic names. Specific epithet refers to Kermit the Frog.

Holotype specimen, locality, horizon, and age: UALVP 40167, right maxilla missing posterior and anterior ends of bone (Fig. 6A–F); Irvine vertebrate microfossil locality, southeastern Alberta, Canada; upper part of Dinosaur Park Formation, Belly River Group; late Campanian (Judithian) in age.

Referred specimens: Dinosaur Park Formation, four localities in Alberta, Canada. (1) Irvine vertebrate microfossil locality (holotype locality): UALVP 40202–40207, UALVP 40037, 40038, 40052, and 40152, maxillae; UALVP 40217, premaxilla; UALVP 40171, 40172, 40211, and 40212, squamosals; UALVP 40170, nasal; UALVP 40173 and 40174, frontoparietals; UALVP 40175, 40213 and 40214, ilia. (2) TMP locality BB 31, Dinosaur Provincial Park: TMP 1985.70.07, maxilla. (3) TMP locality BB 86, Dinosaur Provincial Park: TMP 86.23.32, frontoparietal. (4) Railway Grade locality (= TMP locality BB 102), west of Dinosaur Provincial Park: UALVP 40208 and 40209, maxillae; TMP 1974.10.88, ilium; UALVP 40176, humerus. Oldman Formation, three localities in Alberta, Canada. (1) TMP locality BB 100, Dinosaur Provincial Park: TMP 1986.159.65, maxilla. (2) TMP locality BB 103, northeast of Dinosaur Provincial Park: TMP 86.178.14, ilium. (3) UALVP unnumbered locality along South Saskatchewan River, 5 miles upstream from Sandy Point: UALVP 40168, maxilla. Unit uncertain (either Dinosaur Park Formation or Oldman Formation), two localities in southeastern Alberta, Canada. (1) UALVP locality BGN-2: UALVP 40215, ilium. (2) UALVP locality RCF-1: UALVP 40216, ilium.

Distribution: Late Cretaceous (middle to late Campanian or Judithian); Dinosaur Park and Oldman Formations, Belly River Group; southeastern Alberta, Canada. Note that although the holotype locality is late Campanian in age, other occurrences for which ages are reliably known are stratigraphically lower and the oldest of these extend back into the latest middle Campanian (see Fig. 4).


A
B
PZM
PPal
PFr
C
1
2
3
6
D
PPal
MO
3*
5
LH
E
2
5
PPal
F
1
PPal
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LH
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G
PZM
MO
I
J
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H
4
LH
PPt
K
1 mm
N
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L
M
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Figure 6: *(overleaf)*
Holotype and referred maxillae of *Hensonbatrachus kermiti* new genus and species, from the Late Cretaceous (middle–late Campanian or Judithian) of southeastern Alberta, Canada. All specimens are from the Dinosaur Park Formation. Unless noted otherwise, images are photographs and depict specimens lightly dusted with ammonium chloride to enhance details and texture. A–F, Nearly complete right maxilla (holotype), UALVP 40167, in labial (A–B) and lingual (C–D) views and, with anterior to left, in dorsal (E) and dorsolingual and slightly anterior (F) views (images in B and D are scanning-electron micrographs). G–H, Incomplete right maxilla, UALVP 40202, in labial (G) and lingual (H) views. I–K, Incomplete left maxilla, UALVP 40203, with hair inserted into canal extending through bone below posterior part of orbital margin, in labial (I) and lingual (J) views and, with anterior to right, in dorsal (K) view. L–O, Incomplete left maxilla, UALVP 40209, in labial (L) and lingual (M) views and, with anterior to right in dorsal (N) and dorsal and slightly lingual (O) views. Images are at same scale. Abbreviations: LH, lamina horizontalis; MO, margo orbitalis; PFr, processus frontalis; PPal, processus palatinus; PPt, processus pterygoideus; and PZM, processus zygomatico-maxillaris. Numbered arrows: 1, canal for ductus nasolacrimalis extending through base of processus palatinus; 2, dorsally open groove for ductus nasolacrimalis extending along margo orbitalis; 3, lingual exit for ductus nasolacrimalis as a foramen (asterisk denotes location where thin flange of bone was accidentally broken away from dorsoanterior rim of foramen); 4, lingual exit for ductus nasolacrimalis as a trough; 5, smooth and thin dorsal edge of processus zygomatico-maxillaris lacking any evidence of direct sutural contact dorsally with squamosal; 6, roughened lingual surface, presumably for bony or ligamentous contact with pterygoid or ligamentous contact with squamosal; and 7, unnamed small pit behind processus pterygoideus.

Diagnosis: Differs from other anurans, especially those known from the North American Cretaceous, by a unique suite of features. Body size: moderate (i.e., estimated snout–vent length of 75–115 mm). Cranial ornament: premaxilla is unornamented, whereas maxilla, nasal, squamosal, and frontoparietal are broadly ornamented externally with pit-and-ridge style ornament consisting of moderately deep, irregular-shaped pits and short grooves enclosed by moderately tall, thick, and vermiform ridges. Dentition: maxilla and premaxilla bear teeth; maxillary teeth (no intact examples known for premaxilla) relatively short, weakly pedicellate, and labiolingually bicuspid with disc-shaped cuspules. Maxilla: robust in build; pre- and postorbital regions (i.e., processus frontalis and processus zygomatico-maxillaris, respectively) relatively tall and similar in height, suborbital region relatively deep between margo orbitalis and dorsal surface of lamina horizontalis, and margo orbitalis moderately concave; processus palatinus weakly developed as a narrow, tapered prong that extends dorsoanteriorly and barely projects past dorsal edge of processus frontalis; ductus nasolacrimalis extends as an enclosed canal through base of processus palatinus and as a dorsally open groove along dorsal surface of margo orbitalis; dorsal edge of processus zygomatico-maxillaris labiolingually thin and smooth with no indication (i.e., a sutural surface) of direct bony contact with squamosal; lingual surfaces of processus zygomatico-maxillaris and of pars facialis below posterior portion of margo orbitalis roughened, presumably for ligamentous or direct bony contact with pterygoid or ligamentous contact with squamosal; variable presence of one or more foramina in labial surface of maxillary pars facialis below posterior part of margo orbitalis that connect with canal extending through bone to open in lingual surface of suborbital region; lamina horizontalis a prominent ledge that is moderately deep, lingually wide, and approximately triangular in cross section, with lingual surface flattened and facing ventrolingually, ventral surface narrow and dorsally concave, and dorsal surface shallowly concave to nearly flat; and processus pterygoideus weakly developed as a small, flattened, scoop-like process that barely projects lingually. Premaxilla: bears elongate processus lateralis. Squamosal: lamella alaris expanded into broad, externally ornamented plate that covers most of lateral surface of bone, except for distal end of processus posterolateralis, approximately C-shaped in lateral outline, with deeply concave posterior margin and smooth dorsal margin indicating no direct bony contact with frontoparietal; processus zygomaticus absent and no sutural surface present along ventral margin of bone for direct bony contact with maxilla; and processus posterolateralis a stout prong. Nasal: moderate in size and subtriangular or sickle-shaped in outline. Frontoparietal: bilaterally paired and in weakly sutured medial contact at least posteriorly; moderately narrow in dorsal or ventral outline; tectum supraorbitale present; processus paraoccipitalis posteriorly short and triangular in dorsal or ventral outline; and ventral surface bears anterior and posterior incrassations, both developed as flattened bony patches on median portion of bone and continuous across skull midline, with posterior incrassation subcircular in ventral outline and anterior incrassation more elongate. Ilium: iliac portion of acetabular surface subtriangular in lateral outline and its borders fully contained within dorsal, anterior, and ventral boundaries of acetabular region; dorsal prominence a raised, mediolaterally compressed ridge along dorsal surface of acetabular region and bearing at its anterior end a low, knob-like dorsal tubercle with a flattened top; short oblique groove present and accompanied by low medial crest; iliac shaft slightly compressed mediolaterally, with shallow trough extending along long axis on both lateral and medial surfaces; and no dorsal crest or inter-iliac tubercle.

Description

This new anuran is known by isolated and incomplete cranial (maxillae, premaxilla, squamosals, nasal, and frontoparietals) and postcranial (humerus and ilia) bones that can be associated and differentiated from homologous elements of other anurans in the same deposits on the basis of their larger size, presence of teeth (premaxilla and maxillae), distinctive pattern of external cranial ornament (maxillae, squamosals, nasal, and frontoparietals), complementary structures (i.e., lack of sutural facets on maxilla and squamosal for direct bony contact between those elements), and element-specific features (e. g., form of lamina horizontalis and processus pterygoideus on maxilla, shape of squamosal, and form of dorsal prominence and tubercle on ilium).

Maxilla (Figs. 6–7)

The most nearly complete maxillary specimen is the holotype UALVP 40167 (Fig. 6A–F). This is a right maxilla that is broken anteriorly through the bone in front of the processus palatinus and posteriorly just behind the processus pterygoideus. A crack extends vertically through the bone in the orbital region. The tooth row also is broken anteriorly and posteriorly, and no intact teeth are preserved. The holotype is relatively large compared to most other North American Cretaceous anuran maxillae and has the following preserved dimensions: length = 16.0 mm, maximum height of preorbital region (measured from ventral edge of crista dentalis to apex of processus palatinus) = 6.0 mm, maximum height of postorbital region (measured from ventral edge of crista dentalis to apex of processus zygomatico-maxillaris) = 6.2 mm, and minimum depth of orbital region (measured from ventral edge of crista dentalis to lowest point along margo orbitalis) = 4.5 mm. Comparisons with other anurans suggest that UALVP 40167 would have been at least 20 mm long when intact and potentially longer if, as in some anurans, the postorbital region extended any distance posteriorly. The referred maxillae include a range of different-sized specimens that are informative for estimating maximum size and for documenting additional aspects of maxillary structure. Based on the heights of their respective postorbital regions, the largest (UALVP 40202; Fig. 6G–H) and smallest (UALVP 40152; Fig. 7A–B) of the referred maxillae are about 20% larger and 45% smaller, respectively, than the holotype. Unless indicated otherwise, the description below is a composite.

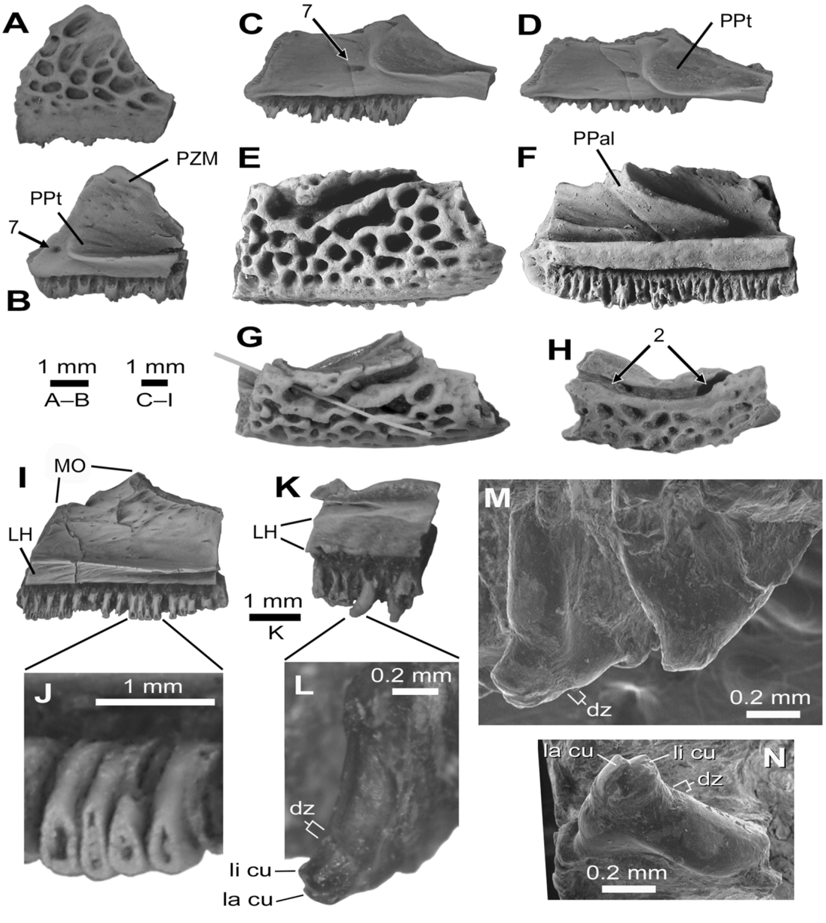

Figure 7:
Referred maxillae and maxillary teeth of *Hensonbatrachus kermiti* new genus and species from the Late Cretaceous (middle–late Campanian or Judithian) of southeastern Alberta, Canada. Most specimens are from the Dinosaur Park Formation except UALVP 40168, which is from the Oldman Formation. Unless noted otherwise, images are photographs and depict specimens lightly dusted with ammonium chloride to enhance details and texture. A–B, Incomplete left maxilla, UALVP 40152, in labial (A) and lingual (B) views. C–D, incomplete left maxilla, UALVP 40206, in lingual (C) and lingual and slightly dorsal (D) views. E–G, incomplete right maxilla, UALVP 40168, in labial (E) and lingual (F) views and, with hair inserted into canal extending through bone below anterior part of orbital margin and with anterior to right, in dorsolabial (G) view. H, Incomplete left maxilla, UALVP 40052, in dorsolabial view and *(continued overleaf)*

(continued from overleaf) with anterior to left. I–J, Incomplete left maxilla, UALVP 40204, entire specimen in lingual (I) view and close up (J) of tooth pedicels lacking crowns in oblique (lingual and slightly ventroposterior) view. K–N, Fragmentary maxilla, side uncertain, UALVP 40038, entire specimen in lingual view (K), close up (photograph) of one intact tooth (L) in oblique (lingual and either anterior or posterior) view, close up (scanning-electron micrograph) of both intact teeth (M) in oblique view and similar orientation to previous image, and close up (scanning-electron micrograph) of same intact tooth (N) depicted in image L, but rotated 180º and in slightly more apical aspect. Images are at different scales. Dental abbreviations: dz, dividing zone between crown and pedicel; la cu, labial cuspule; and li cu, lingual cuspule. Other abbreviations and numbered arrows follow Fig. 6.

When viewed in labial or lingual aspect, the pars facialis portion of the maxilla is moderately tall. The holotype shows that the pre- and postorbital regions are of comparable height and that these enclose a moderately deep and concave margo orbitalis between them. Several referred maxillae preserve more of the preorbital (e. g., UALVP 40168, Fig. 7E–G) or postorbital (e. g., UALVP 40206, Fig. 7C–D) regions, but not enough to establish the exact forms or relative lengths of those regions. Although the preserved portion of each maxillary specimen has a relatively robust build, breakage of the anterior and posterior ends implies that the bone was less robust (likely thinner and, perhaps, lower) in these regions. In dorsal aspect, the holotype maxilla is broadly curved labially. In all specimens, most of the labial surface of the bone bears a distinctive pit-and-ridge style ornament consisting of moderately deep and wide, irregular-shaped pits and short grooves that are enclosed by moderately tall, thick, and vermiform ridges. The pitted pattern is best developed in the orbital region, whereas the grooved pattern tends to dominate across the pre- and postorbital regions. Ornament does not extend ventrally onto the labial surface of the crista dentalis; instead, that region forms a relatively smooth band along the ventral-most portion of the maxilla. The characteristic pit-and-ridge style ornament is consistent across the preserved size range of specimens.

In lingual aspect, the processus palatinus is not especially prominent. This process is best preserved on the holotype, where it is developed as a narrow, tapered prong having a gutter-like posterodorsal surface. The process extends dorsoanteriorly along the lingual wall of the pars facialis and the anterior portion of the margo orbitalis, and its blunt end barely projects past the dorsal edge of the preorbital region. The ductus nasolacrimalis is visible and prominently developed on all maxillae preserving the orbital region. Along its anterior portion, the duct extends as an enclosed canal through the distal portion of the processus palatinus (Fig. 6C–D, F). Upon exiting that process, the duct continues posteriorly along the more lingual portion of the margo orbitalis as a deep, moderately wide groove (Figs. 6E–F, 7H). Along much of its length, this groove is open dorsally, but bony overgrowths partially roof the duct in places. The duct terminates posteriorly by opening lingually along the posterior third of the orbital region, either through a foramen or a trough (cf., UALVP 40167, Fig. 6C vs. UALVP 40202, Fig. 6H). Where the duct extends along the margo orbitalis, the bone in that region tends to be thickened lingually and might have a roughened texture; this condition is especially pronounced in UAVLP 40202 (Fig. 6H). Posterior to the ductus nasolacrimalis, several specimens (e. g., UALVP 40203 and 40168, Figs. 6I–K and 7E–G, respectively) are perforated by a canal that extends obliquely (anteriorly and ventrally) through the pars facialis between a foramen in the lingual surface of the margo orbitalis and one or two foramina that open in the labial surface just below the margo orbitalis.

The processus zygomatico-maxillaris is intact on the holotype (Fig. 6C–D) and the anterior portion of that process is preserved in several referred specimens (e. g., UALVP 40202 and 40203, Fig. 6H and J, respectively). Collectively, these specimens show that the process is broadly convex dorsally in labial or lingual outline and has a labiolingually thin, smooth dorsal edge that lacks any trace of an attachment surface for contacting the complementary processus zygomaticus on the squamosal. More ventrally, however, the lingual surfaces of the processus zygomatico-maxillaris and the adjacent portion of the pars facialis below the margo orbitalis have a roughened texture (Fig. 6C–D, J), suggesting that this region was in bony or ligamentous contact with an adjacent skull bone. For reasons discussed below (see Discussion), we propose that element was either the pterygoid or squamosal. The lamina horizontalis is a prominent ledge that is moderately deep (i.e., accounts for about one-quarter of the minimal depth of the suborbital region) and lingually wide. It is approximately triangular in cross section, having its lingual surface flattened and facing ventrolingually, its ventral surface (sulcus dentalis) narrow and dorsally concave, and its dorsal surface (including the groove for the pars palatina palatoquadrati) shallowly concave to nearly flat. The groove for the pars palatina palatoquadrati terminates anteriorly at a pit in the floor of the recessus vaginiformis immediately behind the base of the processus palatinus. The posterior end of the lamina horizontalis is slightly elaborated to form a processus pterygoideus; although this process is weakly developed on all specimens, it is relatively more prominent on smaller maxillae (e. g., Figs. 6M–O, 7B–D vs. Fig. 6D–F, H). On all specimens, the processus pterygoideus is small, narrow, barely protrudes lingually, and resembles a slightly flattened scoop. Its lingual and posterior edges are broadly convex and its dorsal surface is shallowly concave, smooth, and tilted slightly ventrally. Behind the processus pterygoideus, a small, unnamed pit perforates the lingual surface of the pars facialis. No specimen preserves enough of the postorbital region to establish whether the posterior end of the maxilla was contacted by the quadratojugal.

The total number of maxillary teeth is unknown because all specimens are missing the anterior and posterior ends of the tooth row. The specimen with the most nearly complete tooth row, the holotype, has about 40 loci that are occupied mostly by tooth shafts without crowns and also by some empty tooth slots. In preserving a posteriorly incomplete section of tooth row behind the level of the processus pterygoideus, UALVP 40206 (Fig. 7C) shows that the tooth row extended well behind the level of that process. Preserved tooth bases in all specimens indicate that the teeth are pleurodont, small, closely spaced, and relatively uniform in size along the tooth row (e. g., Figs. 6C, 7I). The tooth shafts are expanded labiolingually, are compressed mesiodistally, and are somewhat oval or subtriangular in cross section, with the lingual portion narrower than the labial (Fig. 7J). Where shafts are well preserved, the apical edges are in the form of a smooth rim, which implies that the missing crowns were not solidly attached to the shaft. This is corroborated by one specimen (UALVP 40038, Fig. 7K–N) that preserves two intact teeth, both of which are weakly pedicellate (i.e., with a barely discernable, mineralised dividing zone between the shaft and crown; see Discussion for additional comments about this condition). On this specimen, each tooth crown is labiolingually bicuspid and its cuspules are disc-shaped (i.e., moderately expanded mesiodistally and have broadly convex apical edges) and are separated by a shallow, median sulcus that extends mesiodistally across the apical surface of the crown.

Premaxilla (Fig. 8A–C)

The sole available specimen, UALVP 40217 (Fig. 8A–C), is an incomplete right premaxilla missing its medial end, the dorsal end of its pars facialis (= alary process of some authors), the lateral end and ventral edge of its crista

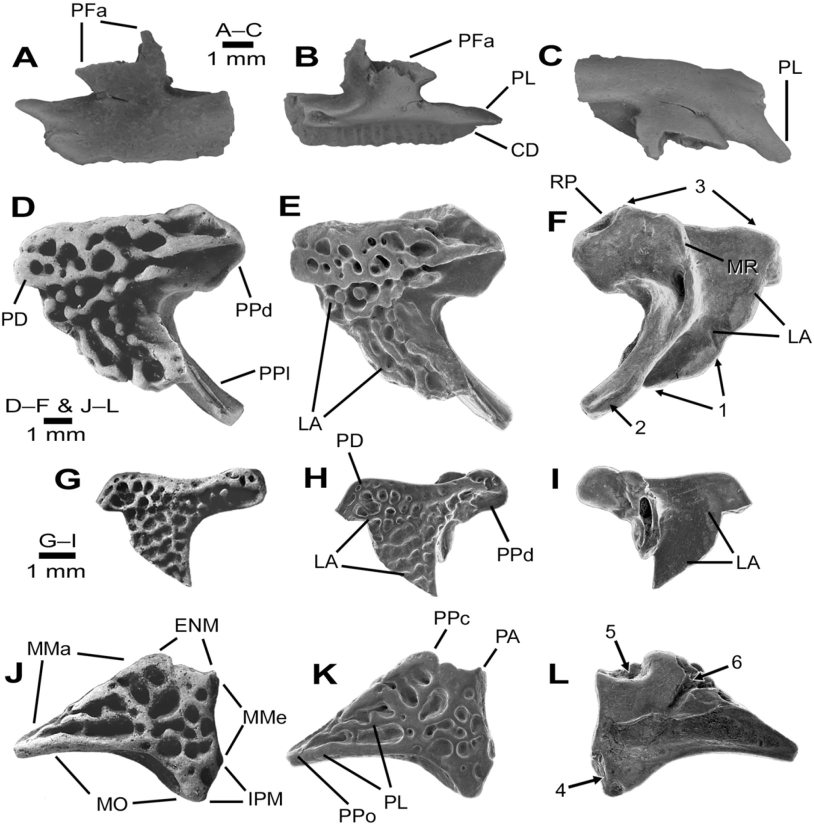

Figure 8:
Referred premaxilla, squamosals, and nasal of *Hensonbatrachus kermiti* new genus and species from the Late Cretaceous (middle–late Campanian or Judithian) of southeastern Alberta, Canada. All specimens are from the Dinosaur Park Formation. Unless noted otherwise, images are photographs and depict specimens lightly dusted with ammonium chloride to enhance details and texture. A–C, Incomplete right premaxilla, UALVP 40217, in labial and slightly dorsal (A), lingual (B), and dorsal (C) views. D–F, Nearly complete, large, left squamosal, UALVP 40171, in lateral (D–E) and medial (F) views (images in E and F are scanning-electron micrographs). G–I, Incomplete, smaller, left squamosal, UALVP 40172, in lateral (G–H) and medial (I) views (images in H and I are scanning-electron micrographs). J–L, Nearly complete, left nasal, UALVP 40170, in dorsal (J–K) and ventral (L) views (images in K and L are scanning-electron micrographs). Images are at different scales. Abbreviations: Premaxilla: CD, crista dentalis; PFa, pars facialis; PL, processus lateralis. Squamosal: LA, lamella alaris; MR, medial ramus; *(continued overleaf)*

(continued from overleaf) PD, processus dorsalis; PPd, processus posterodorsalis; PPl, processus posterolateralis; RP, ramus paroticus. Nasal: ENM, external narial margin; IPM, inner posterior margin; MMa, margo maxillaris; MMe, margo medialis; MO, margo orbitalis; PA, processus anterior; PL, processus lateralis; PPc, processus parachoanalis; and PPo, processus paraorbitalis. Numbered arrows: (squamosal, 1–3 and nasal, 4–6): 1, smooth ventral edge of lamella alaris, lacking any evidence of direct sutural contact ventrally with maxilla; 2, facet on medial surface of processus posterolateralis, presumably for contact with quadratojugal; 3, smooth dorsal edge of lamella alaris, lacking any evidence of direct sutural contact dorsomedially with frontoparietal; 4, facet for overlapping contact with sphenethmoid and/or frontoparietal; 5, external cranial ornament extending past underlying original border of external narial margin; and 6, unidentified grooves in ventral surface.

dentalis, and all its teeth. When oriented with its pars palatinum in the horizontal plane, UALVP 40217 has a maximum width (as measured between the broken medial end of the bone and the intact tip of the processus lateralis) of 7.7 mm and a maximum height (as measured between the broken ventral edge of the crista dentalis and the broken dorsal end of the pars facialis) of 2.5 mm. The pars dorsalis and crista dentalis portions of the bone are relatively shallow in labial or lingual view and are broadly convex in dorsal or ventral view. The entire labial surface is smooth and devoid of ornament. The lack of external ornament on this specimen is not a major impediment to associating it with the other skull bones attributed to the species because anuran premaxillae typically remain smooth or are only weakly ornamented even when the maxillae, cheek, and skull-roof bones are extensively ornamented. The provenance, relatively large size, and dentate nature of this premaxillary specimen support assigning it to *H. kermiti*. The preserved portion of the pars palatinum is a shallow shelf that is moderately broad lingually. Too much of the medial end of the pars palatinum is missing to determine the extent to which that portion of the shelf was expanded lingually and whether or not it bore a prominent processus palatinus. A stout, elongate, and tapered processus lateralis projects posterolaterally from the lateral end of the pars palatinum. The pars facialis arises about midway across the preserved width of the bone. Although an unknown dorsal portion of that process is missing, enough of its base is preserved to establish that the process projected dorsally and slightly posteriorly, was labiolingually compressed and moderately broad, and appears to have widened or flared laterally a short distance above the base. The only indications of teeth are faint remnants of tooth bases along the lingual surface of the crista dentalis. About eight loci are preserved and several more probably were present along the missing medial portion.

Squamosal (Fig. 8D–I)

Four specimens are available, all from the left side. The most nearly complete and informative of these is UALVP 40171 (Fig. 8D–F). This specimen is relatively robust and large. As oriented in the corresponding figures, UALVP 40171 has a maximum length of 7.7 mm and a maximum height of 7.5 mm. The lamella alaris is a broad, plate-like structure that covers most of the lateral surface of the bone except for approximately the distal half of the processus posterolateralis. The lateral surface of the lamella alaris bears ornament similar to that on the maxilla except that, in some places, the ridges are partially excavated and broken into short pillars of bone. In lateral or medial outline, UALVP 40171 is approximately C-shaped: its dorsal margin is shallowly concave and horizontal; its processus dorsalis extends anteriorly for a short distance; its anterior margin is broadly convex and descends posteroventrally; and its posterior margin is deeply concave, being bracketed above by the moderately deep and posteriorly directed processus posterodorsalis and below by a combination of the posteroventral portion of the lamella alaris and the posteroventrally and slightly medially directed processus posterolateralis. Based on comparisons with extant anurans, the concave posterior margin of the squamosal in life probably bordered the anterior portion of the cartilaginous tympanic annulus. There is neither an obvious processus zygomaticus along the anteroventral portion of the squamosal nor any development of a sutural surface in that region for direct bony contact ventrally with the maxilla. The medial surface of UALVP 40171 is smooth. The extent to which the lamella alaris has expanded anteriorly and the form of the processus posterolateralis are especially evident in medial view. The latter is a stout, rod-like process that extends posteroventrally beyond the ventral margin of the lamella alaris. The ventroposterior end of the processus posterolateralis is blunt and medially bears a shallow, elliptical facet that, in life, presumably articulated with the quadratojugal, although no example of the latter has been identified in samples available to us. More dorsoanteriorly, the processus posterolateralis gives rise to a pair of recurved bony flanges that extend along the medial surface of the squamosal. At the divergence of these flanges, there is a deep and dorsally elongate fossa. The posterior flange follows along the posterior edge of the squamosal, where it extends partway along the ventral edge of the processus posterodorsalis. The anterior flange (= medial ramus of Clarke 2007) extends dorsally and slightly posteriorly, and, closer to the dorsal edge of the squamosal, it grades into the ramus paroticus (= otic plate of some authors). The latter is a medially directed flange that posterodorsally bears a weakly inflated bulge with a shallow sutural surface that, in life, presumably contacted the complementary pars contacta on the otoccipital. More laterally, the smooth and dorsally directed dorsal edge of the lamella alaris indicates that this surface was free and, unlike in casque-headed anurans, it did not arch over the otoccipital to suture or fuse with the posterolateral corner of the frontoparietal. The two unfigured specimens UALVP 40211 and 40212 are the posterodorsal portions of squamosals similar in size and structure to UALVP 40171.

The fourth example, UALVP 40172 (Fig. 8G–I), is a smaller squamosal that preserves the dorsal and posterior portions of the bone, but is missing much of the anterior and ventral portions. This specimen is 4.9 mm in preserved length or about 65% the size of UALVP 40171. Overall, the two squamosals are similar in their preserved structure and form, although the smaller UALVP 40172 differs in the following aspects: the bone is less robust, the sculpture is less prominent (i.e., pits and ridges are relatively shallower) and its ridges are continuous, the dorsal edge of the bone is slightly more concave, the posterior edge of the bone is less concave, and the processus posterodorsalis is relatively longer and shallower. These differences likely are size-related, with differences in the outlines of the dorsal and posterior edges and the proportions of the processus posterodorsalis also reflecting less expansion of the lamella alaris in those regions.

Nasal (Fig. 8J–L)

The only example, UALVP 40170 (Fig. 8J–L), is a virtually complete left nasal bearing dorsal ornament similar to that on the maxilla. The specimen is relatively robust, shallowly convex dorsally, and large. As oriented in the corresponding figures, its maximum dimensions are 7.7 mm wide and 5.4 mm long. The nasal is subtriangular or sickle-shaped in dorsal or ventral outline. In dorsal or ventral view, the margo medialis is moderately elongate, extends anteroposteriorly, and is shallowly concave. Its medial surface is vertical and relatively smooth. The surface texture and the shallowly concave outline of the margo medialis indicate that the nasals were not sutured across the skull midline, although they could have abutted against one another along the anterior and posterior ends of their respective medial margins. Behind the margo medialis, the margin of the nasal is straighter and deflected more laterally in dorsal aspect. When seen in ventral view, it is evident that this more posterior surface (= inner posterior margin of Clarke 2007) is inclined dorsally and bears a small sutural surface, indicating that it overlapped either the sphenethmoid or the frontoparietal. More laterally, the margo orbitalis is broadly concave in dorsal or ventral outline. Its posterior face is ventrally thickened and is shallowly concave in cross section; its lower rim extends slightly farther posteriorly than does its dorsal rim. The processus lateralis is prominently developed as a laterally projecting, triangular prong that terminates in a processus paraorbitalis; the tip of the latter is broken, meaning that the process paraorbitalis likely was more pointed in life. The margo maxillaris region along the anterior surface of the processus paraorbitalis is indented by a shallow concavity, but it is unknown whether or not that surface was in direct bony contact with the processus palatinus on the maxilla or formed part of the ductus nasolacrimalis in that region. At the anterolateral and anteromedial corners of the nasal, each of the processus parachoanalis and the processus anterior, respectively, are just tiny, anteriorly projecting nubs. Between these small processes, the external narial margin extends for a short distance posteromedially. In dorsal aspect, the external narial margin is irregular and shallowly concave in outline, but, in ventral view (Fig. 8L), it is evident that profile is the result of the original, more smoothly and deeply concave margin having been overgrown by the dorsal ornament. The ventral surface of the nasal is indented by a broad, shallow trough that parallels the margo orbitalis. Perpendicular to that trough, there is a Y-shaped configuration of narrower grooves that extend anterolaterally to the edge of the bone.

Frontoparietal (Fig. 9A–G)

The frontoparietal is known from three fragments that collectively document much of the anterior and posterior regions; the median portion corresponding to about the posterior half of the orbital region (i.e., from behind the processus lateralis superior forward to about midway along the margo orbitalis) is not preserved. UALVP 40173 (Fig. 9A–B) is the anterior portion (about the anterior one-quarter) of a right frontoparietal, 7.3 mm in maximum preserved length, that is missing the anterior-most end and posteriorly is broken transversely through the anterior portion of the margo orbitalis. The anterior portion of the margo orbitalis and a lesser amount of the medial edge are intact. TMP 1986.23.32 (Fig. 9C–D) is the more posterior portion of a right frontoparietal that preserves part of the bone between the orbital region and the posterior end, and measures 6.8 mm in maximum preserved length. It is broken anteriorly at a shallowly oblique angle behind the base of the processus

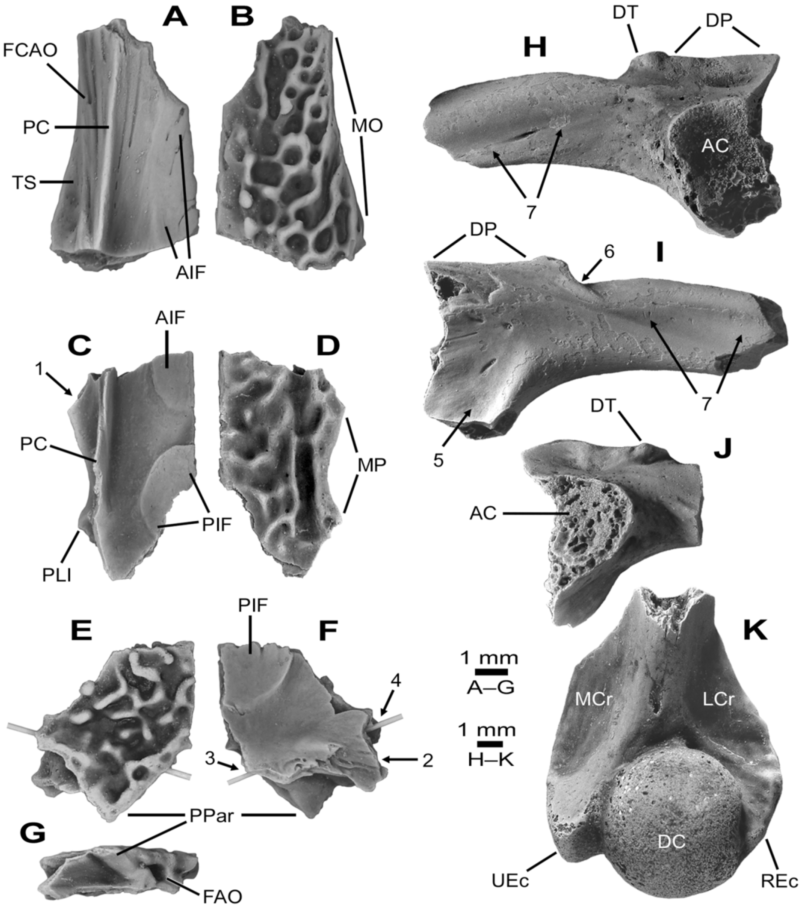

Figure 9:
Referred frontoparietals, ilia, and humerus of *Hensonbatrachus kermiti* new genus and species from the Late Cretaceous (middle–late Campanian or Judithian) of southeastern Alberta, Canada. All specimens are from the Dinosaur Park Formation. Images are photographs and depict specimens lightly dusted with ammonium chloride to enhance details and texture. A–B, Incomplete, large, right frontoparietal preserving anterior portion of bone but missing anteriormost end, UALVP 40173, in ventral (A) and dorsal (B) views. C–D, Incomplete, smaller, right frontoparietal preserving area adjacent to orbital margin, TMP 1986.23.32, in ventral (C) and dorsal (D) views. E–G, Incomplete, smaller, left frontoparietal preserving posterior portion, UALVP 40174, in dorsal (E) and ventral (F) views, both with hair inserted through the arterial canal extending posteromedially to anterolaterally through the bone between the foramen *(continued overleaf)*

(continued from overleaf) arteriae occipitalis and the foramen arteriae temporalis, and in posterior (G) view. H–I, Incomplete left ilium, TMP 1974.10.88, in lateral (H) and medial (I) views. J, less nearly complete right ilium missing most of shaft, UALVP 40175, in lateral view. K, Distal end of left humerus, UALVP 40176, in ventral view. Images are at different scales. Abbreviations: Frontoparietal: AIF, anterior incrassatio frontoparietalis; FAO, foramen arteriae occipitalis; FCAO, foramen for the canalis arteriae orbitonasalis; MO, margo orbitalis; PC, pars contacta; PIF, posterior incrassatio frontoparietalis; PPar, processus paraoccipitalis; and TS, tectum supraorbitale. Ilium: AC, acetabulum; DP, dorsal prominence; DT, dorsal tubercle. Humerus: DC, distal condyle; LCr, lateral crest; MCr, medial crest; REc, radial epicondyle; and UEc, ulnar epicondyle. Numbered arrows (frontoparietal, 1–4 and ilium, 5–7): 1, broken base of ?processus lateralis superior; 2, broken base of ?processus lateralis inferior; 3, hair entering foramen arteriae occipitalis; 4, hair exiting foramen for the canalis arteriae temporalis; 5, no inter-iliac tubercle on medial surface of acetabular region; 6, medial crest paralleling short oblique crest; and 7, shallow trough extending along long axis of iliac shaft on lateral and medial surfaces.

lateralis superior and posteriorly at a steeper oblique angle behind the processus lateralis inferior. The posterior portion of the margo prootica and a short portion of the medial edge are intact. UALVP 40174 (Fig. 9E–G) is the posterolateral corner of a left frontoparietal that is 5.4 mm long in maximum preserved length. Most of its edges are broken except for a short anterior section of the medial margin as well as the median and lateral portions of the posterior margin.

Judging by relative sizes of homologous structures and by proportions and thicknesses of the bone, the three specimens are from different-sized individuals: UALVP 40173 and TMP 1986.23.32 are from the largest and smallest individuals, respectively, whereas UALVP 40174 is from an individual slightly larger than the one represented by TMP 1986.23.32. Collectively, these three specimens reveal that, when complete, the frontoparietals were paired and not in contact anteriorly across the skull midline. Instead, they were weakly sutured together more posteriorly, were moderately narrow in dorsal or ventral outline, and dorsally bore ornament similar to that on the other sculpted cranial bones. UALVP 40173 and TMP 1986.23.32 further show that the pars contacta on the ventral surface is in the form of a narrow, moderately deep flange and that more laterally a tectum supraorbitale is present. UALVP 40173 also shows that the foramen for the canalis arteriae orbitonasalis opens ventrally in the anterior portion of the tectum supraorbitale and that, in dorsal or ventral outline, the margo orbitalis is shallowly concave. TMP 1986.23.32 is important for demonstrating that the ventral surface of the frontoparietal bears both an anterior and a posterior incrassatio frontoparietalis, neither of which is complete. The posterolateral portion of the anterior incrassation is preserved at the level of what we interpret as the broken base of the processus lateralis superior, whereas, farther back, the anterolateral portion of the posterior incrassation is preserved. Each incrassation is developed as a shallow patch of bone that projects slightly below the rest of the ventral surface of the frontoparietal and has a flat ventral surface surrounded by a shallow, but generally well-defined rim that is convex in ventral outline. Both incrassations are located well medial to the pars contacta and are bisected by the medial edge of the frontoparietal, indicating that both the anterior and the posterior incrassations were continuous across the skull midline in life (i.e., they were not paired from side-to-side). The other two frontoparietal specimens preserve some of the missing portions of both incrassations. UALVP 40173 preserves a faint trace of the more anterior portion of the anterior incrassation, which, under low-angle light, can be seen to be elongate (it spans between the broken anterior and posterior ends of the specimen) with its lateral margin curving gently medially. Although the anterior end of this incrassation is lacking, the structure clearly would have been elongate and much more so than the posterior incrassation. Thanks to TMP 1986.23.32 and UALVP 40174 preserving overlapping portions of the relevant regions, it is evident that the posterior incrassation is subcircular in outline and, when the frontoparietals were articulated, that incrassation would have been slightly broader than long. UALVP 40174 is further informative for showing that the posterior portion of the frontoparietal lacks an elevated crest (= frontoparietal-otoccipital ridge of Clarke 2007) extending posterolaterally across its dorsal surface and also that the processus paraoccipitalis projects posteriorly, is robust and anteroposteriorly short, and resembles an equilateral triangle in dorsal or ventral outline. The posteromedian surface of that process is perforated by a moderately large foramen arteriae occipitalis. A hair inserted through that foramen (Fig. 9E–F) can be pushed laterally and slightly anteriorly through a bony canal (= occipital canal of some authors) that is roofed dorsally by bone before exiting through the foramen for the canalis arteriae temporalis in the broken base of the processus lateralis inferior.

Ilium (Fig. 9H–J)

The most nearly complete specimen, TMP 1974.10.88 (Fig. 9H–I), is a left ilium that preserves a considerable amount of the posterior portion of the shaft and much of the acetabular region, but not the posterior and ventral edges. This specimen is robust and large, measuring 17 mm in preserved length; depending on how much of the shaft is missing, the intact bone could have been 25 mm or longer. The other six specimens are comparable in size and build, but preserve only the posterior-most or basal portion of the shaft. Some, such as UALVP 40175 (Fig. 9J), have a more nearly intact acetabular region. Collectively, the seven specimens show that the acetabular region is subtriangular in lateral or medial outline. In lateral view, the iliac portion of the acetabulum is also subtriangular in outline, with a bluntly rounded anterior end; its borders lie well within the dorsal, anterior, and ventral boundaries of the acetabular region. Outside of the acetabulum, the pre-acetabular region is relatively narrow anteroposteriorly, more so than the depths of the sub- and supra-acetabular regions, which are subequal to one another. The medial surface of the acetabular region is shallowly concave and lacks a medially expanded inter-iliac tubercle. Along its dorsal margin, the acetabular region bears a moderately high, ridge-like dorsal prominence that extends anteriorly past the level of the anterior rim of the acetabulum. At its anterodorsal end, the dorsal prominence bears a dorsal tubercle in the form of a moderately swollen, slightly elongate, and raised knob with a slightly flattened top. The base of this dorsal tubercle is slightly offset laterally. More ventrally, a shallow oblique or spiral groove wraps around the anterolateral base of the dorsal prominence, continues anteriorly and slightly medially across the dorsal surface at the junction between the acetabular region and iliac shaft, and barely extends onto the dorsomedial surface of the shaft. Where it extends along the dorsal and medial surfaces of the shaft, this groove is flanked medially by a low, but distinct ridge extending from the anteromedial corner of the base of the dorsal prominence. The structure of the iliac shaft is best seen in TMP 1974.10.88. In that specimen, the preserved portion of the shaft is shallowly arched dorsally in lateral or medial view, is dorsoventrally deep and mediolaterally compressed, and its dorsal and ventral surfaces are broadly convex in cross section. A shallow trough extends anteroposteriorly along both the lateral and medial surfaces of the shaft. No dorsal crest is present and no ridges or protuberances occur on either the medial or lateral surfaces of the shaft.

Humerus (Fig. 9K)

The sole available example, UALVP 40176 (Fig. 9K), is the distal end of a left humerus that is broken through the shaft at about the proximal limits of the medial and lateral crests; it is also missing the dorsal edge of the former crest. Having a maximum preserved length and width of 11.4 and 8.3 mm, respectively, UALVP 40176 is relatively large, at least compared to most known North American Cretaceous anuran humeri. When viewed in ventral aspect, the distal condyle is a solidly ossified and almost perfectly rounded ball, the ventral surface of the cubital fossa is flattened, and a small foramen perforates the shaft just proximal to the cubital fossa. The ulnar epicondyle has a subpointed distal end that is more pronounced than the broadly and asymmetrically convex distal end of the radial epicondyle. The medial and lateral crests are similarly broad, yet their outer edges differ: the medial crest has a thin and smooth edge, whereas the edge of the lateral crest is dorsoventrally thickened and bears low knobs, presumably for enhanced muscle attachment. On the dorsal surface (not figured), the olecranon scar is large and subtriangular in outline, but not especially pronounced. Compared to the broad distal end, the broken end of the shaft is comparably narrow, having a diameter of 3.1 mm or about 37% of the maximum width across the medial and lateral crests.

Discussion

Diagnostic features and comparisons

Introductory remarks and comparative taxa and specimens

Although *H. kermiti* is known only from isolated bones, these exhibit a unique suite of body-size and osteological features that serve to differentiate this taxon from all other anurans known to us and warrant formal taxonomic recognition of this new genus and species. Considering their temporal and geographic proximities, comparisons with other anuran taxa and fossils from the latter part (Campanian and Maastrichtian) of the Late Cretaceous in western North America are particularly relevant. Those taxa and fossils are listed below.

(1) *Theatonius lancensis* Fox 1976b, known by maxillae (including the holotype), frontoparietals, and probable squamosals (Fox 1976b; Gardner 2008), and *Paradiscoglossus americanus* Estes & Sanchíz 1982, known by ilia (including the holotype) and questionably humeri (Estes & Sanchíz 1982; Gardner 2008), with both species being from the late Maastrichtian of Wyoming.

(2) *Palaeobatrachus occidentalis* Estes & Sanchíz 1982, known by ilia (including the holotype) and questionably a fused atlas + first trunk ver-

tebra, from the late Maastrichtian of Wyoming and late Maastrichtian and/or early Palaeocene of Montana (Estes & Sanchíz 1982; Gardner 2008).

(3) *Scotiophryne pustulosa* Estes 1969, known by ilia (including the holotype), maxillae, squamosals, nasals, frontoparietals, and questionably humeri, and an *Eopelobates*-like taxon, also known by many of the same elements, with both taxa having been reported from numerous Campanian to late Maastrichtian and/or early Palaeocene localities in the Western Interior, especially in Montana and Wyoming (e. g., Estes 1964, 1969; Breithaupt 1985; DeMar & Breithaupt 2006, 2008; Gardner 2008; Gardner & DeMar 2013).

(4) An unnamed taxon (= "new gen. and sp. A"; Gardner 2005, his Table 10.1), known by maxillae, squamosals, nasals, frontoparietals, and ilia, being best known from the Dinosaur Park Formation (hereafter this taxon is referred to as the "unnamed Dinosaur Park Formation taxon").

(5) Numerous indeterminate, but distinctive maxillae and ilia from the late Maastrichtian of Wyoming (Estes 1964; Gardner 2008), from the middle–late Campanian Dinosaur Park and Oldman Formations in Alberta (Gardner & Brinkman, work in progress), from the middle–late Campanian Judith River Formation in Montana (Sahni 1972), and from both the early Campanian Wahweap Formation and the middle–late Campanian Kaiparowits Formation in Utah (Roček *et al.* 2010).

The family-level affinities of the above-mentioned taxa and specimens are largely uncertain (e. g., see Gardner 2008; Roček *et al.* 2010) and, for that reason, we conservatively treat them as Anura *incertae sedis* in this paper. The sole possible exception is *P. occidentalis*, which has been regarded as a palaeobatrachid (e. g., Estes & Sanchíz 1982; Sanchiz 1998; Gardner 2008), although Wuttke *et al.* (2012) recently raised concerns about that familial assignment. We exclude *Nezpercius dodsoni* Blob *et al.* 2001 from the above list because, although that species was described as an anuran originally, the trio of distinctive ilia upon which it is based have since been shown to be from a urodele (Gardner *et al.* 2010). Removal of *N. dodsoni* from Anura means that *H. kermiti* is the first unequivocal anuran to be named from the Campanian of North America.

Relative and absolute size of Hensonbatrachus kermiti

One of the most striking features of *H. kermiti* is the large size of its elements, at least relative to other anuran fossils co-occurring in the same localities and known from elsewhere in the North American latest Cretaceous. When dimensions such as total length of the maxilla or depth of the acetabulum on the ilium are compared, bones of *H. kermiti* are between 1.5x and 3x larger than the homologous elements from most other anurans from the North American Late Cretaceous. The only other North American latest Cretaceous anuran specimens of comparable size are some Maastrichtian maxillae and ilia of the *Eopelobates*-like taxon from Wyoming (e. g., Gardner 2008, his Fig. 13.3) and some indeterminate maxillae and ilia from the Campanian of Montana and Utah (e. g., Sahni 1972, his Fig. 7P–Q; Roček *et al.* 2010, their Figs. 14q, 15Be) and the late Maastrichtian of Wyoming (Gardner 2008, his Fig. 13.4). In the absence of an articulated skeleton, absolute body size (measured in terms of snout–vent length) cannot be measured directly for *H. kermiti*. Using formulae presented by Esteban *et al.* (1995) for estimating body size in the extant European anuran *Rana temporaria* and our measurements taken from ilia and the one humerus of *H. kermiti*, we calculated the following snout–vent length estimates for the latter species: 78.6 to 87.8 mm based on the posterior depth of the iliac acetabulum (= measurement 16 or "Acetab" of Esteban *et al.* 1995), 101.5 mm based on the maximum length of the humeral distal condyle (= measurement 15 or "Lcondyle" of Esteban *et al.* 1995), and 116.2 mm based on the maximum width across the distal end of humerus (= measurement 14 or "Wcondyle" of Esteban *et al.* 1995). We also obtained similar body-size estimates by comparing the same *H. kermiti* ilia and humerus directly to different-sized, articulated skeletons of extant North American *Lithobates* species. Extant anurans range in adult body size from about 10–300 mm, with most species falling in the 20–80 mm range (Mattison 2011). With an estimated body size of 75–115 mm, *H. kermiti* can be described as a larger, medium-sized anuran. In terms of present day Albertan anurans, *H. kermiti* is comparable in adult body size to the toads *Anaxyrus boreas* (55–125 mm) and *Anaxyrus cognatus* (45–110 mm) and to the frogs *Lithobates pipiens* (50–100 mm) and *Rana pretiosa* (45–100 mm) (all size ranges from Russell & Bauer 1993).

Osteological features of Hensonbatrachus kermiti

Besides relative or absolute body size, *H. kermiti* also differs from other North American latest Cretaceous anurans in a unique combination of osteological features. None of these features can be surveyed for every other known or suspected North American latest Cretaceous anuran because many of those taxa are known from fewer parts of the skeleton (e. g., no cranial bones are available for *P. americanus* and *P. occidentalis*, and no ilia are available for *T. lancensis*). Even with those uncertainties, there are an impressive number of cranial and iliac features that collectively serve to diagnose *H. kermiti*. These features are discussed below in four groups ranked in descending order of usefulness in differentiating *H. kermiti* from other North American latest Cretaceous anurans.

I. Osteological features known only for Hensonbatrachus kermiti *among other North American latest Cretaceous anurans*: The features discussed below can be compared to two or more of the other North American latest Cretaceous anuran taxa and, within this temporally and geographically constrained grouping, are only known for *H. kermiti*.

(1) Pattern of cranial ornament. In *H. kermiti*, the maxilla, squamosal, nasal, and frontoparietal are broadly ornamented externally with pit-and-ridge style ornament consisting of moderately deep, irregular-shaped pits and short grooves enclosed by moderately tall, thick, and vermiform ridges. Pit-and-ridge cranial ornament is common among extant and fossil anurans, so the mere presence of this kind of ornament is not particularly diagnostic. However, specific and consistent differences in the arrangements and relative sizes of pits and ridges help differentiate *H. kermiti* from other North American latest Cretaceous anurans having pit-and-ridge cranial ornament. In those latter taxa—including the *Eopelobates*-like taxon (Gardner 2008, his Fig. 13.3A, C–D, and F), the unnamed Dinosaur Park Formation taxon (Gardner 2000, his Fig. 12-4A–B, D–E, and G), and indeterminate Campanian maxillae from Montana and Utah (Sahni 1972, his Fig. 7L, P; Roček *et al.* 2010, their Figs. 15Ba, e, and 16Am)—cranial ornament tends to have a more regular polygonal or net-like arrangement vs. the irregular or wavy pattern seen in *H. kermiti*; their pits and ridges also tend to be relatively narrower and shallower. External surfaces of cranial bones in other North American latest Cretaceous anurans differ even further in being smooth (e. g., indeterminate Campanian maxillae figured by Sahni (1972, his Fig. 7N) and by Roček

et al. (2010, their Figs. 15Ak–l and 16Aa) and late Maastrichtian maxillae figured by Gardner (2008, his Fig 13.4G, I)), in having a roughened, striated, or pockmarked texture (e. g., indeterminate Campanian maxillae figured by Roček *et al.* (2010, their Fig. 15An–o) and late Maastrichtian maxillae figured by Gardner (2008, his Fig 13.4A, C, and E)), or in bearing pustulate or tuberculate ornament (e. g., *S. pustulosa* and *T. lancensis*; Estes 1969, his Fig. 2a, d–e; Fox 1976b, his Figs. 1–2; Gardner 2008, his Figs. 13.1L, N, P, Q, and S and 13.2A, E–F, G, and I; Roček *et al.* 2010, their Fig. 16Aj–l).

(2) Proportions of maxillary pre-, post-, and suborbital regions and outline of margo orbitalis. As in extant anurans, there is considerable variation among North American latest Cretaceous anuran maxillae in the heights of the pre- and postorbital regions, the depth of the suborbital region between the margo orbitalis and lamina horizontalis, and the outline of the margo orbitalis. As best shown by the holotype maxilla, the pre- and postorbital regions in *H. kermiti* are relatively tall and similar in height, the suborbital region is relatively deep between the margo orbitalis and the dorsal surface of the lamina horizontalis, and the margo orbitalis is moderately concave. In other adequately known North American latest Cretaceous maxillae, the preorbital region typically is taller to varying degrees than the postorbital region. For example, it is slightly taller in *Scotiophryne* (Estes 1969, his Fig. 2d–e; Gardner 2008, his Fig. 13.1L–O), moderately taller in *Theatonius* (Fox 1976b, his Fig. 1; Gardner 2008, his Fig. 13.2A–B) and the *Eopelobates*-like taxon (Gardner 2008, his Fig. 13.3A–B), and considerably taller in an indeterminate late Maastrichtian maxilla (Gardner 2008, his Fig. 13.4I–J). The depth of the suborbital region between the margo orbitalis and lamina horizontalis typically is relatively shallower than in *H. kermiti* and, in some, it is markedly shallower (e. g., Gardner 2008, his Fig. 13.4F and J). Coincident with the postorbital region becoming lower relative to the preorbital region, the margo orbitalis also tends to become less concave.

(3) Groove for nasolacrimal duct in maxilla open dorsally along most of margo orbitalis. Some North American latest Cretaceous anurans have a groove in the margo orbitalis that appears to have housed a posterior extension of the nasolacrimal duct. Because both the presence and relative length of this groove have received little attention in the anuran literature, variation in this feature among extant anurans is largely unknown. Among North American latest Cretaceous anurans, however, this dor-

sally-open groove is known to extend along much of the margo orbitalis in *H. kermiti*, whereas the groove is limited to the more anterior portion of the margo orbitalis in *T. lancensis* (Gardner 2008, his Fig. 13.2C), the *Eopelobates*-like taxon (Gardner 2008, his Fig. 13.3B), and the unnamed Dinosaur Park Formation taxon (Gardner 2000, his Fig. 12-4C).

(4) Form of lamina horizontalis on maxilla. This ridge or shelf-like structure extends along the anterior and median portions of the lingual surface of the maxilla above the tooth-bearing region. Among North American latest Cretaceous anurans, the most weakly developed lamina horizontalis occurs in *T. lancensis*, where the structure is little more than an indistinct, rounded ridge (Fox 1976b, his Fig. 1; Gardner 2008, his Fig. 13.2B and D). In others, the lamina horizontalis is more prominently developed and considerable variation is evident in its relative depth and width as well as in the form of its surfaces; these features usually are best expressed in the suborbital region. For example, the lamina horizontalis can be a shallow, but lingually broad shelf (e. g., Roček *et al.* 2010, their Fig 15Ak–l), its depth and width can be subequal (e. g., Gardner 2008, his Fig. 13.3B), or it can be deeper than it is wide (as in *H. kermiti*; Fig. 4C and E); its lingual face can be flattened (as in *H. kermiti*; Fig. 4C), shallowly convex (e. g., Gardner 2008, his Fig. 13.1O), or more steeply convex (e. g., Gardner 2008, his Fig. 13.3B). In *H. kermiti*, the lamina horizontalis is a prominent ledge that is moderately deep (i.e., accounts for about one-quarter of the minimal depth of the suborbital region) and lingually wide (but having width less than depth), and is approximately triangular in cross section, with its lingual surface flattened and facing ventrolingually, its ventral surface narrow and dorsally concave, and its dorsal surface shallowly concave to nearly flat. Although some of the above-listed features can be seen in certain other North American latest Cretaceous anuran maxillae (e. g., a similarly deep lamina horizontalis occurs in some indeterminate Campanian and late Maastrichtian maxillae; Sahni 1972, his Fig. 7Q; Gardner 2008, his Fig. 13.4B, D and F), none have a lamina horizontalis that exactly matches the condition in *H. kermiti*.

(5) Form of processus palatinus on maxilla. In anurans, the processus palatinus extends dorsoanteriorly and medially along the lingual surface of the preorbital region and might be involved in articulating, either directly or indirectly, with the nasal. Typically in North American latest Cretaceous anurans, the processus palatinus is prominently developed (i.e., some

combination of being dorsally elongate, lingually broad, and having a prominent, trough-like dorsal surface). Extreme examples of a well-developed processus palatinus include an indeterminate late Maastrichtian maxilla, in which the processus is an elongate and triangular prong that extends dorsoanteriorly well beyond the dorsal edge of the preorbital region (e. g., Gardner 2008, his Fig. 13.4I–J), and *T. lancensis*, in which the process is shorter, but stouter and broader, and projects more lingually (e. g., Gardner 2008, his Fig. 13.2A–D). Despite its relatively large size and robust build, the maxilla of *H. kermiti* has a comparatively weaker processus palatinus in the form of a narrow and tapered prong that extends dorsoanteriorly and barely projects past the dorsal edge of the preorbital region.

(6) Form of processus pterygoideus on maxilla and nature of maxillary contacts with pterygoid and squamosal. The anuran maxilla always articulates lingually with the pterygoid and variably articulates dorsally with the squamosal (e. g., Trueb 1973). Maxilla-pterygoid articulation involves the anterolaterally projecting ramus maxillaris (= anterior ramus of some authors) of the pterygoid extending along the junction between the lingual surface of the maxillary pars facialis and the dorsal surface of the lamina horizontalis in the suborbital region. The posterior end of the lamina horizontalis in some anurans is elaborated lingually to form the processus pterygoideus, which is overlapped by the ramus maxillaris of the pterygoid and thereby contributes to the contact between those two elements. Where present in anurans, direct maxilla-squamosal contact occurs between the dorsal end of the processus zygomatico-maxillaris on the maxilla and the ventral edge of the complementary processus zygomaticus on the squamosal. Contact surfaces between the maxilla and the other two bones can be either smooth or roughened for sutural contact. Among North American latest Cretaceous anurans, most maxillae exhibit some combination of a lingually projecting and usually triangular processus pterygoideus, indicating enhanced maxilla-pterygoid contact, and a sutural facet extending anteroposteriorly along the dorsal edge and onto the dorsolingual portion of the processus zygomatico-maxillaris, indicating firm contact with the squamosal. Both of those conditions occur in *S. pustulosa* (e. g., Estes 1969, his Fig. 2c and f; Gardner 2008, his Fig. 13.1 N–O), the *Eopelobates*-like taxon (e. g., Gardner 2008, his Fig. 13.3B), the unnamed Dinosaur Park Formation taxon (e. g., Gardner 2000, his Fig. 12-4C), and in some indeterminate Campanian (Sahni 1972, his Fig. 7M;

Roček *et al.* 2010, their Fig. 15Ba and e) and late Maastrichtian maxillae (e. g., Gardner 2008, his Fig. 13.4D). Other indeterminate late Maastrichtian maxillae have a prominent processus pterygoideus, but lack any evidence of a contact surface dorsally for articulation with the squamosal (e. g., Gardner 2008, his Fig. 13.4F and H). Conversely, *T. lancensis* dorsally has a sutural surface for squamosal contact, but lacks a processus pterygoideus (e. g., Fox 1976b, his Fig. 1; Gardner 2008, his fig. 13.2 B–D); in that taxon, a lingually projecting and oval-shaped facet located slightly above where the processus pterygoideus normally would occur probably served as a point of articulation with the pterygoid. Compared to the above-listed taxa and specimens, maxillae of *H. kermiti* are distinctive in three attributes. First, the dorsal edge of the processus zygomatico-maxillaris is labiolingually thin and smooth with no indication (i.e., a sutural surface) for having directly contacted the squamosal. This interpretation is supported by the associated squamosals (see next point) that lack any indication of having been in direct, bone-to-bone contact ventrally with the maxilla. Second, the processus pterygoideus is reduced to a small, scoop-like process that is barely expanded lingually. Such a process might still have underlapped the pterygoid, but, if so, it would have contributed minimally, if at all, to the maxilla-pterygoid contact. Judging by the shallowly concave dorsal surface of the lamina horizontalis, the ramus maxillaris probably retained its contact more anteriorly along that ledge. Third, across the posterior portion of the suborbital region and onto the anterior part of the processus zygomatico-maxillaris, the lingual surface of the pars facialis is roughened, and especially so on larger maxillae, in a manner that suggests that the area was in ligamentous or sutural contact with an adjacent element. The two most likely options are that this region of the maxilla was in bony or ligamentous contact with the pterygoid or in ligamentous contact with the squamosal. Either pattern of contact would have helped brace the maxilla lingually, which might have been necessary to stabilise the tall postorbital portion of that bone and to compensate for the lack of direct bone-to-bone contact dorsally with the squamosal.

(7) Form and contacts of squamosal. Anuran squamosals typically are described as being approximately tri-radiate or T-shaped in lateral aspect (e. g., Trueb 1973; Clarke 2007), consisting of the following major components: an anteriorly or anteroventrally directed processus zygomaticus (= zygomatic ramus or process of some authors) that might articulate

with the maxilla; a ventroposteriorly directed processus posterolateralis (= ventral ramus, mandibular ramus, or squamosal shaft of some authors) that might articulate with the quadratojugal; and a posteriorly directed processus posterodorsalis (= posterior, prootic, or otic ramus of some authors) that medially bears the ramus paroticus for bracing the squamosal against the otoccipital. Considerable variation is seen among extant anurans in the shapes, proportions, and contacts of those components (e. g., Lynch 1971; Trueb 1973; Clarke 2007). Among North American latest Cretaceous anurans for which reasonably complete squamosals are known, there are two basic patterns. In *S. pustulosa* and the *Eopelobates*-like taxon (e. g., Gardner 2008, his Figs. 13.1Q–R and 13.3D–E, respectively), the lamella alaris is somewhat bar-like in lateral or medial outline, being much narrower anteroposteriorly than it is tall, and also is bent or curved posteriorly midway along its height, with the portion below the bend formed by the processus zygomaticus and the portion above the bend formed by the processus posterodorsalis. The ventral portion of the processus zygomaticus is anteroposteriorly expanded, is slightly thickened mediolaterally, and its ventral surface is shallowly concave for sutural articulation with the complementary processus zygomatico-maxillaris on the maxilla. The dorsal end of the processus posterodorsalis is narrow and convex in outline. The processus posterolateralis is an anteroposteriorly-compressed flange that, because of its narrow form and delicate build, almost invariably is broken close to its base in fossil specimens; in life, the processus posterolateralis would have projected posteroventrally and been clearly visible in lateral aspect. The squamosal of *H. kermiti* differs substantially as follows: the lamella alaris is expanded into a broad plate that is approximately C-shaped in lateral outline with a deeply concave posterior margin; the processus zygomaticus is absent and no sutural surface is present along the ventral margin of the bone for direct, bone-to-bone contact with the maxilla; and the processus posterolateralis is a stout prong. Both kinds of squamosals are similar in having the external surface of the lamella alaris ornamented—although ornament patterns differ among the taxa—and in having a smooth, dorsal margin indicating that the lamella alaris did not arch dorsomedially to contact the frontoparietal. The three squamosals known for *T. lancensis* (Fox 1976b, his Fig. 2; Gardner 2008, his Fig. 13.2F) also have a broad lamella alaris that is ornamented externally, but cannot be compared further because of their fragmentary nature.

(8) Frontoparietal incrassations. On the ventral surface and medial to the pars contacta, anuran frontoparietals can bear one or more broad, flat to shallowly concave patches of bone that project slightly below, or are indented into, the ventral surface of the frontoparietal. Although once thought to represent imprints of the dorsal surface of the brain (e. g., Špinar 1976), subsequent work using developmental series of extant anurans demonstrated that these incrassations result from frontoparietal bone infilling fenestrae or gaps in the dorsal wall of the underlying endocranium (Jarošová and Roček 1982). Variation in the number, position, and shapes of frontoparietal incrassations occurs in extant anurans and these attributes appear to be taxon-specific (e. g., Špinar 1976; Jarošová & Roček 1982). Among North American latest Cretaceous anurans for which frontoparietals are adequately known, two general arrangements are seen. Either a single, anteroposteriorly elongate and mediolaterally broad incrassation is present—as in *T. lancensis* (e. g., Gardner 2008, his Fig. 13.2J and H), the unnamed Dinosaur Park Formation taxon (e. g., Gardner 2000, his Fig. 12-4H), and the *Eopelobates*-like taxon (e. g., Gardner 2008, his Fig. 13.3G)—or two narrower incrassations are present, a subcircular one posteriorly and a more elongate one anteriorly, as in *H. kermiti*. In both these arrangements, each incrassation is bisected sagittally by the inter-frontoparietal suture, indicating that each incrassation was continuous across the skull midline. Other arrangements documented for anurans include the anterior incrassation being continuous across the midline, but the posterior incrassation being bilaterally paired and vice versa (e. g., Špinar 1976, his Pl. II.3–4 and Fig. 2a, respectively). We have not seen either of those tripartite arrangements among the limited sample of anuran frontoparietals available to us from the North American latest Cretaceous.

(9) Dorsal prominence and dorsal tubercle on ilium. Anuran ilia variably have a raised flange or ridge, called the dorsal prominence, on the dorsal surface of the acetabular region. Also, a knob-like process called the dorsal tubercle (= dorsal protuberance or tuber superius of some authors) might be present on the dorsal surface of the dorsal prominence or on the posteriormost surface of the dorsal crest. This tubercle serves as the attachment point for three muscles (gluteus maximus, ilio-tibialis, and ilio-femoralis) responsible for extension and flexion of the hind limb (Přikryl *et al.* 2009). The presence or absence, form, and position of the dorsal tubercle and, to a lesser extent, also the dorsal prominence varies among

anurans; historically, these kinds of differences were widely used for recognising fossil species (see review and critique by Bever 2005). Among North American latest Cretaceous anurans, the dorsal tubercle is a common, but not universal feature. In fact, it is absent in *S. pustulosa* (e. g., Estes 1969, his Fig. 1), the *Eopelobates*-like taxon (e. g., Gardner 2008, his Fig. 13.3H–I), the unnamed Dinosaur Park Formation taxon (e. g., Gardner 2000, his Fig. 12-4J–K), and from some indeterminate Campanian (e. g., Sahni 1972, his Fig. 7G–K; Roček *et al.* 2010, their Figs. 13a–e, 14r–t, and 15Af) and late Maastrichtian ilia (e. g., Gardner 2008, his Fig. 13.4K–L). In *P. americanus* and *P. occidentalis*, the dorsal tubercle is present as a low, moderately elongate knob positioned slightly anterior to the level of the anterior rim of the acetabulum (e. g., Estes & Sanchíz 1982, their Figs. 2B and 4C, respectively); in the former species, the tubercle lies along the posterior-most end of the dorsal crest, whereas, in the latter species, it lies on the dorsal surface of the acetabular region. Among the Campanian ilia figured by Roček *et al.* (2010), where present, the dorsal tubercle consistently lies along the dorsal surface of the acetabular region, but ranges in its expression from a low, indistinct bump to a tall, medio-laterally compressed knob that is subtriangular to almost square in lateral outline. Compared to these species, the condition in *H. kermiti* shows the following distinctive features: the dorsal surface of the acetabular region bears a moderately high, ridge-like dorsal prominence that extends anteriorly past the level of the anterior rim of the acetabulum and, at its anterodorsal end, bears a dorsal tubercle that is moderately broad, tall, and elongate, has a slightly flattened dorsal surface, and is slightly offset laterally.

(10) Form of iliac shaft. Typically in anurans, the iliac shaft (excluding any crests or ridges that might be present) is subcircular to oval in cross section and has convex lateral and medial sides. This is the case for most North American latest Cretaceous ilia, including the holotype and referred ilia of *S. pustulosa*, *P. americanus*, and *P. occidentalis* (e. g., Estes 1969, his Fig. 1; Estes & Sanchíz 1982, their Fig. 1), ilia of the *Eopelobates*-like taxon (e. g., Gardner 2008, his Fig. 13.3H–I) and the unnamed Dinosaur Park Formation taxon (e. g., Gardner 2000, his Fig. 12-4J–K), indeterminate late Maastrichtian ilia (e. g., Gardner 2008, his Fig. 13.4K–L), and all of the indeterminate Campanian ilia figured by Sahni (1972) and Roček *et al.* (2010). However, in *H. kermiti,* the iliac shaft is moderately com-

pressed mediolaterally and its lateral and medial surfaces are indented by a shallow trough that extends forward along both surfaces.

II. Osteological features that differentiate Hensonbatrachus kermiti *from some other North American latest Cretaceous anurans*: Two features are somewhat useful for identifying *H. kermiti* because, although each is shared with some North American latest Cretaceous anurans, they are absent in others.

(1) Maxilla robustly constructed. This is a qualitative and admittedly subjective feature that undoubtedly is correlated, at least in part, with the moderately large size of the maxilla and its well-developed external ornament in *H. kermiti*. Larger examples of *Eopelobates*-like maxillae (e. g., Sahni 1972, his Fig. 7P–Q) and some indeterminate Campanian (e. g., Roček *et al.* 2010, their Figs. 14q and 15Be) and late Maastrichtian maxillae (e. g., Gardner 2008, his Fig. 13.4A–D) are similarly robust. Other North American latest Cretaceous maxillae, even accounting for the smaller sizes of many of these, have a somewhat less robust build. Few examples of delicate maxillae are known to us (but see Roček *et al.* 2010, their Fig. 15Ak), which is not surprising considering that fossils in vertebrate microfossil localities are subjected to a variety of physical stresses—both before and during deposition (e. g., scavenging, scattering, transport, and re-working; Eberth 1990), and later, when the fossiliferous matrix is processed to recover specimens—that can damage or destroy even fairly robust fossils.

(2) Oblique groove present. An oblique groove (= spiral groove of some authors) is a common iliac feature among Mesozoic and some Cenozoic anurans (see Roček *et al.* 2012). It originates on the lateral surface of the supra-acetabular region, crosses over the dorsal margin at the junction between the acetabular region and shaft, and continues anteriorly or anteroventrally onto the medial surface of the posterior portion of the shaft. The oblique groove can be faint or deep, might not extend any significant distance onto the lateral surface of the shaft, or it can be bordered anteromedially by a faint ridge (Roček *et al.* 2010, 2012, 2013). As noted by Henrici (2002: 252) for the Eocene pelobatoids *Eopelobates wagneri* and possibly *Eopelobates grandis*, the oblique groove can vary “from being barely visible to a deep groove” even within a species. In extant anurans, the oblique groove occurs in the pelobatoids *Pelobates*, *Scaphiopus*, and some *Megophrys* species (Roček *et al.* 2013) and it also has been reported in one individual of the discoglossid *Bombina orientalis*

(Henrici and Haynes 2006). Dissections of *Pelobates* revealed that the oblique groove is associated with the iliac externus muscle, which is important for protracting the thigh (Přikryl *et al.* 2009). We interpret the groove that crosses the dorsal surface of the junction between the acetabular region and the shaft in ilia of *H. kermiti* as the oblique groove because it occurs in approximately the same position as that groove in other anurans and its anteromedial portion is bordered by a distinct crest. Compared to other anurans, however, the oblique groove in *H. kermiti* differs in having its posterior end on the anterolateral corner of the dorsal prominence, not slightly lower on the lateral surface of the supra-acetabular expansion proper. Among other North American latest Cretaceous anurans, an oblique groove is present in *S. pustulosa* (e. g., Estes 1969, his Fig. 1; Roček *et al.* 2010, their Figs. 13a–b and d and 14k–l and t), some ilia of the *Eopelobates*-like taxon (but weakly developed in the specimen figured by Gardner (2008, his Fig. 13.3H–I)), and some of the indeterminate Campanian ilia reported by Roček *et al.* (2010: 388), but it is absent from other taxa and specimens. It has previously been noted (Roček *et al.* 2010, 2012) that an oblique groove and a dorsal tubercle rarely occur together on the same ilium among extant and most fossil anurans. If correctly identified, the presence of an oblique groove in *H. kermiti* represents one of the few known instances in which both of those structures co-occur in the same taxon (for other fossil examples, see Roček *et al.* 2010: 388).

III. Osteological features that differentiate Hensonbatrachus kermiti *from only one other North American latest Cretaceous anuran*: Six features are of more restricted diagnostic utility for *H. kermiti* because nearly all other North American latest Cretaceous anurans also possess the same features. However, for each feature, a different version occurs in one of the three named late Maastrichtian species. As such, *H. kermiti* can be further differentiated from that trio of species as indicated below.

(1) From *T. lancensis* (Fox 1976b, his Figs. 1–2; Gardner 2008, his Fig. 13.2A–E and G–J) in having maxillary teeth (vs. teeth absent), in having medial contact between the paired frontoparietals limited to the more posterior portion of those bones (vs. in contact along entire length of medial edge), and in having frontoparietals that are moderately narrow in dorsal or ventral outline (vs. relatively broader, especially across post-orbital region).

(2) From *P. americanus* (Estes & Sanchíz 1982, their Fig. 1A–B; Gardner 2008, his Fig. 13.2K–L) in lacking a dorsal crest on ilium (vs. crest present).

(3) From *P. occidentalis* (Estes & Sanchíz 1982, their Fig. 1C–F; Gardner 2008, his Fig. 13.1A–D) in having the acetabular surface on the ilium subtriangular in lateral outline and its borders fully contained within the dorsal, anterior, and ventral boundaries of the acetabular region (vs. acetabulum more bell-shaped and relatively larger, with ventral margin displaced below the ventral limit of the subacetabular region) and in having medial surface of acetabular region bearing only a small, subtriangular inter-iliac scar (vs. broader and medially expanded inter-iliac tubercle).

IV. Osteological features more useful for differentiating Hensonbatrachus kermiti *from anurans outside of the North American latest Cretaceous*: The features considered in this section are less useful for differentiating among North American latest Cretaceous anurans because they either are known from too few specimens and taxa or they are invariant among currently available samples. However, all these features are known to vary among extant and other fossil anurans, so they remain useful for diagnosing *H. kermiti* when making broader comparisons. As additional fossil specimens and taxa are discovered, we anticipate that at least some of these features will prove to be more variable among North American latest Cretaceous anurans and, thus, more useful for differentiating among these taxa. These features are briefly discussed below.

(1) Form and size of teeth. Anurans primitively possess teeth on the premaxilla and maxilla, and these teeth primitively are relatively short, are pedicellate (i.e., with a division between the shaft or pedicel and the crown), and their crowns are labiolingually bicuspid (e. g., Trueb 1973; Cannatella 1985). In the classic "textbook" account of pedicelly, a fibrous and ring-like dividing zone completely encircles the tooth, where it forms a somewhat flexible and pronounced "waist" or indentation between the crown and pedicel (e. g., Parsons & Williams 1962, their Figs. 1–5 and 7; Duellman & Trueb 1986, their Figs. 15–20). Yet, as noted by Greven (1989: 452), "The dividing zone, however, shows a considerable variability, especially in Anura … ranging from broad distinct uncalcified rings to traces difficult to see by light microscopy" (for examples, see Greven & Laumeier 1987; Fabrezi 2001). The two intact maxillary

teeth known for *H. kermiti* each have a less pronounced dividing zone (cf., Fig. 7L–N vs. the more pronounced dividing zone in extant anuran teeth depicted by Parsons & Williams 1962, their Figs. 3 and 7); elsewhere in this paper, we have used the term “weakly pedicellate” for the condition in *H. kermiti*. Some anurans have teeth that are non-pedicellate (i.e., the pedicel and crown form one solid unit), bear monocuspid or conical crowns, are elongate (so called “fang-like” teeth), or display some combination of these derived conditions. As an extreme example, the extant ceratophryids (*sensu* Frost *et al.* 2006) *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus* bear teeth that are non-pedicellate, monocuspid, and fang-like (e. g., Lynch 1971, his Figs. 13D, 74 and 76; Fabrezi 2001, his Fig. 4d–f). Although few examples of premaxillae are known for North American latest Cretaceous anurans, enough maxillae are available to show that for those anurans having maxillary teeth (i.e., not *Theatonius*), their teeth typically are small, pedicellate, and have labiolingually bicuspid crowns. The one exception known to us is a recently identified, incomplete anuran maxilla (TMP collection) from a new locality in the Dinosaur Park Formation of southeastern Alberta, which is notable for having fully non-pedicellate teeth, although they remain relatively small and retain labiolingually bicuspid crowns. This new specimen demonstrates that tooth form is at least somewhat more variable among North American latest Cretaceous anurans than previously known and, thus, could be diagnostically useful.

(2) Variable presence of one or more foramina in labial surface of maxillary pars facialis below posterior part of margo orbitalis. This feature is intraspecifically variable within *H. kermiti*. It is not seen in any other North American latest Cretaceous anuran maxillae known to us, nor are we aware of it having been reported in any other anurans. The “maxillary foramen” of Maglia (1998, her Fig. 3), which, according to her taxon-character matrix, occurs in the discoglossid *Discoglossus pictus* and in some pelobatids (*Spea* and one species of *Scaphiopus)* is situated much farther anteriorly in the labial surface of the maxilla and, thus, does not appear to be homologous with the above-described foramina in *H. kermiti*. Because this feature appears to be unique to *H. kermiti*, we include it in the specific diagnosis, although we recognise that it is of limited use for identifying individual maxillary specimens because it is only variably present within the species.

(3) Elongate processus lateralis on premaxilla. As noted above, few well-preserved examples of this bone are known for North American latest Cretaceous anurans. The one available example for *H. kermiti* is notable for having an elongate processus lateralis. The relative length of that process varies among extant anurans, although generally it is short (e. g., Clarke 2007).

(4) Nasal moderate in size and subtriangular or sickle-shaped in outline. The size of the nasal, its dorsal or ventral outline, and the relative sizes of its processes vary considerably among anurans (e. g., Cannatella 1985; Ford 1990; Clarke 2007). For North American latest Cretaceous anurans, reasonably well-preserved nasals are known for *H. kermiti* and the *Eopelobates*-like taxon (Gardner 2008, his Fig. 13.3C). Both have moderate-sized nasals, but the nasal is subtriangular or sickle-shaped in the former, whereas it is more club-shaped in the latter, having an expanded medial portion and a narrower lateral portion. Among extant and other fossil anurans, additional shapes are seen such as: crescentic-, spindle-, or bar-shaped; square; or even reduced to a splint.

(5) Processus paraoccipitalis on frontoparietal posteriorly short and triangular. At its posterolateral corner, the anuran frontoparietal can bear a posteriorly directed processus paraoccipitalis (= posterolateral process of Henrici and Haynes 2006). Where it is present, the length and outline of this process vary. The existence of a processus paraoccipitalis can be demonstrated for only two species of North American latest Cretaceous anurans. In *H. kermiti,* it is a posteriorly short and triangular process, whereas in the unnamed Dinosaur Park Formation taxon (Gardner 2000, his Fig. 12-4G–H), it is an elongate spike.

(6) Tectum supraorbitale present on frontoparietal. The tectum supraorbitale (= supraorbitale flange of some authors) is variably present among anurans (e. g., Cannatella 1985; Henrici and Haynes 2006). Among North American late Cretaceous anurans, enough of the relevant region of the frontoparietal is known for *H. kermiti*, *T. lancensis* (Fox 1976b, his Fig. 2; Gardner 2008, his Fig. 13.2G–J), the *Eopelobates*-like taxon (Gardner 2008, his Fig. 13.3F–G), and the unnamed Dinosaur Park Formation taxon (Gardner 2000, his Fig. 12-4 G–H) to demonstrate that all these taxa possess a tectum supraorbitale.

Higher-level relationships and comparisons

The higher-level relationships of *Hensonbatrachus* are uncertain because of its fragmentary nature and its lack of any obvious and compelling apomorphies that support membership within any currently recognised anuran family. Assessing the phylogenetic relationships of *Hensonbatrachus* with any degree of rigour will require including it in a large-scale cladistic analysis that has suitably broad taxonomic representation of fossil and extant anurans. Although several taxon-character matrices exist that potentially could be used as a starting point for such an analysis (e. g., Gao & Wang 2001; Frost *et al.* 2006; Báez 2013), it has been our first-hand experience that simply "plugging" an additional taxon—especially one known from such limited material—uncritically into an existing matrix (i.e., without evaluating character-state descriptions, polarities, and scores for taxa) rarely yields informative results. For the purposes of this paper, we are content with highlighting and commenting on features that are potentially informative for evaluating the higher-level relationships of *Hensonbatrachus* and comparing it to relevant anuran taxa.

Before proceeding further, it is worth emphasising that although the broad patterns of anuran relationships are becoming better understood, there is less resolution and agreement at lower levels. Monophyly and membership for many of the traditionally recognised families (e. g., Duellman & Trueb 1986; Sanchiz 1998) and patterns of relationships among those families are contentious. Cladistic analyses aimed at examining relationships among anurans at various levels (e. g., all anurans or just a particular family) generally have focused on extant taxa and, with few exceptions, have not been able to survey all species within the group of interest. Many of the synapomorphies identified in cladistic analyses involve attributes that cannot be easily assessed in fossil anurans (e. g., soft tissue and larval features) or involve portions of the skeleton that are rarely preserved in the fossil record. The latter is particularly relevant to fossil taxa such as *Hensonbatrachus* that are only known from isolated bones. One key point that cladistic analyses have helped illuminate is that there is extensive homoplasy among many anuran characters. An important implication of that finding for studies of fossil anurans is that, in many cases, the presence of any one derived state cannot be used unambiguously to assign a species or genus to a particular clade because the same condition often occurs in members of other clades. Finally, we note that, for some characters, their described states are overly generalised, their distributions are not well documented, and/or their polarities are not agreed upon. The above points are worth bearing in mind for the remainder of this section.

The presence in *Hensonbatrachus* of a well-ossified distal condyle on its humerus is a derived feature (e. g., Báez & Basso 1996) supporting inclusion of this genus within the large "archaeobatrachian"-"mesobatrachian"-neobatrachian clade. For those more basal anurans in which the distal end of the humerus is known—the Jurassic *Notobatrachus* (e. g., Báez & Nicoli 2004, their Fig. 4), *Prosalirus* (e. g., Jenkins & Shubin 1998, their Fig. 2M–N), and *Vierella* (e. g., Báez & Basso 1996, their Fig. 6)—the distal condyle is poorly ossified. This feature cannot be scored for the Early Cretaceous genus *Yizhoubatrachus*, but other aspects of its skeletal anatomy suggest that it lies basal to the "archaeobatrachian"-"mesobatrachian"-neobatrachian clade (see Gao & Chen 2004, their Fig. 4). Within that clade, the position of *Hensonbatrachus* is uncertain, in part, because it exhibits a mix (albeit limited) of conflicting character states and, in part, because many of the apomorphies for groups within that clade cannot be scored for *Hensonbatrachus*.

Assignment of *Hensonbatrachus* to Neobatrachia or "advanced frogs"—a group that contains over 95% of extant anuran species and most of the recognised families (Frost *et al.* 2006)—can be neither accepted nor rejected for two reasons. First, neither of the two putative osteological synapomorphies for Neobatrachia—presence of a neopalatine (e. g., Ford & Cannatella 1993; Trueb 1993) and third distal carpal fused to other carpals (Ford & Cannatella 1993)—can be scored for *Hensonbatrachus*. In any case, neither apomorphy is unique to neobatrachians because, according to Frost *et al.* (2006), the former is synapomorphic for a more inclusive neobatrachian-pelobatoid-pelodytoid clade (their Acosmanura) and the latter occurs convergently in *Pelodytes*. Second, *Hensonbatrachus* possesses no derived features that are unequivocally diagnostic or even particularly suggestive for any neobatrachian clade (for an example of using the latter approach to provisionally determine the higher-level affinities of fragmentary Cretaceous anuran bones, see Szentesi and Venczel 2010). Assignment of *Hensonbatrachus* to Neobatrachia is not constrained by the latter clade's known temporal record because pre-Campanian occurrences are known from South America (Aptian; Báez *et al.* 2009), Africa (Albian–Cenomanian; Báez & Werner 1996), and Europe (Santonian; Szentesi & Venczel 2010). By contrast, the widely held interpretation that neobatrachians have a Gondwanan origin (e. g., Duellman & Trueb 1986; Feller & Hedges 1998) and the fact that the earliest accepted appearance of neobatrachians in the North American fossil record does not occur until at least the Eocene (see Roček & Rage 2000, their Table 2), suggest it is unlikely that *Hensonbatrachus* is a neobatrachian. Based on its geological age (Campanian) and geographical occurrence, membership in one of the less derived anuran groups seems more probable.

The most primitive of those anuran groups are the "archaeobatrachians" (= archaic or primitive frogs of some authors). This almost certainly is a paraphyletic assemblage (e. g., Ford & Cannatella 1993; Gao & Wang 2001; Gao & Chen 2004; Báez 2013; see historical review by Frost *et al.* 2006: 41–45) that, for the purposes of this discussion, consists of the following taxa: the Early Cretaceous *Mesophryne*, the Recent *Ascaphus*, the Recent and subfossil *Leiopelma*, the Cretaceous Gobiatidae, and the Middle Jurassic–Recent Discoglossidea *sensu lato*. *Mesophryne* was described by Gao & Wang (2001) and placed by them (their Fig. 6) as the basal-most archaeobatrachian. That genus and *Hensonbatrachus* share no compelling synapomorphies. *Hensonbatrachus* primitively differs from *Mesophryne* in having external cranial ornament and in lacking direct maxilla-squamosal contact, but is more derived in having an elongate processus lateralis on the premaxilla (polarities for those characters follow Gao & Wang 2001).

Leiopelma and *Ascaphus* (for osteological descriptions and illustrations, see Ritland 1955; Stephenson 1960; Worthy 1987; Trueb 1993; Clarke 2007) are widely regarded as the most primitive of living anurans and these genera have been placed in cladistic analyses either as sequential taxa (e. g., Cannatella 1985; Ford & Cannatella 1993) or as sister taxa comprising the monophyletic Leiopelmatidae (e. g., Báez & Basso 1996; Gao & Wang 2001; Frost *et al.* 2006; Clarke 2007). A total of ten osteological synapomorphies have been proposed for the *Ascaphus* + *Leiopelma* clade (Báez & Basso 1996; Gao & Wang 2001; Frost *et al.* 2006; Clarke 2007). Few, if any, of these are unique to these genera, including the three apomorphies that can be scored for *Hensonbatrachus*: an elongate processus lateralis (= lateral process of Gao & Wang 2001) on the premaxilla (Báez & Basso 1996; Gao & Wang 2001) also occurs in *Bombina* (Clarke 2007); an essentially straight anterior margin of the nasal (Gao & Wang 2001) also occurs, for example, in *Eopelobates* and at least some pipids (Gao & Wang 2001); and processus anterior (= rostral process of Gao & Wang 2001) absent from nasal also occurs, for example, in *Alytes*, *Pipa*, and *Pelodytes* (Gao & Wang 2001). Compared to that small roster of homoplasious resemblances, *Hensonbatrachus* differs from *Ascaphus* and *Leiopelma* in a number of features including: external cranial ornament present; maxilla has a tall postorbital region; frontoparietals in medial sutured contact posteriorly and bear a tectum supraorbitale; and ilia have an oblique groove and a dorsal prominence and tubercle. Aside from the tectum supraorbitale, which is universally accepted as a derived anuran feature (e. g., Cannatella 1985; Báez & Basso 1996; Maglia 1998; Gao & Wang 2001), polarities of the remaining features are less well agreed upon and, in our opinion, deserve further evaluation. For example, the dorsal tubercle has been regarded as a primitive salientian feature based on comparisons with ilia of *Triadobatrachus* and *Czatkobatrachus* (e. g., Báez & Basso 1996; Gao & Wang 2001), yet, as noted by Roček *et al.* (2013), the relevant tall and knob-like structure in these proto-frogs (see Evans and Borsuk-Białynicka 1998, their Fig. 1) is located farther anteriorly than in anurans and, based on that positional difference, might not be homologous with the dorsal tubercle of anurans. In stem-anurans, the presence of a dorsal tubercle cannot be determined for *Vierella* because the relevant part of the ilium is not known (see Báez & Basso 1996, their Fig. 7); in the others, a dorsal tubercle is reportedly absent in *Yizhoubatrachus* (Gao & Chen 2004), whereas it is developed only as a slightly raised and roughened patch in *Prosalirus* (e. g., Jenkins & Shubin 1998: 504, their Fig. 2O) and in some, but not all, specimens of *Notobatrachus* (Báez & Nicoli 2004: 267, their Fig. 3C).

Monophyly of Gobiatidae has never been demonstrated, but, for the purposes of this discussion, we follow Roček (2008) in regarding them as a family containing a trio of Asian Cretaceous genera and best known from the Late Cretaceous of Mongolia and Uzbekistan (for other reported Asian occurrences, see Sanchiz 1998). The suggestion of Winkler *et al.* (1990) that some isolated anuran bones from the Albian of Texas, USA, might belong to this group is intriguing, but remains unverified. Although once considered to be intermediate between leiopelmatids and discoglossids (Roček & Nessov 1993) or a subfamily within Discoglossidae *sensu lato* (Sanchiz 1998), subsequent studies have advocated a more basal position for gobiatids: Wang (2004: his Fig. 2) presented a cladogram without any supporting information that placed *Gobiates* basal to *Mesophryne*, whereas Roček (2008: 589) suggested that gobiatids were more closely related to and primitive relatives of *Ascaphus* and *Leiopelma*. Many gobiatid species are known only by isolated cranial and postcranial bones (e. g., Roček & Nessov 1993; Sanchiz 1998; Roček 2008), but incomplete, three-dimensionally preserved skulls and postcrania are available for some species in the type genus *Gobiates* (e. g., Borsuk-Białynicka 1978, her Pl. 15; Špinar & Tatarinov 1986, their Figs 2–3; Roček 2008, his Fig. 2) and for the monotypic *Cretasalia* (Gubin 1999, his Pl. 7). Roček (2008: 587–589) listed 19 characters of varying polarities as being diagnostic for Gobiatidae. Of the eight features that can be scored for *Hensonbatrachus*, it exhibits the gobiatid condition only for the following three: frontoparietals paired; frontoparietals in medial contact posteriorly and separated more anteriorly by a fontanelle; and ilium bears a dorsal tubercle. Roček (2008) regarded the first feature as primitive, the second as derived, and did not comment on the polarity of the third. Regardless of their polarities, each of those features is sufficiently widespread among anurans that their presence in *Hensonbatrachus* cannot be taken as evidence for a particularly close relationship between that genus and gobiatids. As for the other five key gobiatid features that can be scored for *Hensonbatrachus*, the condition in the new genus differs as follows: no direct maxilla-squamosal contact (vs. broad contact in gobiatids); nasals triangular in outline (vs. crescentic); pre- and postorbital regions of maxilla similarly tall and margo orbitalis concave (vs. postorbital region low and margo orbitalis nearly straight); maxilla bears weakly-developed processus pterygoideus (vs. process absent); and humerus bears weakly-developed radial epicondyle (vs. epicondyle absent). *Hensonbatrachus* and many gobiatids (*Gobiates* and *Cretasalia*) are superficially similar in having pit-and-ridge style external cranial ornament; however, as is evident in published images (e. g., Borsuk-Białynicka 1978, her Pl. 15; Roček & Nessov 1993, their Pls. 1 and 5; Špinar & Tatarinov 1986, their Figs. 2–3; Gubin 1999, his Pl. 7; Roček 2008, his Fig. 2B), neither of those gobiatid genera exhibit the distinctive pattern seen in *Hensonbatrachus* and, as noted by Gubin (1999), cranial ornament is less extensive in *Cretasalia*. *Gobiatoides* differs markedly from its congeners and *Hensonbatrachus* in entirely lacking cranial ornament. Other notable differences between *Hensonbatrachus* and gobiatids include a larger estimated snout–vent length of 75–115 mm for *Hensonbatrachus* (vs. a reported snout–vent length of about 50 mm for *Gobiates*; Roček 2008); broad sutural surface along lingual surface of maxillary pars facialis presumably for bony or ligamentous contact with pterygoid or ligamentous contact with squamosal in *Hensonbatrachus* (vs. no such sutural surface reported for gobiatids despite the complete lack of a processus pterygoideus); and squamosal in *Hensonbatrachus* has greatly expanded lamella alaris and bone is C-shaped in lateral outline (vs. lamella alaris more bar-shaped and tilted posteriorly).

Discoglossids are a problematic group, the membership and monophyly of which are contentious (see reviews by Frost *et al.* 2006; Clarke 2007). In its broadest sense and as it has traditionally been viewed (e. g., Duellman & Trueb 1986; Sanchiz 1998), Discoglossidae *sensu lato* includes four extant Eurasian genera (*Alytes*, *Bombina*, *Barbourula*, and *Discoglossus*) plus some combination of about a dozen fossil genera that range in age from the Middle Jurassic to the Pliocene. Cladistic analyses—most of which have only included extant genera—have variously supported or rejected monophyly of the family (e. g., Gao & Wang 2001; Roelants & Bossuyt 2005; Clarke 2007 vs. Cannatella 1985; Ford & Cannatella 1993; Frost *et al.* 2006). For the purposes of this discussion, we view Discoglossidae in its broader sense, but without necessarily accepting all assignments of fossil genera—especially the North American latest Cretaceous genera *Paradiscoglossus* and *Scotiophryne*—to that family. Gao & Wang (2001) and Clarke (2007) collectively identified a total of 17 synapomorphies for Discoglossidae. Most of these relate to features that can only be scored from articulated skeletons (e. g., position of nasal capsules and relative positions of scapula and coracoids) or from bones (e. g., vomer, quadratojugal, braincase, cleithrum, coracoid, and vertebrae) that are not available for *Hensonbatrachus*. All four synapomorphies listed by Gao & Wang (2001) and 11 synapomorphies listed by Clarke (2007) cannot be scored for *Hensonbatrachus*. For the remaining two synapomorphies listed by Clarke (2007), the humerus of *Hensonbatrachus* exhibits the non-discoglossid condition for the relative size of the distal condyle (i.e., small, less than 60% the distal width of the humerus vs. the discoglossid condition of greater than 66%), yet its ilium exhibits the derived condition of having a dorsal tubercle and prominence, but no dorsal crest. However, that combination of iliac features is so widely distributed among anurans (e. g., some extant species of pelobatids and in many families of neobatrachians) that it is hardly compelling for assigning *Hensonbatrachus* to Discoglossidae. *Hensonbatrachus* differs from extant and many fossil discoglossids in some combination of the following features: inferred larger body size, external cranial ornamentation present, maxilla has reduced processus pterygoideus and its pre- and postorbital regions are similarly high, squamosal has expanded lamella alaris and is C-shaped in lateral outline, no direct maxilla-squamosal contact, and frontoparietal has tectum supraorbitale. The European Oligocene-Pliocene discoglossid genus *Latonia* (see Roček 1994) shows the most similarities to *Hensonbatrachus*, but even these differ from the conditions found in the latter. Examples of these similarities, and how they differ in details, include the following: large body size (but the maximum snout–vent length of 200 mm in *Latonia* considerably exceeds what is estimated *Hensonbatrachus*), cranial ornament present (variably present in *Latonia* and it can be in the form of pits and ridges, grooves and ridges, or tubercles), postorbital portion of the maxilla tall (but often taller than the preorbital region in *Latonia* instead of being approximately the same height as in *Hensonbatrachus*), and tectum supraorbitale present on the frontoparietals (but this shelf is relatively wider in *Latonia* than in *Hensonbatrachus*). *Latonia* differs further from *Hensonbatrachus* in having a prominent processus pterygoideus on the maxilla, in having a more T-shaped squamosal with a less expanded lamella alaris, and in having the frontoparietals solidly fused.

"Mesobatrachians" or "transitional frogs" are another probably paraphyletic assemblage of anurans that are more derived than archaeobatrachians yet less derived than neobatrachians and that conventionally (and as viewed in this paper) contains Pipoidea and Pelobatoidea (e. g., Ford & Cannatella 1993; see historical review by Frost *et al.* 2006: 45–50). *Hensonbatrachus* can be excluded from Pipoidea (i.e., Pipidae + Palaeobatrachidae + Rhinophrynidae) based on its primitive retention of paired frontoparietals as opposed to the fused or azygous frontoparietals that are synapomorphic for pipoids (e. g., Ford & Cannatella 1993; Henrici 1998; Gao & Wang 2001; Báez & Pugener 2003). *Hensonbatrachus* differs further from all three pipoid families in having a tall postorbital region on its maxilla; from palaeobatrachids and pipids in primitively lacking the expanded inter-ilia tubercle that occurs in these clades (e. g., Sanchiz 1998; Báez *et al.* 2012); from palaeobatrachids in lacking osseous knobs at the lingual base of the marginal teeth, a feature that is characteristic for palaeobatrachids (Roček 2004, his Fig. 8C-b; Venczel 2004) and undoubtedly derived; and from pipids in lacking any of the iliac features (e. g., a tall dorsal prominence that is triangular or nearly square in lateral aspect, a dorsal crest that is tilted laterally, or a lateral oblique ridge along the base of the shaft in front of the acetabulum) that are characteristic in some combination for many pipids (Báez *et al.* 2012) and probably derived. The primitive retention of pedicellate and labiolingually bicuspid teeth differentiates *Hensonbatrachus* both from the Cenozoic rhinophrynids *Rhinophrynus* and *Chelomophrynus* (e. g., Henrici 1991) and those pipids (e. g., *Hymenochirus* and some species of *Pipa*; e. g., Cannatella & Trueb 1988) that are edentulous as well as from palaeobatrachids and those pipids (e. g., *Xenopus*, *Silurana*, and the remaining species of *Pipa*; Cannatella &

Trueb 1988) that have non-pedicellate and monocuspid teeth. The presence of pedicellate, bicuspid teeth in several Mesozoic pipoids, such as the Late Jurassic probable rhinophrynid *Rhadinosteus* and the Early Cretaceous *Neusibatrachus* and *Thoraciliacus* (e. g., Henrici 1998; Trueb 1999; Báez & Sanchiz 2007) indicates that both loss of teeth and the appearance of non-pedicellate, monocuspid teeth almost certainly occurred independently several times within Pipoidea.

The other conventionally recognised mesobatrachian group, Pelobatoidea *sensu lato*, has also been problematic in that its monophyly, the number of families it contains, and its higher-level relationships with other anurans have been contentious (see review by Frost *et al.* 2006). For the purposes of this discussion, we follow the most recent cladistic analysis for the group to include representative fossil and extant genera (Henrici & Haynes 2006) in recognising Pelobatoidea as a monophyletic group containing the three families Megophryidae, Pelobatidae, and Pelodytidae. Many of the proposed synapomorphies for Pelobatoidea (= Anomocoela of Frost *et al.* 2006) are larval and soft-tissue features that are unavailable for fossils. In addition, most of the adult, osteological synapomorphies (e. g., Gao & Wang 2001; Henrici & Haynes 2006) involve postcranial elements (e. g., sternum, vertebrae, and ribs) that unfortunately are not available for *Hensonbatrachus*. One feature of *Hensonbatrachus* that is suggestive of membership within Pelobatoidea is the presence of an oblique groove, a feature of uncertain polarity that, among extant frogs (Roček *et al.* 2013), is known for the pelobatids *Pelobates* and *Scaphiopus* and some species of the megophryid *Megophrys* (Roček *et al.* 2013), but also as a rare individual variant in the discoglossid *Bombina orientalis* (Henrici & Haynes 2006); it also occurs in some fossil *Eopelobates*. Three of the seven synapomorphies listed by Henrici & Haynes (2006) for the pelobatid subclade of (*Scaphiopus* (*Macropelobates* (*Pelobates* + *Eopelobates*))) are seen in *Hensonbatrachus*, as follows: external cranial ornament present, tectum supraorbitale present on frontoparietal, and occipital canal in frontoparietal roofed by bone and exits laterally. None of these features is unique to that clade, so their presence in *Hensonbatrachus* is not especially compelling for assigning it to that clade.

Another fossil anuran taxon of uncertain affinities, *Hatzegobatrachus* from the Maastrichtian of Romania, deserves to be considered because of its geological age and also because the holotype and only known ilium (Venczel & Csiki 2003, their Figs. 1A and 2A) somewhat resembles ilia of *Hensonbatra-*

chus in having a low, mediolaterally compressed ridge extending along the dorsal surface of the acetabular region. In *Hatzegobatrachus*, however, that dorsal ridge is interpreted as being the entire dorsal tubercle (= dorsal protuberance of Venczel & Csiki 2003) and is tilted laterally. This differs from the condition in *Hensonbatrachus* in which the superficially similar dorsal ridge is actually the dorsal prominence, is not tilted laterally, and anterodorsally bears a knob-like dorsal tubercle. Other differences are that the medial surface of the acetabular region on the ilium of *Hatzegobatrachus* bears a small inter-ilia tubercle (absent from *Hensonbatrachus*), the iliac shaft of *Hatzegobatrachus* has convex lateral and medial sides (not indented by a shallow trough as in *Hensonbatrachus*), and *Hatzegobatrachus* is considerably smaller than *Hensonbatrachus*, with an estimated snout–vent length of just 30 mm (Venczel & Csiki 2003).

To summarise the above, the limited osteological information currently available for *Hensonbatrachus* places it within the clade of “archaeobatrachians”-“mesobatrachians”-neobatrachians, but its more precise relationships within that clade are uncertain. In lacking features that are diagnostic for gobiatids (e. g., maxillae retains processus pterygoideus and has no sutural connection with squamosal) and for pipoids (frontoparietals are primitively paired), *Hensonbatrachus* cannot be assigned to either of those groups, both of which are well-represented in the Cretaceous of Laurasia (e. g., Roček & Rage 2000; Roček 2008). As for the remaining families, *Hensonbatrachus* exhibits a mix of features that neither compellingly support nor exclude its membership within any of these groups. In terms of its overall resemblance, *Hensonbatrachus* looks most similar to pelobatoids in a mix of features (primitive, derived, and of uncertain polarities) such as: moderate body size; extensive external cranial ornament in a pit-and-ridge pattern; teeth are present; frontoparietals are paired, are in sutured contact posteriorly, have a tectum supraorbitale, and their occipital canal is roofed with bone; and ilium has an oblique groove and lacks a dorsal crest. None of these features are compelling because all occur in various combinations in many other anuran clades. The higher-level relationships of *Hensonbatrachus* likely will remain obscure until additional material becomes available and it can be incorporated into a suitably rigorous cladistic analysis. For the time being, we conservatively classify the genus as Anura *incertae sedis*.

Distribution and lifestyle

As currently documented by fossil occurrences, *H. kermiti* has a restricted distribution. It is reliably known from nine localities in southeastern Alberta, Canada, that extend from the upper part of the Oldman Formation into the upper (but not uppermost) part of the Dinosaur Park Formation. Based on current age estimates for those strata (see Fig. 4), this equates to a narrow temporal range of about 76–77 million years ago within the middle-late Campanian. We have not yet seen any diagnostic *H. kermiti* specimens in samples from other anuran-bearing localities of similar age farther to the south, such as in the Judith River Formation of Montana, the Kaiparowits Formation of Utah, or the Aguja Formation of Texas, nor have we seen specimens in samples from localities lower down in the Belly River Group of Alberta.

The lack of iliac specialisations such as an inter-iliac tubercle or dorsal crest that are suggestive of enhanced swimming or jumping capabilities (for a discussion of the possible functional significance of those iliac features, see Szentesi & Venczel 2010), coupled with other features such as its moderate body size, the relatively robust build of its bones, and the presence of external cranial ornamentation, all point to *H. kermiti* being a medium-sized, generalised, ground-dwelling frog. The relatively robust and tall maxillary structure of *H. kermiti* suggests it could have consumed correspondingly larger prey. However, its primitive retention of “normal” teeth and lack of other cranial specialisations (e. g., enhanced sutural contact or fusion of skull bones) normally associated with strengthening of the skull suggest it remained a generalist and opportunistic feeder that, presumably, favoured a typical anuran diet of invertebrates. This differs from the feeding strategies of some anurans, such as the extant ceratophryids *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus*, which are pugnacious lie-in-wait predators that use their specialised fang-like (non-pedicellate, monocuspid, and elongate) teeth to subdue large prey.

Our understanding of Campanian anuran assemblages in the North American Western Interior is still limited (for a recent summary, see Gardner and DeMar 2013), yet it is becoming evident from a recent survey of the Utah record (Roček *et al.* 2010) and our on-going studies in Alberta that both regions supported moderately diverse anuran assemblages during the middle-late Campanian. There are some intriguing similarities between the Utah and Alberta assemblages (e. g., presence of the *Eopelobates*-like taxon) and between these assemblages and the better documented, younger late Maastrichtian (and possibly early Palaeocene) assemblages of Wyoming and Montana (e. g., presence of the *Eopelobates*-like taxon and, at least in Utah, also the presence of *S. pustulosa*). Not surprisingly, there also are differences among those assemblages. One unexpected recent finding is the recognition of two distinctive kinds of edentulous anuran maxillae, one in the Dinosaur Park Formation of Alberta and the second, which is nearly identical to those of the late Maastrichtian *T. lancensis*, in the Kaiparowits Formation of Utah (Gardner *et al.*, work in progress). Future work on those and other Late Cretaceous anuran assemblages in the North American Western Interior promises to provide additional insights into the evolutionary history of anurans.

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Literature cited

Báez A.M. (2013). Anurans from the Early Cretaceous Lagerstätte of Las Hoyas, Spain: new evidence on the Mesozoic diversification of crown-clade Anura. *Cret. Res.*, 41, 90–106.

Báez A.M. & Basso N.G. (1996). The earliest known frogs of the Jurassic of South America: review and cladistic appraisal of their relationships. *Münchner Geowiss. Abh. (A)*, 30, 131–158.

Báez A.M. & Nicoli L. (2004). A new look at an old frog: the Jurassic *Notobatrachus* Reig from Patagonia. *Ameghiniana*, 41, 257–270.

Báez A.M. & Pugener A. (2003). Ontogeny of a new Palaeogene pipid frog from southern South America and xenopodinomorph evolution. *Zool. J. Linn. Soc.*, 139, 439–476.

Báez A.M. & Sanchiz B. (2007). A review of *Neusibatrachus wilferti*, an Early Cretaceous frog from the Montsec Range, northeastern Spain. *Acta Paleontol. Pol.*, 52, 477–487.

Báez A.M. & Werner C. (1996). Presencia de anuros ranoideos en el Cretácico de Sudan. *Ameghiniana*, 33, 460.

Báez A.M., Moura G.J.B. & Gómez R.O. (2009). Anurans from the Lower Cretaceous Crato Formation of northeastern Brazil: implications for the early divergence of neobatrachians. *Cret. Res.*, 30, 829–846.

Báez A.M., Gómez R.O. & Taglioretti M.L. (2012). The archaic ilial morphology of an enigmatic pipid frog from the upper Pleistocene of the South American pampas. *J. Vertebr. Paleontol.*, 32, 304–314.

Béland P. & Russell D.A. (1978). Paleoecology of Dinosaur Provincial Park (Cretaceous), Alberta, interpreted from the distribution of articulated vertebrate remains. *Can. J. Earth Sci.*, 15, 1012–1024.

Bever G.S. (2005). Variation in the ilium of North American *Bufo* (Lissamphibia; Anura) and its implications for species-level identification of fragmentary anuran fossils. *J. Vertebr. Paleontol.*, 25, 548–560.

Blob R.W., Carrano M.T., Rogers R.R., Forster C.A. & Espinoza N.R. (2001). A new fossil frog from the Upper Cretaceous Judith River Formation of Montana. *J. Vertebr. Paleontol.*, 21, 190–194.

Borsuk-Białynicka M. (1978). *Eopelobates leptocolaptus* sp. n. – the first Upper Cretaceous pelobatid frog from Asia. *Palaeontol. Pol.*, 38, 57–63.

Breithaupt B.H. (1985). Nonmammalian vertebrate faunas from the Late Cretaceous of Wyoming. *Wyoming Geol. Assoc., Thirty-sixth Ann. Field Conf. Guidebook*, 159–175.

Brinkman D.B. (1990). Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, 78, 37–54.

Brinkman D.B., Russell A.P., Eberth D.A. & Peng J. (2004). Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, 213, 295–313.

Cannatella D.C. (1985). *A phylogeny of primitive frogs (Archaeobatrachians)*. PhD dissertation, University of Kansas, Lawrence, Kansas, USA, 1–404.

Cannatella D.C. & Trueb L. (1988). Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zool. J. Linn. Soc.*, 94, 1–38.

Clarke B.T. (2007). Comparative morphology and amphibian taxonomy: an example from the osteology of discoglossoid frogs. In: *Amphibian Biology, Volume 7, Systematics* (eds. Heatwole H & Tyler MJ). Surrey Beatty & Sons, Chipping Norton, 2465–2612.

Currie P.J. & Koppelhus E.B (eds.). 2005. *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*. Indiana University Press, Bloomington, Indiana, USA, 1–648.

Davis B.M. (2007). A revision of “pediomyid” marsupials from the Late Cretaceous of North America. *Acta Paleontol. Pol.*, 52, 217–256.

DeMar D.G., Jr. & Breithaupt B.H. (2006). The nonmammalian vertebrate microfossil assemblages of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming. *New Mexico Mus Nat Hist Sci Bull.*, 35, 33–53.

DeMar D.G., Jr. & Breithaupt B.H. (2008). Terrestrial and aquatic vertebrate paleocommunities of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming. In: *Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography* (eds. Sankey JT & Baszio S). Indiana University Press, Bloomington, Indiana, USA, 78–103.

Dodson P. (1983). A faunal review of the Judith River (Oldman) Formation, Dinosaur Provincial Park, Alberta. *The Mosasaur*, 1, 89–118.

Duellman W.E. & Trueb L. (1986). *Biology of Amphibians*. McGraw-Hill, New York, New York, USA, 1–670.

Eberth D.A. (1990). Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, 78, 1–36.

Eberth D.A. (2005). The geology. In: *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed* (eds. Currie PJ & Koppelhus EB). Indiana University Press, Bloomington, Indiana, USA, 54–82.

Eberth D.A. & Brinkman D.B. (1997). Paleoecology of an estuarine, incised-valley fill in the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) of southern Alberta, Canada. *Palaios*, 12, 43–58.

Eberth D.A. & Hamblin A.P. (1993). Tectonic, stratigraphic, and sedimentological significance of a regional discontinuity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. *Can. J. Earth Sci.*, 30, 174–200.

Eberth D.A., Braman D.R. & Tokaryk T.T. (1990). Stratigraphy, sedimentology and vertebrate paleontology of the Judith River Formation (Campanian) near Muddy Lake, west-central Saskatchewan. *Bull. Can. Petrol. Geol.,* 38, 387–406.

Eberth D.A., Currie P.J. Brinkman D.B., Ryan M.J., Braman D.R., Gardner J.D., Lam V.D., Spivak D.N. & Neuman A.G. (2001). Alberta's dinosaurs and other fossil vertebrates: Judith River and Edmonton groups

(Campanian-Maastrichtian). In: *Mesozoic and Cenozoic Paleontology in the Western Plains and Rocky Mountains* (ed. Hill CL). Guidebook for the Field Trips, Society of Vertebrate Paleontology 61st Annual Meeting. *Mus. Rockies Occ. Paper*, 3, 47–75.

Esteban M., Castanet J. & Sanchiz B. (1995). Size inferences based on skeletal fragments of the common European frog *Rana temporaria* L. *Herpetol. J.*, 5, 229–235.

Estes R. (1964). Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. *Univ. Calif. Publ. Geol. Sci.*, 49, 1–180 + 5 plates.

Estes R. (1969). A new fossil discoglossid frog from Montana and Wyoming. *Breviora*, 328, 1–7.

Estes R. & Sanchíz B. (1982). New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. *J. Vertebr. Paleontol.*, 2, 9–20.

Evans S.E. & Borsuk-Białynicka M. (1998). A stem-group frog from the Early Triassic of Poland. *Acta Paleontol. Pol.*, 43, 573–580.

Fabrezi M. (2001). Variación morfológica de le dentición en anuros. *Cuad. Herpetol.*, 15, 17–28.

Feller A.E. & Hedges S.B. (1998). Molecular evidence for the early history of living amphibians. *Mol. Phylogen. Evol.*, 9, 509–516.

Ford L.S. (1990). *The phylogenetic position of poison-dart frogs (Dendrobatidae): reassessment of the neobatrachian phylogeny with commentary on complex character systems.* PhD dissertation. University of Kansas, Lawrence, Kansas, USA, 1–307.

Ford L.S. & Cannatella D.C. (1993). The major clades of frogs. *Herpetol. Mono.*, 7, 94–117.

Fox R.C. (1976a). Upper Cretaceous and Paleocene vertebrate paleontology in Alberta. *Geol. Assoc. Can., Mineral. Assoc. Can., and Edmonton Geol. Soc. Ann. Meet., Field Trip A-6 Guide Book*, 1–25 + 1 fig.

Fox R.C. (1976b). An edentulous frog (*Theatonius lancensis*, new genus and species) from the Upper Cretaceous Lance Formation of Wyoming. *Can. J. Earth Sci.*, 13, 1486–1490.

Fox R.C. (1979a). Mammals from the Upper Cretaceous Oldman Formation, Alberta. I. *Alphadon* Simpson (Marsupialia). *Can. J. Earth Sci.*, 16, 91–102.

Fox R.C. (1979b). Mammals from the Upper Cretaceous Oldman Formation, Alberta. II. *Pediomys* Marsh (Marsupialia). *Can. J. Earth Sci.*, 16, 103–113.

Fox R.C. (1979c). Mammals from the Upper Cretaceous Oldman Formation, Alberta. III. Eutheria. *Can. J. Earth Sci.*, 16, 114–125.

Fox R.C. (1980). Mammals from the Upper Cretaceous Oldman Formation, Alberta. IV. *Meniscoessus* Cope (Multituberculata). *Can. J. Earth Sci.*, 17, 1480–1488.

Fox R.C. (1981). Mammals from the Upper Cretaceous Oldman Formation, Alberta. V. *Eodelphis* Matthew, and the evolution of the Stagodontidae (Marsupialia). *Can. J. Earth Sci.*, 18, 350–365.

Frampton E.K. (2006). *Taphonomy and palaeoecology of mixed invertebrate-vertebrate fossil assemblage in the Foremost Formation (Cretaceous, Campanian), Milk River Valley, Alberta.* M.Sc. thesis, University of Calgary, Calgary, Alberta, Canada, 1–294.

Frost D.R., Grant T., Faivovich J., Bain R.H., Haas A., Haddad C.F.B., De Sá R.O., Channing A., Wilkinson M., Donnellan S.C., Raxworthy C.J., Campbell J.A., Blotto B.L., Moler P., Drewes R.C., Nussbaum R.A., Lynch J.D., Green D.M. & Wheeler W.C. (2006). The amphibian tree of life. *Amer. Mus. Nat. Hist. Bull.*, 297, 1–370.

Gao K.-Q. & Chen S. (2004). A new frog (Amphibia: Anura) from the Lower Cretaceous of western Liaoning, China. *Cret. Res.*, 25, 761–769.

Gao K. & Fox R.C. (1991). New teiid lizards from the Upper Cretaceous Oldman Formation (Judithian) of southeastern Alberta, Canada, with a review of the Cretaceous record of teiids. *Ann. Carnegie Mus.*, 60, 145–162.

Gao K. & Fox R.C. (1996). Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bull. Carnegie Mus. Nat. Hist.*, 33, 1–107.

Gao K.-Q. & Fox R.C. (1998). New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Paleocene, Alberta and Saskatchewan, Canada, and phylogenetic relationships of Choristodera. *Zool. J. Linn. Soc.*, 124, 303–353.

Gao K.-Q. & Wang Y. (2001). Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaeobatrachian anuran clades. *J. Vertebr. Paleontol.*, 21, 460–476.

Gardner J.D. (2000). *Systematics of albanerpetontids and other lissamphibians from the Late Cretaceous of western North America.* PhD dissertation, University of Alberta, Edmonton, Alberta, Canada, 1–577.

Gardner J.D. (2003). Revision of *Habrosaurus* Gilmore (Caudata; Sirenidae) and relationships among sirenid salamanders. *Palaeontol.*, 46, 1089–1122.

Gardner J.D. (2005). Lissamphibians. In: *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed* (eds. Currie PJ & Koppelhus EB). Indiana University Press, Bloomington, Indiana, USA, 186–201.

Gardner J.D. (2008). New information on frogs (Lissamphibia: Anura) from the Lance Formation (late Maastrichtian) and Bug Creek Anthills (late Maastrichtian and early Paleocene), Hell Creek Formation, USA. In: *Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography* (eds. Sankey JT & Baszio S). Indiana University Press, Bloomington, Indiana, USA, 219–249.

Gardner J.D. & DeMar D.G., Jr. (2013). Mesozoic and Paleocene lissamphibian assemblages of North America: a comprehensive review. *Palaeobio. Palaeoenv.*, 93, 459–515.

Gardner J.D., Roček Z., Přikryl T., Eaton J.G., Blob R.W. & Sankey J. (2010). Comparative morphology of the ilium of anurans and urodeles (Lissamphibia) and a re-assessment of the anuran affinities of *Nezpercius dodsoni* Blob *et al.*, 2001. *J. Vertebr. Paleontol.*, 30, 1684–1696.

Greven H. (1989). Teeth of extant amphibia: morphology and some implications. In: *Trends in Vertebrate Morphology* (eds. Splechtna H & Hilgers H). Gustav Fischer Verlag, Stuttgart, 451–455.

Greven H. & Laumeier I. (1987). A comparative SEM-study on the teeth of ten anuran species. *Anat. Anz.*, 164, 103–116.

Gubin Y.M. (1999). [Gobiatids (Anura) from the Upper Cretaceous locality Khermeen-Tsav (Gobi Desert, Mongolia)]. Paleontol. Zh., 33, 76–87 [In Russian]; *Paleontol. J.*, 33, 77–87 [English translation].

Haeckel E. (1866). *Generelle Morphologie der Organismen: allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch Begründet durch die von Charles Darwin reformirte Descendenz-Theorie, 2. Bd., Allgemeine Entwickelungsgeschichte der Organismen.* Georg Reimer, Berlin, 1–462.

Henrici A.C. (1991). *Chelomophrynus bayi* (Amphibia, Anura, Rhinophrynidae), a new genus and species from the middle Eocene of Wyoming: ontogeny and relationships. *Ann. Carnegie Mus*., 60, 97–144.

Henrici A.C. (1998). A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument. *J. Vertebr. Paleontol.*, 18, 321–332.

Henrici A.C. (2002). Redescription of *Eopelobates grandis*, a late Eocene anuran from the Chadron Formation of South Dakota. *Ann. Carnegie Mus.*, 71, 241–259.

Henrici A.C. & Haynes S.R. (2006). *Elkobatrachus brocki*, a new pelobatid (Amphibia: Anura) from the Eocene Elko Formation of Nevada. *Ann. Carnegie Mus.*, 75, 11–35.

Holman J.A. (2003). *Fossil Frogs and Toads of North America*. Indiana University Press, Bloomington, Indiana, USA, 1–246.

Holmes R.B., Forster C., Ryan M., & Shepherd K.M. (2001). A new species of *Chasmosaurus* (Dinosauria: Ceratopsia) from the Dinosaur Park Formation of southern Alberta. *Can. J. Earth Sci.,* 38, 1423–1438.

Jarošová J. & Roček Z. (1982). The incrassatio frontoparietalis in frogs, its origin and phylogenetic significance. *Amph.-Rept.*, 3, 111–124.

Jenkins F.A., Jr. & Shubin N.H. (1998). *Prosalirus bitis* and the anuran caudopelvic mechanism. *J. Vertebr. Paleontol.*, 18, 495–510.

Johanson Z. (1996). Revision of the Late Cretaceous North American marsupial genus *Alphadon*. *Palaeontogr. Abt. A*, 242, 127–184.

Kielan-Jaworowska Z., Cifelli R.L. & Luo Z.-X. (2004). *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. Columbia University Press, New York, New York, USA, 1–630.

Lambe L.M. (1902). New genera and species from the Belly River Series (Mid-Cretaceous). *Contrib. Can. Paleontol.*, 3, 23–81 + 21 plates.

Laurenti J.N. (1768). *Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentis Circa Venena et Antidota Reptilium Austriacorum. Joannis Thomae Nobilis de Trattnern, Vienna, 1–214.*

Lynch J.D. (1971). Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.,* 53, 1–238.

Maglia A.M. (1998). Phylogenetic relationships of extant pelobatoid frogs (Anura: Pelobatoidea): evidence from adult morphology. *Univ. Kansas Nat. His. Mus. Sci. Papers*, 10, 1–19.

Mattison C. (2011). *Frogs and Toads*. Natural History Museum, London, UK, 1–192.

McLean J.R. (1971). Stratigraphy of the Upper Cretaceous Judith River Formation in the Canadian Great Plains. *Sask. Res. Council Rep., Geol. Div.*, 11, 1–96.

Meng J. & Fox R.C. (1995). Therian petrosals from the Oldman and Milk River formations (Late Cretaceous), Alberta, Canada. *J. Vertebr. Paleontol.*, 15**,** 122–130.

Naylor B.G. (1979). The Cretaceous salamander *Prodesmodon* (Amphibia: Caudata). *Herpetol.*, 35, 11–20.

Naylor B.G. (1981). A new salamander of the family Batrachosauroididae from the late Miocene of North America, with notes on other batrachosauroidids. *PaleoBios*, 39, 1–14.

Panton J.H. (1884). Fragmentary leaves from the geological records of the Great Northwest. A paper read before the Society on the evening of 24 January 1884. *Manitoba Hist. Sci. Soc.* 10, 1–9. Available at: http://peel.library.ualberta.ca/bibliography/1274.html. Last accessed 9 April 2013.

Parsons T.S. & Williams E.E. (1962). The teeth of Amphibia and their relation to amphibian phylogeny. *J. Morphol*., 110, 375–389.

Peng, J. Brinkman D.B. & Russell A.P. (1995). A paleoecological study of vertebrate microfossil assemblages from the lower Judith River Group (Campanian) of southeastern Alberta, Canada. In: *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers* (eds. Sun A & Wang Y) China Ocean Press, Beijing, 185–187.

Peng J., Russell A.P. & Brinkman D.B. (2001). Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide. *Prov. Mus. Alberta Nat. Hist. Occ. Paper*, 25, 1–54.

Přikryl T., Aerts P., Havelková P., Herrel A. & Roček Z. (2009). Pelvic and thigh musculature in frogs (Anura) and origin of anuran jumping locomotion. *J. Anat.*, 214, 100–139.

Rafinesque C.S. (1815). *Analyse de la nature ou Tableau de l'Univers et des corps organises.* Jean Barravecchia, Palermo, 1–224.

Ritland R.M. (1955). Studies on the post-cranial morphology of *Ascaphus truei*. I. Skeleton and spinal nerves. *J. Morph.*, 97, 119–177.

Roček Z. (1981). Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Univ. Carolinae - Biol.*, 1–2, 1–164.

Roček Z. (1994). Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* v. Meyer, 1843. *Geobios*, 27, 717–751.

Roček Z. (2000). Mesozoic anurans. In: *Amphibian Biology, Volume 4, Paleontology: The Evolutionary History of Amphibians* (eds. Heatwole H & Carroll RL). Surrey Beatty & Sons, Chipping Norton, 1295–1331.

Roček Z. (2004). Late Miocene Amphibia from Rudabánya. *Palaeontograph. Ital.*, 90, 11–29.

Roček Z. (2008). The Late Cretaceous frog *Gobiates* from Central Asia: its evolutionary status and possible phylogenetic relationships. *Cret. Res.*, 29, 577–591.

Roček Z. & Nessov L.A. (1993). Cretaceous anurans from Central Asia. *Palaeontogr. Abt. A*, 266, 1–54.

Roček Z. & Rage J.C. (2000). Tertiary Anura of Europe, Africa, Asia, North America, and Australia. In: *Amphibian Biology, Volume 4, Paleontology: The Evolutionary History of Amphibians* (eds. Heatwole H & Carroll RL). Surrey Beatty & Sons, Chipping Norton, 1332–1387.

Roček Z., Eaton J.G., Gardner J.D. & Přikryl T. (2010). Evolution of anuran assemblages in the Late Cretaceous of Utah, USA. *Palaeobio. Palaeoenv.*, 90, 341–393.

Roček Z., Gardner J.D., Eaton J.G. & Přikryl T. (2012). Similarities and differences in the ilia of Late Cretaceous anurans and urodeles. *Bull. Soc. Géol. France*, 183, 529–535.

Roček Z., Gardner J.D., Eaton J.G. & Přikryl T. (2013). Anuran ilia from the Upper Cretaceous of Utah—diversity and stratigraphic patterns. In: *At the Top of the Grand Staircase: The Late Cretaceous of Southern Utah* (eds. Titus AL & Loewen MA). Indiana University Press, Bloomington, Indiana, USA, 273–294.

Roelants K. & Bossuyt F. (2005). Archaeobatrachian paraphyly and the Pangaean diversification of crown-group frogs. *Syst. Biol.*, 54, 111–126.

Russell A.P. & Bauer A.M. (1993). *The Amphibians and Reptiles of Alberta: A Field Guide and Primer of Boreal Herpetology*. University of Calgary Press, Calgary, Alberta, Canada, 1–264.

Russell L.S. (1964). Cretaceous non-marine faunas of northwestern North America. *Roy. Ont. Mus. Life Sci. Contrib.*, 61, 1–24.

Russell L.S. & Landes R.W. (1940). Geology of the southern Alberta Plains. *Geol. Surv. Can. Mem.*, 221: 1–223.

Sahni A. (1972). The vertebrate fauna of the Judith River Formation, Montana. *Bull. Amer. Mus. Nat. Hist.*, 147, 321–412.

Sanchiz B. (1998). Salientia. In: *Encyclopedia of Paleoherpetology*, Part 4 (ed. Wellnhofer P). Verlag Dr. Friedrich Pfeil, München, 1–275.

Scott C.S., Gardner J.D., Clemens W.A. & Cifelli R.L. (2013). Richard Carr Fox, Canadian paleontologist. *Can. J. Earth Sci.*, 50, v–xi.

Špinar Z.V. (1976). Endolymphatic sacs and dorsal endocranial pattern: their significance for systematics and phylogeny of frogs. *Vèstn. Ústřed. Ústavu Geol.*, 51, 285–290 + 2 plates.

Špinar Z.V. & Tatarinov L.P. (1986). A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi Desert. *J. Vertebr. Paleontol.*, 6, 113–122.

Stephenson E.M. (1960). The skeletal characters of *Leiopelma hamiltoni* McCulloch, with particular reference of the effects of heterochrony on the genus. *Trans. Roy. Soc. New Zealand*, 88, 473–488.

Sullivan R.M. (2003). Revision of the dinosaur *Stegoceras* Lambe (Ornithischia, Pachycephalosauridae). *J. Vertebr. Paleontol.*, 23, 181–207.

Szentesi Z. & Venczel M. (2010). An advanced anuran from the Late Cretaceous (Santonian) of Hungary. *N. Jahr. Geol. Paläont. Abh.*, 256, 291–302.

Trueb L. (1973). Bones, frogs, and evolution. In: *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems* (ed. Vial JL). University of Missouri Press, Columbia, Missouri, USA, 65–132.

Trueb L. (1993). Patterns of cranial diversity among the Lissamphibia. In: *The Skull, Volume 2: Patterns of Structural and Systematic Diversity* (eds. Hanken J & Hall BK). University of Chicago Press, Chicago, Illinois, USA, 255–343.

Trueb L. (1999). The Early Cretaceous pipoid anuran, *Thoraciliacus*: redescription, revaluation, and taxonomic status. *Herpetol.*, 55, 139–157.

Venczel M. (2004). Middle Miocene anurans from the Carpathian Basin. *Palaeontograph. Abt. A*, 271, 151–174.

Venczel M. & Csiki Z. (2003). New frogs from the latest Cretaceous of Haţeg Basin, Romania. *Acta Palaeontol. Pol.*, 48, 609–616.

Wang Y. (2004). Taxonomy and stratigraphy of Late Mesozoic anurans and urodeles from China. *Acta Geol. Sinica*, 78, 1169–1178.

Wilson M.V.H., Brinkman D.B. & Neuman A.G. (1992). Cretaceous Esocoidei (Teleostei): early radiation of the pikes in North American fresh waters. *J. Paleontol.*, 66, 839–846.

Winkler D.A., Murry P.A. & Jacobs L.L. (1990). Early Cretaceous (Comanchean) vertebrates of central Texas. *J. Vertebr. Paleontol.*, 10, 95–116.

Worthy T.H. (1987). Osteology of *Leiopelma* (Amphibia: Leiopelmatidae) and descriptions of three new subfossil *Leiopelma* species. *J. Roy. Soc. New Zealand*, 17, 201–251.

Wuttke M., Přikryl T., Ratnikov V.Yu., Dvořák Z. & Roček Z. (2012). Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura). *Palaeobio. Palaeoenv.,* 92, 367–395.

Note added in press

For completeness, we briefly comment below on two relevant papers that were published after our manuscript was accepted.

Dong *et al.* (2013) provided a detailed reconsideration of all known anuran fossils and taxa from the Lower Cretaceous Jehol Group of northeastern China. They argued that all previously named monotypic anuran genera (including several mentioned in our "Higher-level relationships and comparison" section) from that unit pertain to three species of *Liaobatrachus*, recognised a fourth species of *Liaobatrachus*, and presented a cladistic analysis that placed *Liaobatrachus* as a crown-clade anuran in an unresolved trichotomy with leiopelmatids and all other crown frogs. In the expanded sense that those authors view *Liaobatrachus*, that genus remains substantially different from *H. kermiti* in numerous features (e. g., cranial bones unornamented, extensive medial contact between nasals, and no dorsal prominence or tubercle on ilia) and it does not appear to be closely related to *Hensonbatrachus*.

Henrici *et al.* (2013) presented a cladistic analysis that sampled a larger number of extant and fossil pelobatoid taxa than were included in the earlier analysis by Henrici and Haynes (2006). The new analysis continues to support monophyly of Pelobatoidea (= Anomocoela of those authors) and of the three less inclusive clades corresponding to the conventionally recognised families Megophryidae, Pelobatidae, and Pelodytidae (= Pelodytomorpha of those authors); it also documents a wider distribution for the oblique groove within Pelobatoidea than had been previously reported. The Henrici *et al.* (2013) analysis does not appear to provide any compelling suite of apomorphies for assigning *Hensonbatrachus* to Pelobatoidea.

Dong L. Roček Z., Wang Y. & Jones M.E.H. (2013). Anurans from the Lower Cretaceous Jehol Group of western Liaoning, China. *PLoS One*, 8(7): e69723. doi: 10.1371/journal.pone.0069723.

Henrici A.C., Báez A.M. & Grande L. (2013) *Aerugoamnis paulus*, new genus and species (Anura: Anomocoela): first reported anuran from the early Eocene (Wasatchian) Fossil Butte Member of the Green River Formation, Wyoming. *Ann. Carnegie Mus*., 81, 295–309.

Judithemys russelli sp. nov., a new "macrobaenid" turtle from the Late Cretaceous of Saskatchewan, Canada

Donald B. Brinkman

Royal Tyrrell Museum of Palae ontology, PO Box 7500, Drumheller, Alberta, T0J 0Y0, Canada;
E-mail: don.brinkman@gov.ab.ca

Abstract

A nearly complete shell and associated pelvis of a "macrobaenid" turtle from the late Maastrichtian of Saskatchewan is described as *Judithemys russelli* sp. nov. *Judithemys russelli* is similar to *Judithemys backmani* and different from *Judithemys sukhanovi* in having wide vertebral scutes and a fenestrated plastron. It differs from *J. backmani* most strongly in features of the pelvis, particularly in having a longer bridge, and in the shape of the posterior lobe. The presence of a distinct species of *Judithemys* in the late Maastrichtian of Saskatchewan adds to the evidence that "macrobaenids" were dominant members of turtle assemblages in northern regions of the western interior in the Late Cretaceous and Palaeocene.

Introduction

The family "Macrobaenidae" Sukhanov 1964 is a group of turtles characterised by the presence of a low-domed aquatic shell with a reduced, cruciform plastron. Thus characterised, the group includes both large-bodied taxa from the Late Cretaceous and Palaeocene as well as small-bodied taxa from the Early Cretaceous of Asia (Tong & Brinkman 2013). Phylogenetic analyses have concluded that the family is likely paraphyletic (Parham & Hutchison 2003) and I therefore use quotes around the family name to indicate this. These turtles are of considerable phylogenetic interest because they are near

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BIS Verlag, Oldenburg, Germany.

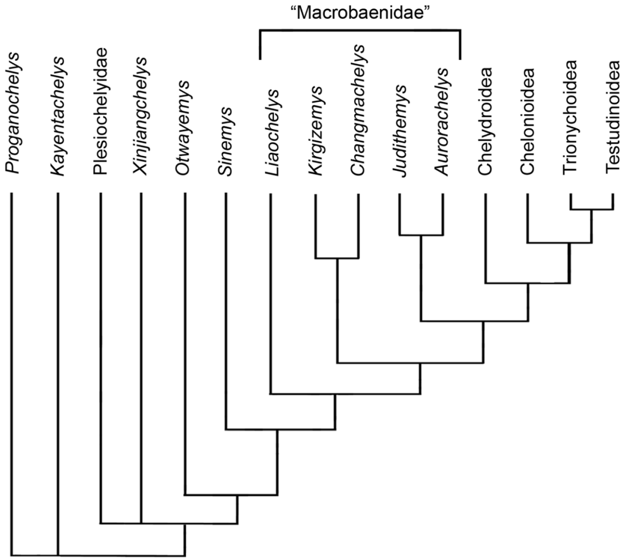

Figure 1:
Cladogram showing the relationships of the "Macrobaenidae" as characterised by Tong and Brinkman (2012). Relationships of taxa included are based on results of PAUP analysis presented by Brinkman *et al.* (2013).

the base of the crown-group cryptodires (Fig. 1) and a close relationship with cheloniid turtles has been suggested (Khozatsky & Nessov 1979). As well as being of phylogenetic interest, the family is biogeographically significant because its presence in both Asia and North America helps document the pattern of interchange of ectothermic mesoreptiles between these two continents (Vandermark *et al.* 2009). Because the family is well represented in the Early Cretaceous of Asia (Sukhanov 2000) and does not occur in North America until the Turonian, it is thought to have had an Asian origin in the Early Cretaceous and to have dispersed into North America during the Late Cretaceous (Hirayama *et al.* 2000; Hutchison 2000; Vandermark *et al.* 2009).

The family "Macrobaenidae" was recognised in North America by Hutchison and Archibald (1986), who concluded that the taxon described by Russell (1934) as *Clemmys backmani* was a member of this family and referred a number of specimens from the Hell Creek and Tullock Formations to this species. The generic affinities of this species were unresolved, which was indicated by placing the generic name "*Clemmys*" in brackets. Later, Parham and Hutchison (2003) described late Campanian "macrobaenid" *Judithemys sukhanovi* on the basis of a complete skeleton and series of shells from the Dinosaur Park Formation of Alberta, Canada. Brinkman *et al.* (2010) included *"Clemmys" backmani* in *Judithemys* and referred two large "macrobaenid" shells from the late Palaeocene of Montana to that species. Subsequently, Brinkman (2013) illustrated a number of "macrobaenid" shells from the Palaeocene of Alberta. Although these specimens differed from the Montana specimens in details of the carapace, the material was also included in the species *Judithemys backmani*.

The delayed recognition of the family in North America was likely in part a result of the improper association of the skull of a true cheloniid with the shell of an *Osteopygis*. The "macrobaenid" affinities of *Osteopygis* were recognised by Parham (2005), who demonstrated that "macrobaenids" and cheloniids differ in features of the plastron, including the presence of a longer contact between the plastron and carapace as well as a sutural contact between opposite hyo- and hypoplastra in "macrobaenids". Based on these features, Parham (2005) argued that the type specimen of *Osteopygis*, a carapace, was a macrobaenid turtle that was incorrectly associated with the skull of a marine turtle.

In this paper, a well-preserved "macrobaenid" shell from the base of the Ravenscrag Formation of Saskatchewan is described as *Judithemys russelli* sp. nov. The shell of *J. russelli* differs from *J. sukhanovi* and *J. backmani* in its proportions, details of the pattern of the scutes on its carapace, and features of the plastron. Although the Ravenscrag Formation is mostly Palaeocene in age, the locality from which the type specimen of *J. russelli* was collected has been interpreted as late Maastrichtian in age based on associated mammal specimens (Johnston & Fox 1984; Fox 1989). As well as adding to our understanding of the diversity of turtles in the late Maastrichtian of the western interior of North America, this specimen provides additional data on the distribution of "macrobaenid" turtles in North America during the Late Cretaceous.

Institutional abbreviations: TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; and YPMPU, Yale Peabody Museum-Princeton University, New Haven, Connecticut, USA.

Systematic palaeontology

TESTUDINES Batsch 1788

Cryptodira Cope 1868

Eucryptodira Gaffney 1975

Centrocryptodira Gaffney & Meylan 1988

"Macrobaenidae" Sukhanov 1964

Genus *Judithemys* Parham & Hutchison 2003

Included species: *Judithemys sukhanovi* Parham & Hutchison 2003; *Judithemys backmani* Russell 1934.

Diagnosis (from Brinkman *et al.* 2010): a "derived macrobaenid" (*sensu* Parham & Hutchison 2003) differing from *Osteopygis* in lacking a strong contact between the first vertebral and the second marginal, in exhibiting a strong visceral ridge on the first costal, and in lacking massive triangular peripherals into which the peg-like thoracic ribs insert deeply. Differs from *Aurorochelys* from the Turonian-Coniacian of Axel Heiberg Island in the Canadian Arctic in the presence of a carapace that is oval, rather than round, in dorsal view.

Remarks: Currently three genera of "macrobaenid" turtles from the Late Cretaceous and Palaeocene of North America have been named: *Aurorachelys* from the Turonian-Coniacian of Axel Heiberg Island in the Canadian Arctic; *Judithemys,* which extends from the late Campanian Dinosaur Park Formation of southern Alberta to the late Palaeocene of North Dakota; and *Osteopygis* from the Late Maastrichtian and Palaeocene of New Jersey. *Aurorachelys* is distinct in having a round carapace. The shells of *Osteopygis* and *Judithemys* are generally similar in proportion but differ in *Osteopygis* through the presence of a relatively wider cervical; a long contact between the first vertebral and the second marginal scutes; and the absence of a visceral ridge on the first costal ribs, which are rounded and peg-like and insert deeply into the massive, triangular peripherals (Brinkman *et al.* 2010). Specimen UALVP 47598 is included in *Judithemys* because the first vertebral has a short contact with the second marginal and because the costal ribs are flattened. In addition, inclusion of UALVP 47598 in *Judithemys* is geographically consistent with the distribution of other species of this genus because it also occurs in the western interior of North America, whereas *Osteopygis* occurs on the east coast of North America.

Judithemys russelli sp. nov.

Figs. 2–4

Etymology: Named after Anthony Russell in honour of his contributions to the study of fossil turtles of western Canada.

Holotype: UALVP 47598, articulated shell and pelvis. Carapace missing left peripherals six to nine and right peripherals five to seven. Plastron missing epiplastra and entoplastron. Pelvis visible in left lateral view.

Locality and horizon: Long Fall Locality, Ravenscrag Formation. The locality is located within the Medicine Hat Brick and Tile Co. Quarry and is 3.5 km WNW of the village of Ravenscrag, Saskatchewan in NW ¼, Sect. 23, Tp. 6, R. 24, W. 4 (Johnson & Fox 1984: their text-fig. 2). The Long Fall locality is a mammal-bearing fossiliferous locality that is within the basal 1.3 m of a ten-meter thick point-bar sequence (Fox 1989: his text-fig. 5). The point-bar sequence containing the Long Fall locality also includes an early Palaeocene mammal-bearing locality, the Rav W-1 locality. However, the Long Fall Locality is considered to be Late Cretaceous age by Johnston and Fox (1984) and Fox (1989) on the basis of its mammalian assemblages.

Diagnosis: A species of the genus *Judithemys* differing from the two recognised species of *Judithemys* in features of both the carapace and plastron. It is similar to *J. backmani* and different from *J. sukhanovi* in having relatively narrower vertebral scutes and a fenestrated plastron. *Judithemys russelli* differs from *J. backmani* in features of the plastron, particularly the longer bridge; the greater contribution of the hyoplastron to the bridge; and the longer posterior lobe with a more rounded posterior end. The carapace also differs in being narrower, in that the anterior portion of the second vertebral scute is constricted relative to the posterior portion, and in the presence of a relatively larger twelfth marginal scute.

Description

As in "macrobaenids" generally, the carapace is low-domed and smooth (Figs. 2A–B). It is relatively narrower than the carapace of *J. backmani* (see Table 1). Also, the posterior edge of the carapace is more strongly angled than in *J. backmani*, which is evenly rounded. A distinct nuchal emargination is absent. The anterolateral edge is thickened but not strongly upturned. The shell has a mid-dorsal depression extending from the first neural to the suprapygal region.

The nuchal is trapezoidal as is typically the case in “macrobaenids.” Nine neurals are present. The first is sub-rectangular, the second to eighth are hexagonal with short anterolateral edges, and the ninth is sub-rectangular. The second neural is particularly long and narrow. The neurals decrease in relative length posteriorly with the eighth neural being slightly wider than long. Two large suprapygals are present, the first being triangular in shape with a concave posterior margin and the second being generally lens-shaped. Eight costals are present. These are fully sutured with the peripherals. The peripheral series of the right side is most complete. It is represented by peripherals one to four, the posterior half of peripheral seven, and peripherals eight to eleven. Judging from the contour of the more anterior and posterior edges of the carapace, the missing peripherals were relatively wide (see also Fig. 3). The pygal is short compared with that of *J. backmani*.

Sulci are deeply impressed. The cervical scute is relatively wide, its width being about five times its length. The first vertebral scute is wider than long, with its lateral edges extending to the lateral edge of the first marginal scute. The second vertebral scute is slightly longer than wide. It differs from that of *J. backmani* in that the anterior portion of the scute is laterally constricted relative to the posterior portion. Vertebral scutes three and four are increasingly shorter and wider. The second to fourth vertebral scutes have increasingly more strongly angled lateral edges, with the fifth scute being distinctly hexagonal in shape.

The first pleural scute extends laterally onto peripherals one and two. Just posterior to peripheral two, the lateral edge of this pleural overlies the contact between the costals and marginals. The lateral edge of the second pleural is also coincident with the contact between the costals and peripherals. Further posteriorly, the pleural scutes extend onto the peripherals.

Marginal scutes are relatively wide. The eighth to eleventh marginals are slightly wider than the anterior marginals, but the difference in size is not great. The twelfth marginal scutes are enlarged compared to the adjacent scutes. In this feature, *J. russelli* differs from both *J. backmani* and *J. sukhanovi*, where the twelfth marginal scute is subequal in size to the eleventh marginal scute.

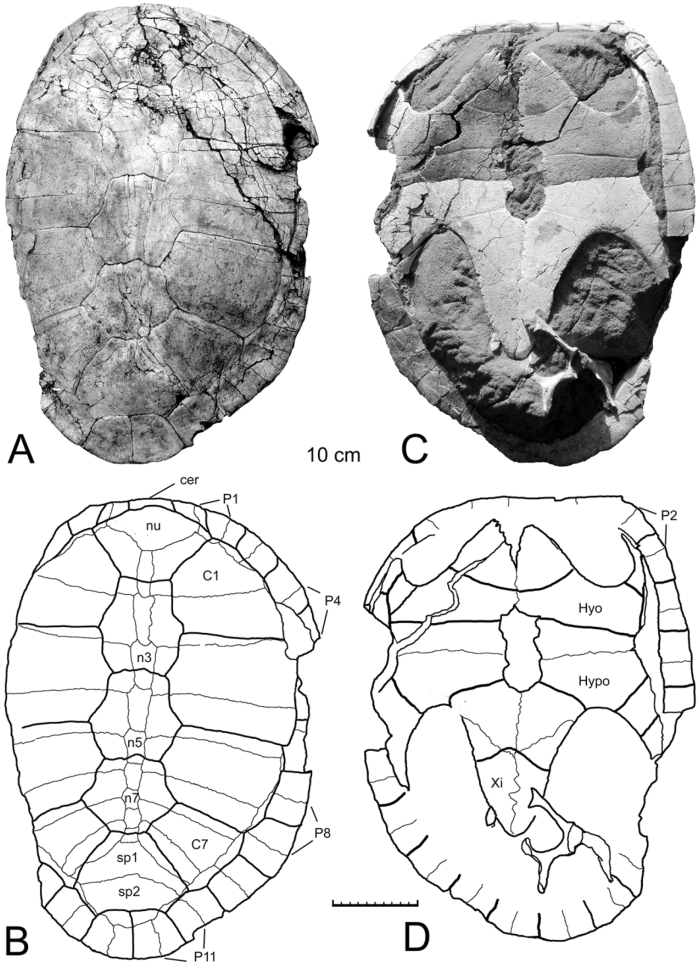

Figure 2:
Judithemys russelli, UALVP 47598, in dorsal and ventral views. A) Dorsal view of carapace, B) illustration of dorsal view of carapace, C) ventral view of plastron, and D) illustration of ventral view of plastron. Abbreviations: C1, first costal; C7, seventh costal; cer, cervical scute; Hyo, hyoplastron; Hypo, hypoplastron; n3, third neural; n5, fifth neural; n7, seventh neural; nu, nuchal; P1, first peripheral; P2, second peripheral; P4, fourth peripheral; P8, eighth peripheral; P11, eleventh peripheral; sp1, first suprapygal; sp2, second suprapygal; Xi, xiphiplastron.

Table 1:
Measurements of three *Judithemys* species (all in cm)

	Judithemys russelli (UALVP 47598)	*Judithemys sukhanovi* (TMP 87.2.1)	*Judithemys backmani* (YPMPU 016235)
Length	50.0	38.5	70.0
Width	38.0 *	32.5	–
Width of plastron	32.0 *	27.0	45.4
Length of plastron	34.0 **	23.5	47.6
Length of bridge	14.2	7.0	12.4
Portion of bridge formed by hyoplastron	8.3	3.7	6.6
Portion of bridge formed by hypoplastron	5.9	3.3	5.8

* Measured on most complete half of shell and doubled
** Length of anterior lobe of plastron estimated

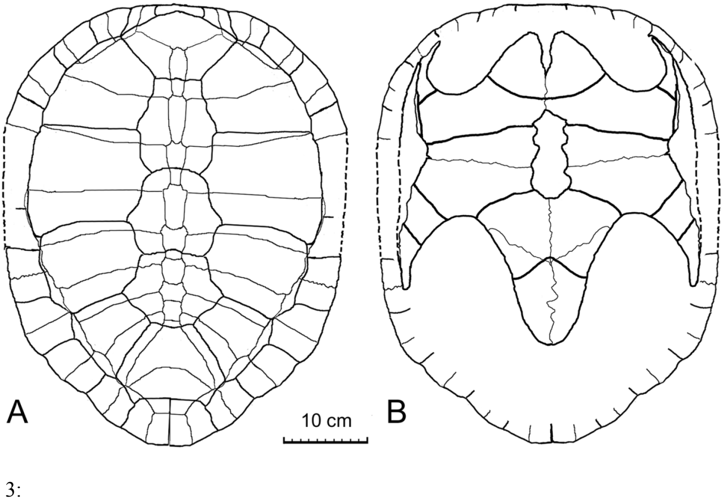

Figure 3:
Reconstruction of the shell of *Judithemys russelli* based on UALVP 47598. A) dorsal view of carapace; B) ventral view of plastron.

The plastron is missing the epi- and entoplastra but is otherwise complete (Figs. 2C–D). Fenestrae are present mid-ventrally and laterally. The mid-ventral fenestra is a relatively narrow, elongate opening and the lateral fenestrae are narrow, crescent-shaped openings. In the presence of a mid-ventral plastral fenestra, *J. russelli* is similar to *J. backmani* and different from *J. sukhanovi*. As in “macrobaenids” generally, the hyoplastron extends anteriorly to the second peripheral and the hypoplastron extends posteriorly to the eighth peripheral. The arrangement of scutes on the plastron agrees with that of other “macrobaenids.”

The most notable difference in the plastron of *J. russelli* compared to that of *J. sukhanovi* and *J. backmani* is the presence of a relatively longer bridge region. This can be quantified by comparing the length of the bridge to the width of the plastron. In *J. sukhanovi* and *J. backmani*, the bridge is 25% and 27% of the width of the plastron, respectively, whereas in *J. russelli* the bridge is 44% the length of the plastron (see Table 1). The plastron of *J. russelli* also differs from that of both *J. sukhanovi* and *J. backmani* in that a greater portion of the bridge is formed by the hyoplastron. In *J. sukhanovi* and *J. backmani*, the hyoplastron forms 53% of the length of the bridge, whereas in *J. russelli* it forms 58% of the length of the bridge. The plastron of *J. russelli* also differs from that of *J. backmani* in the shape of the posterior lobe. In *J. backmani*, the lobe is distinctly triangular in shape, whereas in *J. russelli* it is relatively longer and narrower as well as having a more rounded posterior end. In this feature, *J. russelli* is similar to *J. sukhanovi. Osteopygis* is similar to both *J. backmani* and *J. sukhanovi* in the proportions of its bridge. As reconstructed by Zangerl (1953: his fig. 89), the bridge is 27% of the width of the plastron and the hyoplastron forms 51% of the length of the bridge.

The pelvis is slightly displaced and is visible in lateral view (Fig. 4). The ilium is tall, has a straight anterior edge, and a well-developed posterior process. A sharp flange is present at the base of the posterior process. Such a flange is absent in *J. sukhanovi*. Since pelves are poorly known in other “macrobaenids” turtles, the taxonomic significance of this difference cannot be evaluated.

Discussion

The presence of a "macrobaenid" turtle in the late Maastrichtian of Saskatchewan is expected from their presence in the Hell Creek Formation of Montana (Hutchison and Archibald 1986) and the Scollard Formation of Alberta (Brinkman 2003; Brinkman & Eberth 2006). The widespread distribution of "macrobaenid" turtles in this region of North America is consistent with the hypothesis presented by Brinkman (2003) that "macrobaenid" turtles are latitudinally restricted to the more northerly regions of the western interior of North America during the late Campanian and suggests that this pattern continued throughout the Late Cretaceous and into the Palaeocene.

Figure 4:
Pelvis of *Judithemys russelli*, UALVP 47598, in lateral view.

Judithemys russelli, which is late Maastrichtian in age, is intermediate in age between the late Campanian *J. sukhanovi* and the described specimens of *J. backmani*, which are all Palaeocene in age (Russell 1934; Brinkman *et al.* 2010; Brinkman 2013). However, it is temporally equivalent to the specimens from the Hell Creek of Montana that have been included in *J. backmani* by Hutchison & Archibald (1986) and Holroyd & Hutchison (2002). Although the Hell Creek specimens have not been described in detail, the reconstructions of the shell and plastron published by Holroyd & Hutchison (2002: their Fig. 2) agree with the type specimen of *J. backmani* and the specimens described by Brinkman *et al.* (2010) with respect to features in which *J. russelli* and *J. backmani* differ. The occurrence of both these species in the Late Maastrichtian is the first instance of multiple species of a "macrobaenid" occurring within a limited geographic area at the same time and adds to the evidence that "macrobaenids" were important members of turtle assemblages of Saskatchewan, Montana, and Alberta areas in the Late Cretaceous.

Acknowledgements

The specimen was discovered and collected by Paul Johnston while he was a Masters student at the University of Alberta undertaking a study of late Cretaceous and Early Palaeocene mammals from this area. The name of the locality, Long Fall, derives from a unplanned decent of about ten meters down the slope that occurred while investigating some turtle bones that were seen while looking upwards from the base of the cliff. Fortunately, the fall ended without injury in a spill pile and did not deter Paul from collecting the specimen. Phil Currie and Eva Koppelhus located the unprepared jacket containing this specimen soon after undertaking a reorganisation of unprepared specimens in the collections of the University of Alberta and brought the specimen to light and made it available for study. Karen Adams and Judy Graham prepared the specimen. Their able assistance is greatly appreciated. This paper is dedicated to Tony Russell in honour of his contributions to paleontological research through mentoring students and recent graduates.

Literature cited

Batsch A.J.G.K. (1788). *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Volume 1*. Akademische Buchhandlung, Jena, Germany.

Brinkman D.B. (2003). A review of nonmarine turtles from the Late Cretaceous of Alberta. *Can. J. Earth. Sci.*, 40, 557–571.

Brinkman D.B. (2013). Non-trionychid turtles from the Paleocene of Alberta, Canada. *Can. J. Earth. Sci.*, 50, 282–293.

Brinkman D.B., Yuan C.X., Ji Q., Li D.Q. & You H.L. (2013). A new turtle from the Xiagou Formation (Early Cretaceous) of Changma Basin, Gansu Province, P.R. China. *Palaeobio. Palaeoenv.*, 93, 367–382.

Brinkman D.B. & Eberth D.A. (2006). Turtles of the Horseshoe Canyon and Scollard Formations – further evidence for a biotic response to Late Cretaceous climate change. *Russ. J. Herpetol.*, 13 (suppl.), 11–18.

Brinkman D.B., Densmore M.J. & Joyce W.G. (2010). "Macrobaenidae" (Testudines: Eucryptodira) from the Late Paleocene (Clarkforkian) of Montana and the taxonomic treatment of *"Clemmys" backmani*. *Bull. Peabody Mus. Nat. Hist.*, 5, 147–155.

Cope E.D. (1868). On the origin of genera. *Proc. Acad. Nat. Sci., Phila.*, 1868, 242–300.

Fox R.C. (1989). The Wounded Knee local fauna and mammalian evolution near the Cretaceous-Tertiary boundary, Saskatchewan, Canada. *Palaeontogr. A*, 208, 11–59.

Gaffney E.S. (1975). A phylogeny and classification of the higher categories of turtles. *Bull. Am. Mus. Nat. Hist.*, 155, 389–436.

Gaffney E.S. & Meylan P.A. (1988). A phylogeny of turtles. In: *The phylogeny and classification of the tetrapods. 1. Amphibians, reptiles, birds* (ed. Benton MJ) Clarendon Press Oxford, UK, 157–219.

Hirayama R., Brinkman D.B. & Danilov I.G. (2000). Distribution and biogeography of nonmarine Cretaceous turtles. *Russ. J. Herpetol.*, 7, 181–198.

Holroyd P.A. & Hutchison J.H. (2002). Patterns of geographic variation in latest Cretaceous vertebrates: evidence from the turtle component. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: an Integrated Continental Record of the End of the Cretaceous* (ed. Hartman JH, Johnson KR & Nichols DJ). Geological Society of America Special Paper 361, 177–190.

Hutchison J.H. (2000). Diversity of Cretaceous turtle faunas of eastern Asia and their contribution to the turtle faunas of North America. In: *2000 International Dinosaur Symposium for Kosong County in Korea: Proceedings*. (ed. Yuong-Nam L) Paleontological Society of Korea Special Publication 4, 27–38.

Hutchinson J.H. & Archibald J.D. (1986). Diversity of turtles across the Cretaceous/Tertiary boundary in northeastern Montana. *Paleogeogr., Paleoclimatol., Paleoecol.*, 55, 1–22.

Johnston P.A. & Fox R.C. (1984). Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. *Palaeontogr. A*, 186, 163–222.

Khozatsky L.I. & Nessov L.A. (1979). [Large turtles of the late Cretaceous of middle Asia.] *Akad. Nauk SSSR, Zool. Inst.*, 89, 98–108. (In Russian)

Parham J.F. (2005). A reassessment of the referral of sea turtle skulls to *Osteopygis* (Late Cretaceous, New Jersey, USA). *J. Vertebr. Paleontol.*, 25, 71–77.

Parham J.F. & Hutchinson J.H. (2003). A new eucryptodiran turtle from the Late Cretaceous of North America (Dinosaur Provincial Park, Alberta, Canada). *J. Vertebr. Paleontol.*, 23, 783–798.

Russell L.S. (1934). Fossil turtles from Saskatchewan and Alberta. *Trans. Roy. Soc. Can., Ser. 3, Sect. IV*, 28, 101–110.

Sukhanov V.B. (1964). Subclass Testudinata, Testudinates. In: *Fundamentals of Palaeontology. Amphibians, Reptiles and Birds* (ed. Orlov JA). Nauka Moscow, 354–438. (In Russian)

Sukhanov V.B. (2000). Mesozoic turtles of middle and central Asia. In: *The Age of Dinosaurs in Russia and Mongolia* (eds. Benton MJ, Shishkin MA, Unwin DM & Kurochkin EN). Cambridge University Press Cambridge, UK, 309–367.

Tong H.Y. & Brinkman D.B. (2013). A new species of *Sinemys* (Testudines: Cryptodira: Sinemydidae) from the Early Cretaceous of Inner Mongolia, China. *Palaeobio. Palaeoenv.*, 93, 355–366.

Vandermark D., Tarduno J.A., Brinkman D.B., Cottrell R.D. & Mason S. (2009). New Late Cretaceous macrobaenids turtle with Asian affinities from the High Canadian Arctic: dispersal via ice-free polar routes. *Geol.*, 37, 183–186.

A new, nearly three-dimensional specimen of the skull and anterior body of the Late Triassic ichthyosaur *Macgowania janiceps* (McGowan 1996) from northeastern British Columbia, Canada

Donald M. Henderson

Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, Alberta, T0J 0Y0, Canada;
E-mail: don.henderson@gov.ab.ca

Abstract

Although fairly common, the Early through Late Triassic ichthyosaurs recovered from northeastern British Columbia tend to be partly to heavily eroded, incomplete, poorly articulated, two-dimensional fossils, with only limited details of individual bones being available. In the summer of 2009, an exceptional specimen was discovered by rock climbers on a steeply dipping slope above a stretch of the remote Graham River in northeastern British Columbia in rocks of the Late Triassic Pardonet Formation. Similar cranial proportions; details of the premaxillae, jugals, and prefontals; geographic location; and stratigraphic position of the present specimen match those of *Macgowania janiceps* (McGowan 1996). The present specimen consists primarily of a skull in almost complete articulation in three-dimensions with the individual shapes, sutural contacts, and degrees of overlap between many of the dermal bones and braincase elements being visible. Unfortunately, the preserved mandible is heavily eroded. There is also a partial pectoral girdle and partial vertebral column associated with the skull. This specimen enables the revision of three previously interpreted skull character states as well as providing details on 15 previously unknown ones and one from the post-crania.

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BIS Verlag, Oldenburg, Germany.

Introduction

Ichthyosaur remains have been known from the Triassic marine rocks of northeastern British Columbia since the early 1930s (Sternberg 1931). A series of expeditions to this region in the 1980s and 1990s by staff of the Royal Tyrrell Museum of Palaeontology (RTMP) discovered new, fossil-rich localities and recovered many partial skulls, partial skeletons, and isolated ichthyosaur remains. Much of this collected material represents either new genera or species, or better examples of taxa found elsewhere (e. g., Brinkman *et al.,* 1992, Nicholls & Brinkman 1993, Nicholls & Manabe 2004). Table 1 lists those British Columbia Triassic ichthyosaur specimens identifiable to genus and/or species currently held in the collections of the Royal Tyrrell Museum and demonstrates the richness of the fossil localities. This table is far from being exhaustive because most of the specimens listed are known from three or more individuals of varying degrees of completeness. Additionally, there are many tens of elements identifiable only to family level (e. g., Mixosauridae or Shastasauridae) and many more tens of elements identifiable only as Ichthyosauria indet.

During the same time period that the RTMP was exploring, staff from the Royal Ontario Museum (ROM) in Toronto, Ontario were independently running expeditions to Triassic exposures in areas around Williston Lake, which is also located in the northeastern portion of the province (e. g., McGowan 1991, 1995). In 1996, Chris McGowan of the ROM published a description of an unusual ichthyosaur from middle Norian (specimen number ROM 41992) collected on the shore of Williston Lake. Although coming from the Late Triassic, this specimen possessed features typically seen in later Jurassic ichthyosaurs. It was named *Ichthyosaurus janiceps*, with the generic epithet referring to the well-established genus from the Jurassic and the specific epithet referring to the Roman god with two opposite faces looking back into the Triassic and forward into the Jurassic (McGowan 1996). The skull of this specimen exhibited the typical sort of preservation associated with the marine Triassic material from northern British Columbia—disarticulated, flattened bones, with individual dermal bones blending into one another—making exact shapes and contacts between the bones difficult or impossible to distinguish. However, the relative proportions of the various skull regions and the orbit were distinct enough to merit it being named as a new species. Thirteen years later, ROM 41992 was promoted to being a new genus, *Macgowania*, by Motani (1999). This promotion was based on the unique configuration of the bones forming the manus.

Table 1:
Selected ichthyosaur taxa from the Triassic of northeastern British Columbia identifiable to genus and/or species held in the collections of the Royal Tyrrell Museum of Palaeontology. In most cases, there is more than one specimen of an identified taxon. This list also excludes the many tens of specimens in the collections that are identifiable only to family level (e. g., Mixosauridae or Shastasauridae) or are only identifiable as Ichthyosauria indet.

Catalogue number	**Genus**	**Species**	**Geological formation**
TMP 1994.380.0011	*Callawayia*	*neoscapularis*	Pardonet
TMP 2001.023.0001	*Chaohusaurus*		Sulphur Mountain
TMP 1976.014.0001	*Cymbospondylus*		Toad
TMP 1986.152.0012	*Grippia*	*longirostris*	Sulphur Mountain
TMP 1998.077.0007	*Macgowania*	*janiceps*	Pardonet
TMP 1991.117.0002	*Mixosaurus*		Sulphur Mountain
TMP 1989.000.0018	*Parvinatator*	*wapitiensis*	Sulphur Mountain
TMP 1986.153.0012	*Phalarodon*	*fraasi*	Sulphur Mountain
TMP 1997.074.0035	*Phalarodon*	*nordenskioeldii*	Sulphur Mountain
TMP 1991.117.0006	*Pessosaurus*		Sulphur Mountain
TMP 1994.378.0002	*Shonisaurus*	*sikanniensis*	Pardonet
TMP 1991.121.0001	*Utatsusaurus*		Sulphur Mountain

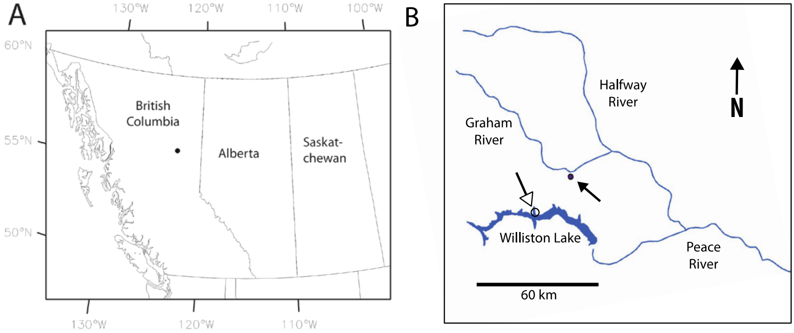

Figure 1
Maps showing where the new specimen of *Macgowania janiceps* (McGowan 1996) was found in 2009. A) Map of western Canada with the dot in northeastern British Columbia marking the fossil locality. B) Small-scale map with the locality of the new fossil highlighted with the solid black arrow pointing to the solid dot. The open circle and open arrow mark the approximate location of the original Royal Ontario Museum specimen of *Macgowania*, ROM 41992.

In August of 2009, members of an outdoor club based in Fort St. John, British Columbia informed staff of the RTMP about the occurrence of two fossils embedded at the top of a steep slope bordering a short stretch of the remote Graham River in northeastern British Columbia (Fig. 1). Of the photographs sent, one showed the heavily eroded spinal column and scattered ribs of a very large ichthyosaur akin to *Shonisaurus* sp., whereas the other showed a nearly complete small ichthyosaur, with the head, shoulders, trunk, and portions of the pelvic regions being preserved and missing only the tail (Fig. 2). This latter specimen was precariously situated on the lower edge of a large slab of weakly attached bedrock and several large cracks running through it were clearly visible. It was obvious that this exceptional specimen was not going to survive another winter exposed to the elements and remain intact.

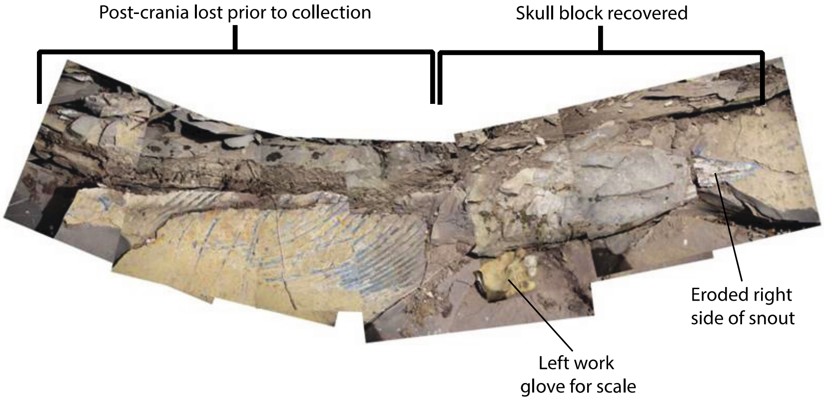

Figure 2
Field photograph of the highly fractured specimen in August 2009. Unfortunately, the postcranial sections fell from the cliff before the collection expedition in September of that year. All the vertebral elements ranging from the anterior caudal region forward were present, along with partial pelvic elements and ribs from both the left and right sides. Forelimb elements might have also been present in the block that the work glove is resting on.

Plans were immediately made for collecting the specimen in September of that year. The remoteness of the region is emphasised by how much travel was required to get to the site. The first leg of travel was to drive from Drumheller, Alberta to Grande Prairie in the northwestern part of the prov-

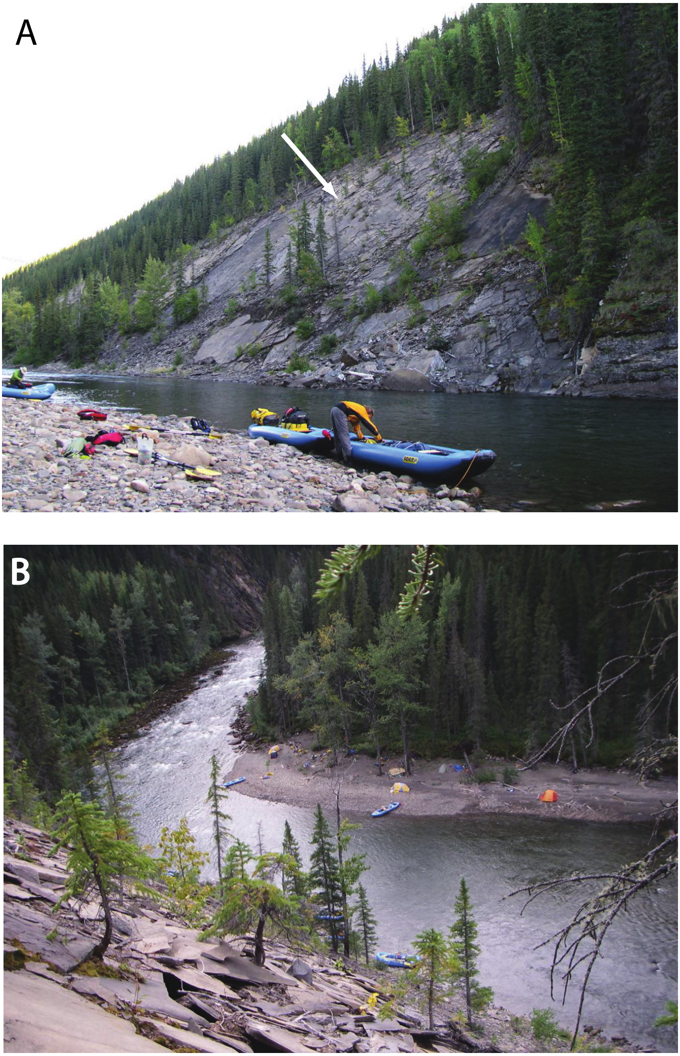

Figure 3
A) View of the steep slope along the southern shore of the Graham River hosting the specimen of what would turn out to be another example of *Macgowania janiceps* (McGowan 1996). The white arrow indicates the position of the ledge where the specimen discovered. B) View from the specimen locality on the cliff showing the campsite on a point bar of the Graham River.

ince. This took ten hours. Another six hours of driving via Fort St. John on the following day brought us to an informal campsite on the banks of the Graham River to meet up with members of the outdoor club. The next morning we set off as a small flotilla of high-tech, inflatable rafts and canoes to arrive eight hours later at a broad gravel point bar and set up camp. The steep, rocky slope hosting the fossils was located directly across the river from the campsite (Fig. 3). Unfortunately, in the time between being informed about the specimens and our arrival on site, most of the postcranial material of the smaller ichthyosaur had fallen away and ended up lost at the bottom of the river. Fortunately, the anterior portion of the trunk region as well as the skull and jaws were still there. Using ropes and climbing gear installed by club members, Jim McCabe (RTMP) and club member Peter Goetz put a plaster jacket on the specimen for protection, and then carefully lowered it with a system of ropes to bring it down off the steep slope.

The following description of this specimen, assigned the RTMP collection number TMP 2009.121.1, reveals new, and hitherto unknown, details about the skulls of ichthyosaurs from this part of the world at this time.

Palaeoenvironmental setting

The animal that is represented by TMP 2009.121.1 inhabited a broad bay, referred to as the Peace River Embayment that is estimated to have been 900 km long in a NNW-SSE direction, and at least 350 km wide (Davies 1997). This basin was situated on the west coast of the ancient supercontinent Pangaea in what is now the British Columbia-Alberta border at a palaeolatitude of approximately 30° north (Davies 1997, his Fig. 13). The climate for the Triassic in general is thought to have been warm and dry (Dickins 1993). Given the arid climate inferred for the region, sediment supply and sedimentation rates are thought to have been low (Davies 1997). The combination of climate and geography is thought to have produced coastal upwellings in the region and would have made the area a biologically productive one (Davies 1997), explaining the abundance of fossil vertebrates. However, these upwellings might have sometimes brought oxygen-depleted water from depth, producing anoxic conditions near the surface and these events might have also been associated with biogenic toxins. Such conditions could explain the mass mortalities observed among ichthyosaurs and fishes as recorded by their abundant fossil remains (Davies 1997). Accreting microcontinents along the western margin of North America during the later Mesozoic and early Tertiary resulted in the folding and uplifting of the formerly flat-lying, continental-shelf sediments (see Chapter 8 in Eyles & Miall 2007). It is on these deformed, eroding cliffs and ridges that the fossils of marine reptiles such as ichthyosaurs are discovered.

Taphonomy

The skull was almost fully preserved in a concretionary nodule that must have formed before the specimen experienced the typical fate of ichthyosaurs in the region of becoming deeply buried and flattened. The early development of this rigid nodule would have acted to maintain the three-dimensional nature of the specimen during subsequent burial and tectonic activity. Unfortunately, the snout was not encased in the nodule and lost substantial bone from its central lateral and dorsal regions because of weathering. The specimen came to rest on the ancient seabed on its left side and this is the side that is best preserved. However, some disarticulation of the specimen did occur. Beginning above the anterior limit of the external naris, the left and right members of the nasals, frontals, and parietals all became detached from one other by varying degrees. The separation was the result of shearing that displaced the right side of the skull dorsally relative to the left side by about 1 cm, although the actual plane of shear was approximately parallel to the inferred bedding plane. The nasals experienced the greatest displacement—on the order of 2 cm. It might be that the more robust postrostral region of skull was better able to resist the forces acting to separate the left and right halves. This shearing resulted in the exposure of the palate to the seabed surface and the subsequent disruption and loss of most of the bones in this region. The right-hand side of the block hosting the specimen shows isolated elements of the right lower jaw scattered across the palate. The majority of the upper and lower teeth have been lost and those that remain are not in their original articulation. Similar to the preservational state of the holotype, and of most other ichthyosaurs (McGowan 1996), the jaws are tightly closed against the cranium. Sitting exposed on a steep, southwest facing slope and exposed to many years of freeze-thaw cycles has led to many small sections of skull and jaw bones disintegrating and falling away. This is especially true of the left mandible, where almost all the bones appear to have been present originally, but most of the dentary as well as the external lateral surfaces of the postdentary bones were lost. The medial external surfaces of these bones are obscured by matrix.

Methods

Measurements were taken using the specifications outlined in McGowan (1996, his Table 1). Snout length was the straight-line distance from the tip of the snout to the posterior edge of the quadrate. As the tip of the dentary was missing, the mandibular tip was assumed to be the same as that of the left premaxilla and jaw length was taken as the distance from that tip to the posterior edge of the angular. Orbit length was the inner diameter measured in the anteroposterior direction. Premaxillary length was taken in two ways: (1) from the tip of the premaxilla to the anterior tip of the maxilla (following McGowan) for ratio comparison purposes and (2) from the rostral premaxillary tip to the posterior-most extent of the bone. Prenarial length was the distance from the tip of the snout to the anterior internal rim of the external naris. The ratios reported in Table 2 were computed as follows: orbital ratio, orbital diameter divided by jaw length; snout ratio, snout length divided by jaw length; premaxillary ratio, premaxillary length divided by jaw length; and prenarial ratio, prenarial length divided by jaw length.

Table 2:
Comparison of dimensions (in cm) and ratios of *Macgowania janiceps* ROM 41992 (McGowan 1996) and TMP 2009.121.1. See Methods for a description of the measurements and calculation of the ratios.

	TMP 2009.121.1.	**ROM 41992**
Skull length	49	50.0
Jaw length	59	50.0 *
Orbital diameter	15	13.5 *
Snout length	30.5	27.0 *
Premaxillary length	21	17.0 *
Orbital ratio	0.268	0.27
Snout ratio	0.545	0.54
Premaxillary ratio	0.348	0.34
Prenarial ratio	0.375	0.31

* Calculated from skull length reported by McGowan (1996) by multiplying by the reported ratio.

Systematic palaeontology

ICHTHYOSAURIA de Blainville 1835

Parvipelvia Motani 1999

Genus *Macgowania* (McGowan 1996)

Specimen: a nearly complete cranium exposed in left dorsolateral view; most of mandible lost because of erosion; ten vertebrae and associated ribs; eroded, incomplete and disarticulated pectoral girdle elements. Collected 2009.

Locality: northeastern shore of the Graham River, approximately 26 km north of the eastern end of Williston Lake, British Columbia: UTM Zone 10, 529,078E, 6,246,975N (World Geodesic System Datum WGS 84) and elevation 849 m.

Distribution: Pardonet Formation, Late Triassic.

Description (Figs. 4 and 5):

Snout

Premaxilla: Parts of both the left and right premaxillae are present, but the former is the best preserved. The anterior tip is intact and the posterior end has only lost small fragments. The full length is 25 cm and the width of the posterior base is in the range of 4–5 cm. Given the state of preservation, it is impossible to give an accurate estimate of the general outline shape of the bone, but it could be described as being an elongate isosceles triangle, with an altitude-to-base length ratio of approximately 1:6. Erosion has removed bone from a region starting at 8 cm from the tip to 20 cm posteriorly. This has resulted in the exposure of the internal edges of the nasals and palatal bones in oblique view as well as irregularly scattered teeth from the left side of the skull. The posterior end of the premaxilla diverges into symmetric dorsal and ventral processes, and the inner margins of these two processes form the dorsal and ventral edges, respectively, of the anterior half of the external naris. The posterior extent of the dorsal process clearly overlaps the left lateral margin of the nasal. This overlapping is only visible on the specimen in the area immediately dorsal to the narial opening. The dorsomedial edge of the dorsal process is eroded and the complete extent of its overlapping cannot be determined. The ventral posterior process can be seen to clearly overlap the anterodorsal portion of the maxilla.

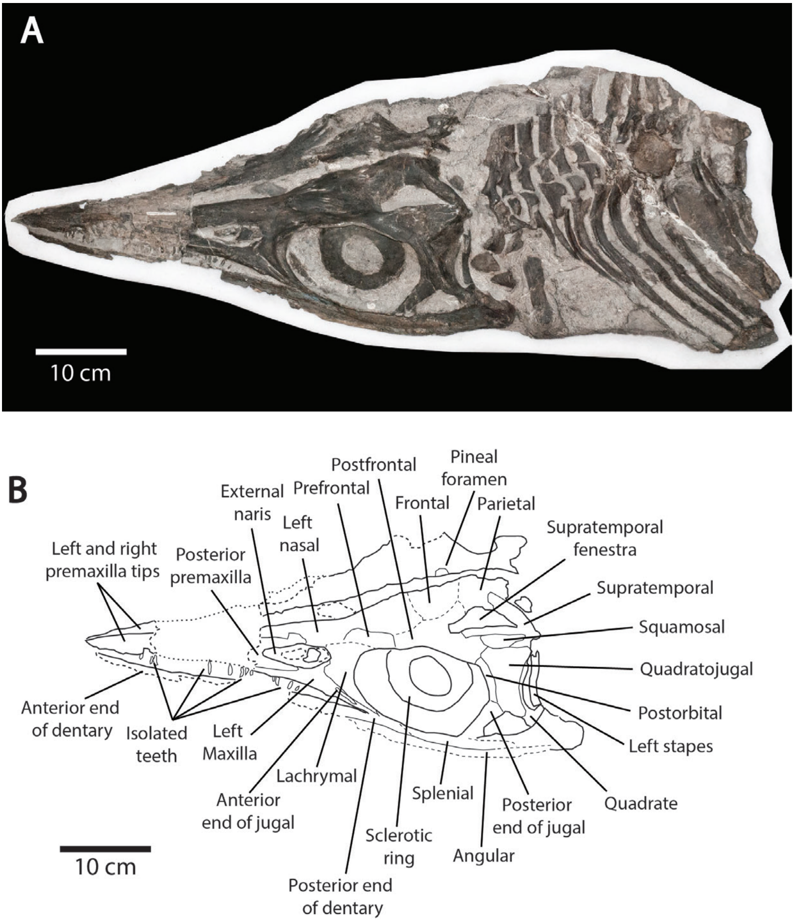

Figure 4
A) Left lateral and dorsal view of the skull, cervical, and pectoral region of *Macgowania janiceps* (McGowan 1996), Royal Tyrrell Museum of Palaeontology specimen number TMP 2009.121.1. B) Tracing of the skull with individual bones highlighted and identified where possible. Dotted lines indicate broken or eroded edges of bones. Dashed lines denote estimated boundaries for fused contacts between skull elements. Unidentified bone shapes are deemed impossible to reliably attach a name to.

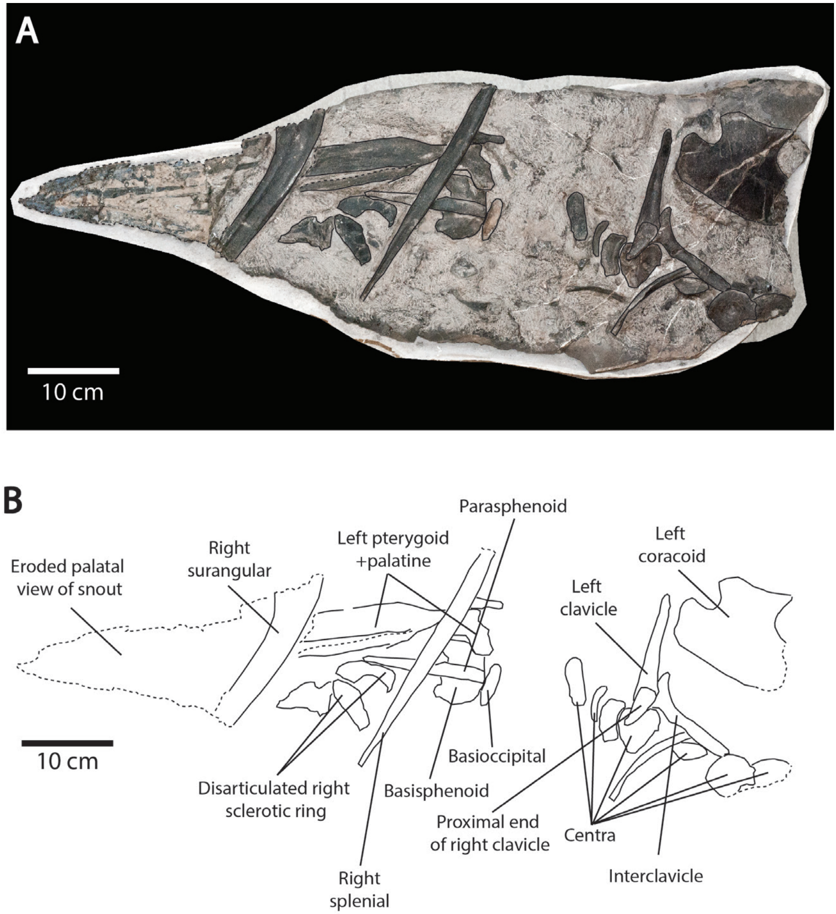

Figure 5:
A) Ventral view of block with scattered cranium, jaw, and pectoral elements of TMP 2009.121.1.
B) Outlines of visible bony elements with identifications where possible. Dashed lines indicate broken or eroded edges of bones.

Maxilla: The general shape of the maxilla is that of a low-altitude, isosceles triangle, with the base of the triangle forming a broad, ventrally concave arc. The altitude-to-base length ratio is between 1:4 and 1:5. The anterior and posterior ends have been eroded away, but it is estimated that only 1–2 cm are missing and its original length is estimated to have been 15 cm. The roots of just two teeth are visible on the ventral edge located below the midpoint of the external naris, with the remainder of the teeth having fallen out sometime after death. Despite being heavily eroded, the plicate condition of the teeth can be faintly seen. The preserved end of the anterior ramus of the maxilla lies 1 cm beyond the anterior-most rim of the external naris. The dorsal edge of the anterior ramus of the maxilla and a narrow, tapered process ascending from the dorsal midpoint of the maxilla together form the posteroventral quarter of the rim of the external naris. The region of the maxilla posterior to the ascending process extends along the full ventral edge of the lachrymal for a distance of not less than 4 cm. There is the possibility that the maxilla extended beyond the base of the lachrymal and under the orbit for a short distance, but with the posterior end missing, this is impossible to be certain. If so, this would be similar to condition seen in *Ichthyosaurus communis* (McGowan & Motani 2003, their Fig. 69). The anterior end of the jugal overlaps the dorsal edge of the posterior process of the maxilla for approximately 4 cm. Again, this overlap might have been more extensive, but, given the erosion, its true extent is unknowable.

Skull roof

Nasal: The exposed contact surfaces between the left and right nasals show very low-amplitude, serrated edges and imply a weak degree of sutural integration. On account of the 12 cm of erosion on the side of the snout, it is impossible to say much more about the nature of the contact between the nasal and the premaxilla other than to note the external overlap of the premaxilla onto the nasal. The lateral margin of the nasal forms a 2-cm segment of the dorsal rim of the external naris immediately posterior to the dorsal process of the premaxilla. The contact point between the nasal and the postfrontal is difficult to discern, but appears to occur above the midpoint of the orbit.

Frontal: Sutural contact between the frontals and their assumed neighbours—the anteriorly located nasals, the laterally located postfrontals, and the posteriorly positioned parietals—is impossible to discern because of extensive fusion of the skull roof. The pineal foramen is assumed to be positioned wholly within the frontals based on the configuration seen in *I. communis* (McGowan & Motani 2003, their Fig. 69). It is a 1.5-cm diameter circular opening that lies centred on an imaginary transverse line joining the anterior-most points of the left and right supratemporal fenestrae (STF).

Circumorbitals

Lachrymal: This is a robust, roughly quadrilateral bone with an arcuate posterior margin centred at the mid-height position of the orbit, with this margin forming most of the anterior quarter of the orbital rim. The extent of the posteroventral ramus of the lachrymal is uncertain because of erosion, but it runs parallel to, and is overlapped by, the jugal for approximately 6 cm. The anterior flange of the lachrymal is overlapped along the ventral 50% of its length by the ascending process of the maxilla. The dorsal 50% of the anterior flange forms the posterior-most portion of the rim of the external naris. The probable contact between the lachrymal and the dorsally bounding prefrontal is obscured by a localised inward crushing of the skull roof in the immediate area of contact between the two bones.

Jugal: The anterior and posterior ends of the jugal are preserved and the full length of the bone measured along the curved, ventral edge of the orbit can be stated as 20.5 cm. However, most of the middle 13 cm has been lost to erosion. The ventral margin of the orbit is defined by a thin ‘skin’ of bone representing the dorsal edge of the jugal, but most of this is embedded in, and obscured by, matrix left in place to protect the remaining bone. The anterior end of the jugal overlaps the suture between the maxilla and the lachrymal for more than half the suture length. The exact extent of the overlap is unknowable because of erosion of all three bones. The posterior 5 cm of the jugal expands to a maximum width of 2 cm to form the contact with the postorbital at the mid-height point of the orbit.

Postorbital: This bone forms a 5-cm arc on the posterior orbital rim from the orbital mid-height to where it contacts the postfrontal. This arc represents about 25% of the length of the dorsal half of the orbital rim. In lateral view, this bone appears to be only 5 mm wide. However, it makes a substantial contribution to the rear wall of the orbit. Unfortunately, matrix retained in the orbit to support the sclerotic ring prevents knowing the full medial extent of the postorbital. The posterolateral edge of the postorbital is overlapped by a substantial portion of the quadratojugal. Posterior contact between the postorbital and the postfrontal is obscured by crushing in the temporal region. The ventral end of the postorbital is overlapped by the jugal.

Postfrontal: The lateral margin of the postfrontal forms the central 50% of the dorsal half of the orbital rim. A small, posteromedially directed process makes a small contribution to the anteromedial margin of the STF, whereas a larger, posterolaterally directed process partially forms the anterolateral margin enclosing the STF. Posterolaterally, the postfrontal contacts the supratemporal, squamosal, quadratojugal, and postorbital. The posterior margin of the postfrontal forms the anterolateral quadrant of the STF rim.

Prefrontal: This bone contributes a 3-cm arc to the anterodorsal rim of the orbit, similar to that seen in *I. communis* (McGowan & Motani 2003, p. 23). In dorsal view, this bone has an irregular, five-sided outline. It overlaps the lateral edge of the nasal. Inward crushing and fracturing of the skull roof in the immediate region of this bone on the left side prevents a more reliable assessment of its original shape. The fluted ornament visible on the dorsal surface of this bone is very similar to, but more extensive than, that illustrated by McGowan (1996, his Fig. 4) for the same bone on ROM 41992.

Sclerotic ring: A complete sclerotic ring is preserved inside the left orbit. It has external and internal diameters of 10 cm and 5 cm, respectively, in the anteroposterior direction. Modest deformation associated with shearing of the skull has altered the presumably original circular shape of the ring and reduced the dorsoventral external and internal diameters to 8 cm and 4 cm, respectively. All scleral plates are in position and tightly associated with one another. It is possible to discern some edges of the plates on the dorsal half of the ring, but most are obscured by fusion, especially in the ventral half. Several of what appear to be edges of the scleral plates are likely to be fractures. The decision to retain most of the matrix in the orbit to support the sclerotic ring means that not much more can be observed. However, in the anterodorsal quadrant of the ring, the plates can be seen to plunge steeply towards the medial wall of the orbit. Unfortunately, their full extent cannot be seen.

Temporal region

Parietals: Extensive fusion between the parietals and adjacent bones prevents identification of their true extent. Together, the left and right parietals form a robust, bar-like, central region with a minimum transverse width (occurring at the anteropostero midpoint of the STF) equal to approximately 40% of the estimated width of the skull table of 16 cm. This skull-width measurement was taken as twice the distance from sagittal midline of the parietals to the dorsolateral rim of the supratemporal bone on the better preserved left side.

Supratemporal: This is a V-shaped bone when viewed dorsally and forms a substantial fraction (almost 50%) of the dorsal rim of the STF rim. It extends along 80% of the dorsolateral edge of the STF and forms 90% of the posterodorsal rim, reaching to within 1 cm of the sagittal midline of the skull. Unfortunately, the combination of fusion and modest crushing has obscured the nature of the contacts with adjacent bones. A laterally directed process contacts the posterior margin of the squamosal.

Squamosal: This is a petal-shaped bone, with the broad, rounded, anterior end making contact with the postfrontal. The tapered posterior end is bounded dorsally by the supratemporal and ventrally by the quadratojugal anteriorly and an extension of the supratemporal posteriorly. Crushing of the dorsal portion of the temporal region obscures any sutural contacts with neighbouring bones, if any unambiguous, unfused sutures were there to begin with.

Quadratojugal: The form of this bone is very similar to that described for *I. communis* (McGowan & Motani 2003, p. 24). It is a broadly fan-shaped bone that gently tapers ventrally and its anterior edge parallels the curvature of the postorbital. This anterior edge is greatly thickened where it overlaps the postorbital and the thickness doubles in going from the dorsal to ventral end. However, there is the suspicion that the variable thickness of this ridge might be associated, in part, with some of the crushing in this region of the skull. Details of the dorsal edge of this bone are also obscured by the crushing.

Quadrate: This bone is substantially overlapped on its lateral side by the quadratojugal. The visible shape of the quadrate is of an open, 5-mm arc that approximates an L-shape and that forms the posterolateral margin of the skull. Exposure of the ventral portion of the left lateral region of the occipital region enables an additional view of the quadrate. This bone narrows ventrally to a circular cross-section of approximately 1 cm immediately above the quadrate-articular joint. The actual joint surface is then expanded to 2.5 cm mediolaterally, similar to that shown for *I. communis* in McGowan and Motani (2003). Tight contact with the articular, in combination with modest crushing in the immediate region of the jaw articulation on the mandible, prevents further details from being observed.

Stapes: A displaced left stapes is visible on the left side of the occipital region. It is an L-shaped bone with a broad, flattened dorsomedial end that would have contacted the opisthotic (McGowan & Motani 2003, their Fig. 31). Retention of matrix around most of this bone as well as the rest of the occipital region, prevents any further description. Although the ventrolateral end of the stapes is in contact with the ventromedial surface of the quadrate, this cannot be the case in the real-life position because the dorsal end of the bone has been rotated so that it projects laterally beyond the posterior margin of the quadrate.

Palate

Pterygoid + palatine: For structural reasons, much of the matrix on the ventral side of the skull has been left in place. This has had the unfortunate effect of hiding many of the edges and distal extremities of the few palatal bones preserved with the specimen. The left members of the pterygoid and palatine are indistinguishably fused together and partly obscured by scattered elements of the right mandible. The right members are either deeply buried in matrix or were lost soon after death. Their general appearance is very similar to that illustrated for *Stenopterygius* (McGowan & Motani 2003, their Fig. 40), but the most significant difference is in the posterior region. Unfortunately, the anterior extent of the pterygoid + palatine is missing and the posterior constriction of the pterygoid is obscured by an overlying, isolated right splenial. The posteromedial process of the pterygoid is robust and almost circular in cross-section. It is displaced ventrally relative to the posterolateral corner of the basisphenoid. The posterolateral process is partly obscured by matrix, but appears to be more robust than that illustrated for *Stenopterygius*.

Basisphenoid: The ventral surface of this bone is well exposed. It has a subrectangular shape that is 7 cm in transverse width and 4 cm long. Two wing-like processes with thickened central axes project symmetrically anterolaterally. The peripheral edges of these processes taper rapidly, giving a bevelled edge. These processes also form a shallow step on their posterior edges where they arise from the posterior third of the basisphenoid. Again, full details of the margins of this bone are obscured by retained matrix.

Basioccipital: The ventral quarter of the basioccipital is visible and is situated immediately posterior to the basisphenoid. It closely resembles the same bone figured for *Opthalmosaurus* (McGowan & Motani 2003, their Fig. 35). It has the form of a very flat (oblate) disk with rounded edges. The transverse width of the visible portion is 5 cm and the anteroposterior thickness is 1 cm. There are a series of concentric, slightly raised rings running circumferentially along the outer surface. In TMP 2009.121.1, the basisphenoid has a much paler colour, suggesting a lesser degree of permineralisation. No other elements of this specimen have this appearance of weakly mineralised bone.

Parasphenoid: This bone is preserved as a short, 12-cm long segment. It originates at the posterior margin of the basisphenoid and continues forward before plunging into the retained matrix under the medial edge of the left pterygoid. It is a constant 1.3 cm in width along its visible extent.

Mandible

Jaw elements: The substantial erosion of the left mandible has resulted in only incomplete views of internal surfaces of a few of the postdentary bones and reliable estimates of their shapes are unobtainable. The inside of the surangular is visible, but the anterior portion of this bone is lost. The lateral surface of the splenial is visible in lateral view because of the loss of the surangular and dentary.

Dentition

It is not possible to reliably infer the shapes or dimensions of any of the preserved teeth because most are either broken off flush with the surface of the rock or still partly embedded in matrix. It is possible to discern faint fluting on some of the less eroded teeth to make the assignment that the teeth show the plicidentine condition (Motani 1999, character 36). Erosional loss of the bone immediately adjacent to teeth, combined with the loss and/or scattering of the teeth, make it impossible to say anything about the nature of their implantation along the jaw margins.

Postcrania

To maintain the structural integrity of the specimen and retain its display quality preservation, most of the matrix lying posterior to skull has been left in place. This has meant that the vertebrae and ribs have only been partly exposed, making it impossible to see their full shape and extent. From these limited views, it does not appear that the forms of these skeletal elements differ from those of other small Triassic ichthyosaurs.

Clavicle: Only the left clavicle appears to be fully preserved and only 12 cm is visible in ventral view. The medial end is 2-cm deep in the dorsoventral direction and this width tapers down to less than 1 cm at the visible distal end. The overall shape is that of a gentle arc with the curvature lying in a transverse plane of the body. There are no longitudinal grooves or any other sort of ornament visible. The medial end of this bone overlaps two-thirds of the anterior transverse bar of the interclavicle. The medial-most 4 cm of the right clavicle is preserved and overlaps the anteromedial surface of the left clavicle. This configuration for these two bones is identical to that illustrated for *I. communis* (McGowan & Motani 2003, their Fig. 56).

Interclavicle: This is a T-shaped bone missing most of the distal left portion of the transverse bar. The full width of the bar is estimated to be 4 cm based on the central portion and the fully preserved left side. The length of the central shaft is 10 cm with a constant width of 1.5 cm. The anterior two-thirds of the shaft has a sub-circular cross-section, whereas the posterior third is flattened. The overall form of this bone is much more elongate than that of *I. communis* (McGowan & Motani 2003, their Fig. 56).

Coracoid: This bone is very similar to that illustrated for *I. communis* (McGowan & Motani 2003, their Fig. 56). The basic shape is that of an oval disk with the anteroposterior diameter estimated to be 16 cm and a mediolateral diameter of 10 cm. The posterior-most 2 cm is missing, but an impression in the matrix enables recognising the full extent. The medial rim appears to have been poorly mineralised because the margin is not sharply defined. There is a smoothly contoured U-shaped notch on the anterolateral edge between the buttress for the scapular facet and the main corpus of the coracoid. This notch is 3.5 cm at its widest point and 2 cm deep. A more open, U-shaped notch is visible on the posterolateral margin adjacent to the base of the humeral facet, but the missing posterior edge precludes any reliable measurement of its dimensions. The facet for scapula is 3 cm long, with no raised rim being apparent. The humeral facet is 5 cm long, again with no visible rim. The basal buttress for the scapular and humeral facets is noticeably thicker than the remainder of the coracoid, possibly twice as thick, but retained matrix prevents knowing the true thickness.

Discussion

Comparisons

It is difficult to make many meaningful osteological comparisons between TMP 2009.121.1 and other Triassic ichthyosaurs recovered from northeastern British Columbia because of the different quality of preservation of the specimens, their ontogenetic-stage differences, and the low number of common elements that are preserved.

Two ichthyosaur genera are known from the same early Norian Pardonet Formation that produced TMP 2009.121.1: *Metashastasaurus neoscapularis* TMP 1994.380.11 (Nicholls & Manabe 2001) and *Shonisaurus sikkaniensis* TMP 1994.378.2 (Nicholls & Manabe 2004). *Metashastasaurus neoscapularis* is a small, probably juvenile, specimen (Nicholls & Manabe, 2001) comprising a crushed, but nearly complete, skull and most of the postcrania. The skull length is approximately 33 cm. Several cranial bones of TMP 2009.121.1 are clearly different from those of *M. neoscapularis*, with the former possessing a broad parietal midline bar as opposed to a narrow one; a V-shaped supratemporal as opposed to a straight, sub-rectangular one; broad frontals, prefrontals, and nasals in contrast to the narrow forms; a slender postorbital with a smooth, arcuate posterior margin in contrast to a wider bone with complex sutural pattern on the posterior margin; and an anteroposteriorly broad, robust lacrimal instead of a slender one, to name just a few. It is unlikely that TMP 2009.121.1 is another example of *M. neoscapularis*.

Shonisaurus sikkaniensis is a very large ichthyosaur with an estimated body length of 23 m (Nicholls & Manabe 2004). It should be noted that this animal was also argued to be a member of the genus *Shastasaurus* (Sander *et al.,* 2007). Unfortunately, the quality of preservation of the skull roof bones is very poor in this specimen and details of the contacts between the various cranial bones are almost impossible to discern (Nicholls & Manabe 2004). Additionally, the great size difference between its 3–4-m long skull and the 49-cm skull of TMP 2009.121.1 would allow for very large ontogenetic changes to significantly affect the shapes and relative proportions of the bones, making any bone-by-bone comparisons between the two futile. Nevertheless, it is unlikely that TMP 2009.121.1 is an example of *S. sikkaniensis*.

Another early Norian ichthyosaurian specimen from the shores of Lake Williston in northeastern British Columbia, but with an unspecified geological formation, is *Hudsonelpidia brevirostris* ROM 41993 (McGowan 1995). This specimen is especially frustrating because it is represented by an almost complete skull and skeleton, but the severe weathering that it experienced before its discovery means that it preserves very little in the way of diagnostic detail. Additionally, the skull is crushed flat and is moderately disarticulated (McGowan 1995, his Fig. 3). It is virtually impossible to make meaningful comparisons between TMP 2009.121.1 and ROM 41993. Indeed, McGowan and Motani (2003, p. 73) make the following damning remark concerning Hudsonelpidiidae and its classification, “A family comprising a single genus named solely for classificational convenience.”

Identification

The loss of substantial portions of the postcranial skeleton and mandible of TMP 2009.121.1 render it difficult to make detailed comparisons between it and other Late Triassic remains for the purposes of identifying the specimen. Especially distressing is the fact that most of the forelimb appeared to be present in a photograph of the specimen before the loss of most of the post-crania soon after its discovery and it was the manus that exhibited autapomorphic characters for the genus *Macgowania* (Motani 1999). Similarly, a cladistic analysis would normally be an option to help place the specimen within the larger systematic picture of ichthyosaurs, but problems with this strategy (see below), led to a different approach in an attempt to make an identification. Using the data provided by McGowan (1996) for ROM 41992, Table 2 compares the proportions of the skull of the new specimen with that of ROM 41992 and it can be seen that the numbers for both specimens are very similar. The difference between the values for the prenarial ratio for TMP 2009.121.1 and ROM 41992 is most likely because of the snout tip of the latter not being preserved, such that the value used by McGowan (1996) for prenarial length (distance between the snout tip and anterior margin of the external naris) being an estimated one. Fig. 1 shows the locality of ROM 41992 as an open circle on the north shore of Williston Lake and that of TMP 2009.121.1 as a solid dot on the south shore of the Graham River. The geographic separation of the two sites is approximately 30 km (Fig. 1). McGowan (1996) states that the age of the bed hosting ROM 41992 is Norian based on conodont analysis. The age of the bed hosting TMP 2009.121.1 is interpreted to be Norian as well given the occurrence of a large, weathered specimen of *Shonisaurus* sp. on the same bedding plane at the site. The latter specimen is known from Norian age rocks in the region (Nicholls & Manabe 2004). The similarity of the proportions, the geographic proximity of the two localities producing the fossils, and their similar geological age suggest that the present specimen is another example of *Macgowania janiceps*.

Cladistic analysis

The specimen TMP 2009.121.1 was scored for characters using the character set of Motani (1999). The hope was to perform a phylogenetic analysis to see where TMP 2009.121.1 would sit in a large-scale ichthyosaur phylogeny. The new specimen enabled the revision of three skull characters and the scoring of 16 characters that were previously coded as unknown for *M. janiceps*. These changes and the new information are summarised in Table 3. Unfortunately, the erosional loss of large parts of the mandible, most of the teeth, all the limbs, and all but one bone of the associated girdles has resulted in a large amount of missing data. TMP 2009.121.1 can only be scored for the first 45 (of 105) characters in the Motani matrix and, with one exception (T-shaped interclavicle; character 45), all these characters are cranial. The amounts and categories of character data that *cannot* be scored for are summarised as follows: 7 of 34 skull characters; 5 of 10 dental characters; 6 of 7 pectoral characters; and all the forelimb, pelvic, hind-limb, and axial characters. Tables 4–6 present those characters of the skull, dental and pectoral regions that can be scored for TMP 2009.121.1. These tables also report the scoring of *Macgowania* (based on ROM 41992) for the same character sets. Shown also in Tables 4 and 5 are grey-coloured cells that highlight those nine skull characters and five dental characters that can be simultaneously scored for TMP 2009.121.1 and *Macgowania*. The large amount of missing data for TMP 2009.121.1 (57% of 105 characters) combined with the large amounts of missing data for other Triassic ichthyosaurs (McGowan & Motani 2003, 160–163) led to the author deciding that any attempt at a cladistic analysis of the specimen would be a futile waste of time that would not contribute to any real advance in our study of the interrelationships of ichthyosaurs.

Significance

The new specimen is significant for two main reasons. First, it provides a clear view of the undeformed dermal bones in their original topological relationships with their neighbours. The vast majority of the ichthyosaurs from the region are preserved with the dermal bones detached from one another to varying degrees (e. g., *M. neoscapularis* [Nicholls & Manabe 2001, their Figs. 2 and 3], *Hudonselpida brevirostris* [McGowan 1995], and *Phalarodon nordenskioeldi* (Nicholls *et al.,* 1999, their Figs. 2–5]). The bones of these specimens are also severely flattened. It could be significant that the ROM specimen of *Macgowania* figured by McGowan (1996, his Fig. 4) shows very little disarticulation compared to other ichthyosaurs from the region and, although it is still very flattened, shares a similar state of cohesiveness as the RTMP specimen. This similar aspect of their preservation suggests that the two skulls possessed the same high degree of fusion between their elements and a similar mechanical strength.

Table 3:
Updates to character-matrix entries for *Macgowania* using the new specimen TMP 2009.121.1. Characters are those of Motani (1999).

Changes to existing character codings

Character no.	Character description	Old value	New value
1	Nature of premaxillary contact with external naris (0 – concave, dorsal process longer; 1 – pointed; 2 – concave, ventral process longer)	2	0
2	Dorsal lamina of maxilla present (0 – absent; 1 – present)	0	1
39	Tooth size relative to skull width (0 – normal; 1 – small)	0	1

New information to replace previously unknown character states

Character no.	Character description	Old value	New value
3	Maxilla-external naris contact (0 – absent; 1 – present)	?	0
5	Nasal-external naris contact (0 – absent; 1 – present)	?	0
6	Wide contact between nasal and postfrontal (0 – absent; 1 – present)	?	1
10	Postfrontal participates in upper temporal fenestra (0 – absent; 1 – present)	?	1
13	Squamosal participates in upper temporal fenestra (0 – present; 1 – absent)	?	1

Table 3:
Continued

Character no.	Character description	Old value	New value
13	Squamosal participates in upper temporal fenestra (0 – present; 1 – absent)	?	1
14	Anterior terrace on upper temporal fenestra (0 – absent; 1 – present)	?	0
15	Frontal widest position (0 – posteriorly; 1 – at nasal suture)	?	1
16	Sagittal eminence (0 – absent; 1 – small; 2 – large)	?	0
17	Parietal ridge (0 – absent; 1 – present)	?	0
18	Parietal supratemporal process (0 – short; 1 – long)	?	0
20	Supratemporal posterior slope (0 – absent; 1 – narrow separation anteriorly; 2 – widely open)	?	0
21	Supratemporal ridge (0 – absent; 1 – present)	?	0
22	Supratemporal ventral process (0 – absent; 1 – present)	?	1
23	Jugal-quadratojugal dorsal contact (0 – absent; 1 – present)	?	1
31	Basioccipital contact (0 – flat or slightly concave; 1 – hemispherical)	?	0
45	Interclavicle (0 – cruciform; 1 – triangular; 2 – T-shaped)	?	2

Table 4:
Matrix showing the amounts and distributions of missing data (question marks) in the character data sets for the skull bones of TMP 2009.121.1 and *Macgowania janiceps* (ROM 41992). The grey regions highlight the limited number of characters that can be scored simultaneously for both specimens. The character numbers are those of Motani (1999).

Character no.	TMP 2009.121.1	ROM 41992
1	0	2
2	1	0
3	0	?
4	1	1
5	0	?
6	1	?
7	0	?
8	1	1
9	1	1
10	1	?
11	1	1
12	1	1
13	1	?
14	0	?
15	1	?
16	0	?
17	0	?
18	0	?
19	?	?
20	0	?
21	0	?
22	1	?
23	1	?
24	1	1
25	0	0
26	?	?
27	?	?
28	?	?
29	?	?
30	?	?
31	0	?
32	?	1
33	0	0
34	0	0

Table 5:
Matrix showing the amounts and distributions of missing data (question marks) in the character data sets for the teeth of TMP 2009.121.1 and *Macgowania janiceps* (ROM 41992). The grey regions highlight the characters that can be scored simultaneously for both specimens. The characters numbers are those of Motani (1999).

Character no.	**TMP 2009.121.1**	**ROM 41992**
35	?	?
36	1	1
37	0	0
38	0	0
39	1	0
40	0	0
41	?	0
42	?	0
43	?	?
44	?	?

Table 6:
Matrix showing the amount of missing data (question marks) in the character data sets for the pectoral girdles of TMP 2009.121.1 and *Macgowania janiceps* (ROM 41992). There are no pectoral characters that can be scored simultaneously for both specimens. The characters numbers are those of Motani (1999).

Character no.	**TMP 2009.121.1**	**ROM 41992**
45	2	?
46	?	2
47	?	1
48	?	0
49	?	3
50	?	?
51	?	1

Second, the specimen provides an accurate indication of the skull shape and size for a small ichthyosaur from northeastern British Columbia. All the previous ichthyosaurs from the region have incomplete skulls that are all disarticulated to a greater degree than that of TMP 2009.121.1, making accurate estimates of their true sizes and shapes problematic. With an the intergirdle trunk length of 71 cm estimated from the field photo (Fig. 2) taken before the loss of most of the postcranial region and, assuming that the ratio of trunk length to caudal length was one-to-one like the Late Triassic (Carnian) ichthyosaur *Californosaurus perrrini* (Kuhn 1934), the total body length associated with the 49-cm skull can be estimated as 190 cm. This sort of information is of use when attempting to study the palaeoecology of a fauna such as that recovered from the Late Triassic marine rocks of northeastern British Columbia by determining the range of body sizes that could occupy the environment. Both skull- and body-size values for the ichthyosaurs of the region also enable estimates to be made of the sizes of prey could be taken by the animals. Additionally, the width of the skull table in TMP 2009.121.1 is greater than that of possibly sympatric and contemporaneous *M. neoscapularis* as indicated by the greater relative width of the skull table bones of the former compared to the latter. This suggests a possible difference in feeding style and/or prey between the two.

The new specimen of *M. janiceps* merits the above descriptive detail because it provides new information on ichthyosaurs from the Triassic of what is now western North America. The ichthyosaur remains from the Triassic of northeastern British Columbia tend to be heavily eroded when found. This is related to how they are found because the only way to efficiently find them in this region is to patiently walk talus and scree slopes above the treeline in the mountainous terrain and to be on the lookout for the bright white to pale blue weathered bone. By the time the fossils are located, they have often lost much of their surface detail. Additionally, the nature of the preservation soon after death is for the specimens to disarticulate, with skull bones separating from one other, heads and jaws detaching from the rest of the body, limbs detaching from girdles, and caudal sections separating from the rest of the body. Rapid burial of these disarticulated remains before they become solidly fossilised tends to flatten them and results in loss of shape information. TMP 2009.121.1 overcomes these problems through its almost three-dimensional skull, with the majority of elements in place and with sharply defined edges. The only complaint with this discovery is that it would have been better to have been found about ten years earlier. Erosion has eaten away at significant portions of the skull and, together with gravity, taken away what could have been the best preserved postcranial remains for a British Columbian Triassic ichthyosaur. At the same time, however, it was erosion that brought the specimen to the surface to make its discovery possible.

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I first contacted Tony Russell in 1992 during my final undergraduate year at the University of Toronto. At that time, I was finishing a degree in geophysics, but was less than satisfied with the subject. I wrote asking how feasible it would be for someone who had studied geology, mathematics, and physics as well as taken a first-year biology course to get into vertebrate palaeontology. Tony advised me that I would need to spend two years getting some more biology and zoology courses under my belt before applying for graduate studies in palaeontology. In the fall of 1993, I followed his advice and registered at the University of Calgary and took, among other courses, Tony's comparative vertebrate morphology course (ZOOL 377) and the fishes, amphibians, and reptiles course (ZOOL 477). Over my two years at Calgary, I regularly pestered Tony with reams of questions about vertebrate functional morphology and evolution, which he patiently answered. In 1995, I was accepted into a PhD program at the University of Bristol, England. I returned to Calgary in 2001 and joined the Russell lab as a postdoc, remaining with the lab until 2006 when I was hired on at the Royal Tyrrell Museum. When Tony went on sabbatical in 2004, I was thrilled to be able to teach the fishes, amphibians, and reptiles course that I had enjoyed ten years earlier, and, with Herb Rosenberg, the comparative vertebrate morphology course as well. I will always be very grateful for the scientific and academic advice and support that Tony has given me over the years.

Literature cited

Blainville H.M.D. (1835). Description de quelques espèces de reptiles de la Californie, précédé de l'analyse d'un systèm général d'erpétologie et d'amphibiologie. *Nouvelles Ann. Mus. Hist. Nat. Paris*, 4, 233–296.

Brinkman D.B., Zhao X.J., & Nicholls E.L. (1992). A primitive ichthyosaur from the Lower Triassic of British Columbia, Canada. *Palaeontol.,* 35, 465 –474.

Davies G.R. (1997). The Triassic of the Western Canada Sedimentary Basin: tectonic and stratigraphic framework, paleogeography, paleoclimate and biota. *Bull. Can. Petrol. Geol.,* 45, 434–460.

Dickins J.M. (1993). Climate of the Late Devonian to Triassic *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* 100, 89–94.

Eyles N. & Miall A. (2007). *Canada Rocks: A Geological Journey.* Fitzhenry and Whiteside Limited, Markham, Ontario.

Kuhn O. (1934). Ichthyosauria. In: *Fossilum Catalogus I: Animalia. Pars 63* (ed. Quenstedt W). W. Junk, Berlin, 75 pp.

McGowan C. (1991). An ichthyosaur forefin from the Triassic of British Columbia exemplifying Jurassic features. *Can. J. Earth Sci.,* 28, 1553–1560.

McGowan C. (1995). A remarkable small ichthyosaur from the Upper Triassic of British Columbia, representing a new genus and species. *Can. J. Earth Sci.,* 32, 292–303.

McGowan C. (1996). A new and typically Jurassic ichthyosaur from the Upper Triassic of British Columbia. *Can. J. Earth Sci.,* 33,24–32.

McGowan C. & Motani R. (2003). *Handbook of Paleoherpetology Part 8: Ichthyopterygia.* Verlag Dr. Friedrich Pfeil, München.

Motani R. (1999). Phylogeny of the Ichthyopterygia. *J. Vertebr. Paleontol.,* 19, 472–495.

Nicholls E.L. & Brinkman D.B. (1993). A new specimen of *Utatsusaurus* (Reptilia: Ichthyosauria) from the Lower Triassic Sulphur Mountain Formation of British Columbia. *Can. J. Earth Sci.,* 30, 486–490.

Nicholls E.L., Brinkman D.B. & Callaway J.M. (1999). New material of *Phalarodon* (Reptilia: Ichthyosauria) from the Triassic of British Columbia and its bearing on the interrelationships of mixosaurs. *Palaeontographica Abt. A,* 252, 1 –22.

Nicholls E.L. & Manabe M. (2001). A new genus of ichthyosaur from the Late Triassic Pardonet Formation of British Columbia: bridging the Triassic-Jurassic gap. *Can. J. Earth Sci.,* 38, 983–1002.

Nicholls E.L. & Manabe M. (2004). Giant ichthyosaurs of the Triassic – a new species of *Shonisaurus* from the Pardonet Formation (Norian: Late Triassic) of British Columbia. *J. Vertebr. Paleontol.,* 24, 839–849.

Sander P. M., Chen X., Cheng L. & Wang, X. (2011). Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. *PLoS ONE,* 6, e19480.

Sternberg C.M. (1931). Two ichthyosaur localities in British Columbia. *Geol. Soc. Amer. Bull.,* 42, 363.

A census of Canadian dinosaurs: more than a century of discovery

Caleb Marshall Brown[1], Michael J. Ryan[2], and David C.Evans[3]

[1] Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, Alberta T0J 0Y0, Canada; E-mail: caleb.brown@gov.ab.ca
[2] Department of Vertebrate Paleontology, Cleveland Museum of Natural History, 1 Wade Oval Drive, University Circle, Cleveland, Ohio 44106, USA; E-mail: mryan@cmnh.org
[3] Department of Natural History, Palaeobiology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6, Canada; E-mail: d.evans@utoronto.ca

Abstract

Canadian rocks preserve a rich fossil history, including diverse assemblages of Late Cretaceous dinosaurs that have been a focal point of dinosaur research for more than a century. This paper reviews the current literature on Canadian non-avian dinosaur occurrences and provides an updated data set of all dinosaur formational occurrences in the country, complete with reference specimens. We discuss this dataset in the context of dinosaur palaeobiology, diversity, patterns of species discoveries, and endemicity/provinciality. To date, 87 named dinosaur species (~11–17% of known global diversity) are known from Canada based on 205 formational occurrences across 23 dinosaur-bearing formations. The current diversity of dinosaurs is heavily dominated by a few geological formations in southern Alberta. However, recent work has extended the known regional and temporal ranges of dinosaur taxa in Canadian Mesozoic rocks outside of these heavily sampled units. Ceratopsia and Pachycephalosauria are often the first taxa discovered and named in these newly explored formations and recent finds of new taxa from well-sampled formations are generally small-bodied (< ~100 kg). Occurrences of most individual dinosaur species are restricted to a single formation, which superficially suggests restricted geographic ranges; however, it is likely that poor sampling and a lack of coeval deposits is at least partially responsible for this pattern. Despite the extraordinary nature of the Albertan dinosaur

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record, poor and unequal sampling still limits our ability to test many interesting palaeobiological questions. Further collection from Mesozoic exposure outside of Alberta and Saskatchewan might provide important discoveries for extending the temporal and biogeographical ranges of Canadian dinosaurs. These prospects include the Canadian Arctic territories, British Columbia, and possibly Northern Ontario.

Introduction

With its vast geographic area and varied geologic history, the sedimentary rocks of Canada preserve an abundance and diversity of fossil resources, including fossil localities of global scientific importance. A number of these sites are recognised, at least in part, for this significance by the United Nations Educational, Scientific and Cultural Organization (UNESCO) as current or prospective World Heritage Sites, including the Ediacaran deposits of Mistaken Point Ecological Reserve, Newfoundland (Narbonne 2005); the Cambrian Burgess Shale of British Columbia (Morris 1992; Briggs & Fortey 2005); the Devonian deposits from Miguasha National Park, Quebec (Schultze & Cloutier 1996); the Carboniferous sites of the Joggins Fossil Cliffs, Nova Scotia (Falcon-Lang & Calder 2004; Falcon-Lang 2006); and, perhaps most prominently, the badlands of Dinosaur Provincial Park, Alberta (Currie & Koppelhus 2005). The fossil-rich deposits of the Late Cretaceous Belly River Group exposed in Dinosaur Provincial Park have produced over 400 articulated dinosaur skulls and skeletons, hundreds of bone beds, and millions of isolated bones, making it one of the richest dinosaur-bearing fossil deposits in the world. The well-preserved specimens collected from here have formed the core of several major museum collections, including the American Museum of Natural History, the Canadian Museum of Nature, the Royal Ontario Museum, and the Royal Tyrrell Museum of Palaeontology, and have provided an extraordinary window into the Cretaceous world. The rocks exposed at Dinosaur Provincial Park are only a small part of a series of Late Cretaceous terrestrial deposits in the Western Interior foreland basin of Alberta and Saskatchewan. These deposits preserve a nearly continuous history of terrestrial faunas for the last 20 million years of the Cretaceous, providing an unparalleled resource for understanding dinosaur palaeoecology, palaeobiology, and extinction. The first officially reported dinosaurs were collected in 1874 by George Mercer Dawson of the British North

American Boundary Survey in southern Saskatchewan in the Wood Mountain area and along the Milk River in southern Alberta (Currie 2005a). Since then, these resources have been nearly continuously collected and researched by generations of Canadian and international scientists up to the present day (Sternberg 1917; Parks 1933, 1935; Langston 1965; Russell 1966; Sternberg 1966; Russell, 1967b; Dodson 1971; Spalding 1999; Currie 2005a). As a result, Canada, and particularly Alberta, hosts one of the best-sampled and most diverse series of dinosaur assemblages in the world.

The dinosaur diversity of Canada has been documented in a number of publications (Langston 1965; Russell 1966; Russell 1967a, 1977; Beland & Russell 1978; Russell 1984; Baszio 1997a). A recent major comprehensive review of the non-avian dinosaur fossil record of Alberta was provided by Ryan and Russell (2001). This publication quickly became widely cited and has served as important benchmark in Canadian dinosaur studies. However, the past decade has witnessed a tremendous increase in scientific research on dinosaurs, with numerous significant advances in Canadian dinosaur palaeontology. This includes both the discovery of many new taxa (e. g., Ryan *et al.* 2010b, 2012a) as well as multiple new fossil localities. Much of this research has been highlighted in recent symposia held at the Royal Tyrrell Museum of Palaeontology, including the Dinosaur Park Symposium (2005), Ceratopsian Symposium (2007), and the International Hadrosaur Symposium (2011), as well as the resulting abstract volumes and books (Braman *et al.* 2005, 2011; Currie & Koppelhus 2005; Braman 2007; Ryan *et al.* 2010b).

The rapid rate of discovery and publication since Ryan and Russell (2001) necessitates a revised compilation of Canadian dinosaur diversity as a whole. This paper aims to update the dinosaur occurrence data of Ryan and Russell (2001) for Alberta and to make taxonomic changes where appropriate. Additionally, we expand the dataset to include dinosaur occurrence data for all dinosaur-bearing formations across Canada. We hope the data provided here will be a useful synthesis for future studies of dinosaur diversity dynamics and palaeobiogeography. We have chosen to concentrate this review on body fossils (skeletons, bones, and teeth only) and only address footprints or other ichnofossils/ichnotaxa, and eggs and/or ootaxa at a broad, occurrence-based (rather than taxonomic) level. This review of Canadian non-avian dinosaur fossil occurrences enables for a brief discussion of several aspects of the distribution and diversity of dinosaur occurrences, including formation-level diversity, historical patterns of discovery, and aspects of provinciality/endemicity.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; CMN, Canadian Museum of Nature, Ottawa (formerly the National Museum of Canada, NMC, and incorporating specimens from the Geological Survey of Canada, GSC); FGM, Fundy Geological Museum, Parrsboro; FMNH, Field Museum of Natural History, Chicago; NHM(UK), Natural History Museum (United Kingdom), London; EM, Eastend Museum, Eastend; NMI, National Museum of Ireland, Dublin; NSM, Nova Scotia Museum, Halifax; RBCM, Royal British Columbia Museum, Victoria; ROM, Royal Ontario Museum, Toronto; RSM, Royal Saskatchewan Museum, Regina; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton; and YG, Yukon Palaeontology Program, Whitehorse.

Methods

The data set of dinosaur skeletal occurrences was compiled from the published literature using Ryan and Russell (2001) as the core of the revised data set. There are several additional occurrences and localities that are known to the authors, but that have not yet been published. Material currently in the process of being collected or studied, but that has not been published is not included in this review. For issues of taxonomic synonymy and nomenclature, the most recent literature is generally followed, except where the authors prefer a previously published taxonomy, which is noted.

For each geological formation, we provide a list of diagnostic reference specimens (the holotype when applicable) as well as a reference to the literature for that occurrence (if applicable). Each reference specimen also includes a general comment on the nature of the material (e. g., tooth, skull, complete, articulated, etc.) and a very general sense of other material assignable to that taxon from the formation where possible. Further information regarding the locality data and collection history of individual reference specimens is available at the specimen repository. Each named taxon also includes a list of synonymies (when appropriate).

The diversity of formations with more than three taxa represented is quantified using five different metrics.

1. *families represented*, the minimum number of families known from the formation;
2. *genera represented*, the minimum number of genera represented in the formation (these do not need to be named genera, but where the occurrence of a suprageneric taxon implies the presence of at least one genus);
3. *genera named*, the number of named genera in the formation;
4. *species represented*, the minimum number of species represented in the formation (these do not need to be named species, but where the occurrence of a supraspecific taxon implies the presence of at least one species); and
5. *species named*, the number of named species in the formation.

We also employ the Paleobiology Database (PBDB; http//www.pbdb.org) to analyse the distribution and number of dinosaur fossil occurrences across Canada. The database was accessed on February 22, 2013 and queried using the Fossil Collection Records search function with the search terms "Dinosauria" and both the Canadian provinces and formation names, which retrieved data for body-fossil occurrences, trace-fossil occurrences, and egg-site occurrences. Body, trace and fossil-egg occurrences were separated. The data were modified to remove the occurrences of avian dinosaurs and to include known sites not represented in the PBDB.

Results

The dinosaurian (exclusive of Aves) faunal list for all Canadian formations is summarised in Table 1. A full breakdown of the taxonomic occurrences, including reference specimens, material represented, and literature references, is provided in the Appendix.

Currently, a total of 87 named (and considered valid) dinosaur species are known from Canada, representing approximately 11–17% of known global dinosaur diversity (Wang & Dodson 2006; Benton 2010). This diversity is derived from 205 documented, unique formational occurrences across 23 dinosaur-bearing formations in four provinces (Alberta, British Columbia, Nova Scotia, and Saskatchewan) and all three northern territories (Fig. 1). Six provinces do not have any dinosaur records: Ontario, Quebec, Manitoba, Newfoundland, New Brunswick, and Prince Edward Island.

Table 1:
Dinosaur species occurrence in Canadian dinosaur-bearing formations listed by region and formation. Occurrences are listed to the lowest taxonomic level. * Formation of provenance for these taxa is uncertain. ** *Arctosaurus* likely does not represent a dinosaur, but rather an indeterminate archosauriform.

Alberta

Clearwater Formation (Albian)

Nodosauridae n. gen et. sp.

Milk River Formation (Santonian)

Hadrosauridae indet.
Acrotholus audeti
Ankylosauridae indet.
Nodosauridae indet.
Gryphoceratops morrisoni
Ceratopsidae indet.
Tyrannosauridae indet.
Ornithomimidae indet.
Milk River Saurornitholestinae gen. et sp.
Milk River Dromaeosauridae gen. et sp.
Milk River Dromaeosaurinae gen. et sp.
Aquilan cf. *Richardoestesia gilmorei*
?Aquilan cf. *Richardoestesia isosceles*
Milk River cf. *Zapsalis* sp.
cf. *Paronychodon lacustris*

Foremost Formation (Campanian)

Hadrosauridae indet.
Colepiocephale lambei
Ankylosauridae indet.
Nodosauridae indet.
Xenoceratops foremostensis
Tyrannosauridae indet.
Saurornitholestes sp.
Richardoestesia sp.
Richardoestesia n. sp.
Paronycodon sp.

Oldman Formation (Campanian)

Albertadromeus syntarsus
Brachylophosaurus canadensis
Hypacrosaurus stebingeri
Pachycephalosauridae indet.
Ankylosauridae indet.
Nodosauridae indet.
Prenoceratops sp.
Centrosaurus apertus
Coronosaurus brinkmani
Albertaceratops nesmoi
Chasmosaurinae indet.
Daspletosaurus torosus
Dromaeosaurus albertensis
Saurornitholestes langstoni
Oldman cf. *Richardoestesia gilmorei*
Richardoestesia isosceles
Paronychodon sp.

Dinosaur Park Formation (Campanian)

Gryposaurus notabilis
Prosaurolophus maximus
Corythosaurus casuarius
Corythosaurus intermedius
Lambeosaurus lambei
Lambeosaurus clavinitialis
Lambeosaurus magnicristatus
Chasmosaurus russelli
Vagaceratops irvinensis
Dromiceiomimus samueli
Ornithomimus edmontonicus
Struthiomimus altus
Ornithomimidae indet.
Gorgosaurus libratus

Table 1: Continued

Parasaurolophus walkeri
Orodrominae incertae sedis
Stegoceras validum
Stegoceras breve
Hanssuessia sternbergi
Pachycephalosaurus?*
Pachycephalosauridae nov. sp.
Euoplocephalus tutus
Dyoplosaurus acutosquameus
Edmontonia rugosidens
Panoplosaurus miris
Unescoceratops koppelhusae
Centrosaurus apertus
Styracosaurus albertensis
*Spinops sternbergorum**
Pachyrhinosaurini indet.
Chasmosaurus belli
Daspletosaurus sp.
Avimimus sp.
Caenagnathus collinsi
Caenagnathus sternbergi
Chirostenotes pergracilis
Elmisaurus elegans
Troodon inequalis
Dinosaur Park cf. *Pectinodon* sp.
Dromaeosaurus albertensis
Zapsalis abradens
Saurornitholestes langstoni
Hesperonychus elizabethae
Richardoestesia gilmorei
Richardoestesia isosceles
cf. *Paronychodon lacustris*
Anchiceratops sp?

Bearpaw Formation (Campanian)

Prosaurolophus sp.
Edmontonia sp.
Stegoceras sp.
Richardoestesia gilmorei
Ceratopsidae indet.
Ornithomimidae indet.

Allison Formation (Campanian)

Orodrominae indet.

Horseshoe Canyon Formation (Camp./Maast.)

Parksosaurus warreni
Edmontosaurus regalis
Saurolophus osborni
Hypacrosaurus altispinus
Prenocephale edmontonense
Euoplocephalus tutus
Edmontonia longiceps
Montanoceratops sp.
Pachyrhinosaurus canadensis
Anchiceratops ornatus
Arrhinoceratops brachyops
Eotriceratops xerinsularis
Dromiceiomimus brevitertius
Ornithomimus edmontonicus
Struthiomimus altus
Daspletosaurus sp.
Albertosaurus sarcophagus
Epichirostenotes curriei
Horseshoe Canyon cf. *Troodon* sp.
HsCF Dromaeosaurinae gen. et sp.
Atrociraptor marshalli
Albertonykus borealis
HsCF cf. *Richardoestesia gilmorei*
cf. *Paronychodon lacustris*

St. Mary River Formation (Camp./Maast.)

Edmontosaurus sp.
Pachyrhinosaurus canadensis
Anchiceratops sp.
Edmontonia cf. *longiceps*
Ornithomimidae indet.
Albertosaurus sp.
Deinonychosauria indet.
Troodon indet.
Richardoestesia sp.

Table 1: Continued

Wapiti Formation (Camp./Maast.)

Hypsilophodontidae indet.
Hadrosauridae indet.
Pachyrhinosaurus lakustai
Pachycephalosauridae indet.
Ankylosauridae indet.
Ornithomimidae indet.
Tyrannosauridae indet.
Dromaeosauridae indet.
Saurornitholestes sp.
Troodontidae indet.
Paronychodon sp.
Richardoestesia gilmorei

Scollard Formation (late Maastrichtian)

Thescelosaurus neglectus
Hadrosauridae indet.
Ankylosaurus magniventris
Pachycephalosauridae indet.
Leptoceratops gracilis
Triceratops sp.
Ornithomimidae indet.
Tyrannosaurus rex
Table 1: Continued
?Caenagnathidae n.sp.
cf. *Troodon*
cf. *Dromaeosaurus albertensis*
cf. *Saurornitholestes langstoni*
cf. *Richardoestesia gilmorei*
cf. *Richardoestesia isosceles*
Paronychodon-like

Willow Creek Formation (Late Maastrichtian)

Hadrosauridae indet.
Prenoceratops sp.
Tyrannosaurus rex

British Columbia

Brothers Peak Formation (Camp./Maast)

Cerapoda indet.

Kaskapau Formation (Turonian)

Hadrosauridae indet.
Tyrannosauridae indet.
Saurornitholestes sp.

uncertain formation

Ornithopoda indet.
Theropoda indet.

Northwest Territories

Summit Creek Formation (Maastrichtian)

Ceratopsia indet.

Nova Scotia

Wolfville Formation (Carnian to Norian)

?Ornithischia indet.

Table 1: Continued

McCoy Brook Formation (Hettangian)

Prosauropod gen. et sp. nov

Nunavut

Kanguk Formation (Late Cretaceous)

Hadrosauridae indet.
Tyrannosaurid indet.

Heiberg Formation (Late Triassic)

Arctosaurus osborni **

Saskatchewan

Dinosaur Park Formation–Saskatchewan (Campanian)

Lambeosaurinae indet.
Centrosaurus apertus
Chasmosaurus sp.
Ornithomimidae indet.
Saurornitholestes langstoni
Troodon formosus
Albertosaurus sp.

Frenchman Formation (late Maastrichtian)

Thescelosaurus assiniboiensis
Edmontosaurus annectens
Pachycephalosauridae indet.
cf. *Ankylosaurus magniventris*
Triceratops horridus
cf. *Torosaurus*
Tyrannosaurus rex
Ornithomimus sp.
Struthiomimus sedens
Chirostenotes sp.
Troodontidae indet.
cf. *Dromaeosaurus* sp.
Saurornitholestes sp.
Richardoestesia sp.
cf. *Paronychodon*

Yukon

Bonnet Plume Formation (Maastrichtian)

Ornithopoda indet.
Hadrosauridae indet.

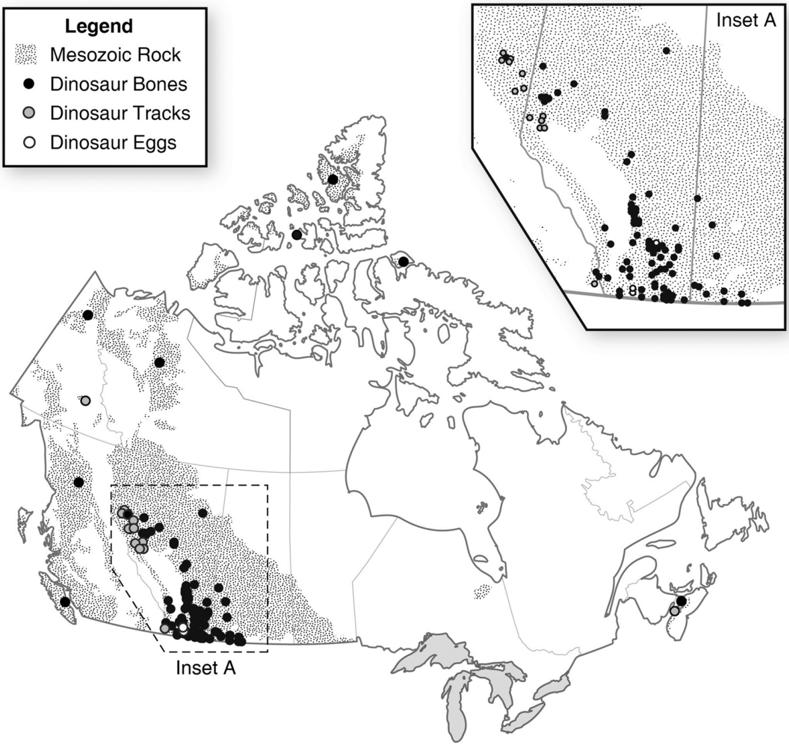

Figure 1:
Map of Canada illustrating currently known dinosaur occurrences and the exposure of Mesozoic rocks. Dinosaur fossil sites are indicated by black (body), grey (track), and white (egg) dots. Mesozoic rock outcrop is indicted with grey stippling. Inset shows highly fossiliferous areas of Alberta, southwestern Saskatchewan, and eastern British Colombia.

The PBDB lists 499 dinosaur occurrences in Canada (Table 2). Alberta has by far the highest number of dinosaur occurrences (476 or 95%), eclipsing the province with the second highest number of occurrences, Saskatchewan (10 or 2%), by more than an order of magnitude (Fig. 2A, Table 2). British Columbia and Alberta have the greatest number of dinosaur-track occurrences, followed by the Yukon and Nova Scotia (Fig. 2A, Table 2). Alberta is, to date, the only province with known dinosaur-egg occurrences. Dinosaur occurrence data derived from the PBDB also show high dominance of occurrences by a single formation, the Dinosaur Park Formation, with 73% (255) of all occurrences for formations with three or more species (Table 3).

Diversity counts for formations with three or more taxa are presented in Table 4. The most diverse assemblage is the Dinosaur Park Formation (*n* = 46 species represented, Campanian), followed in descending order by the Horseshoe Canyon Formation (*n* = 23, late Campanian/early Maastricht ian), the Oldman Formation (*n* = 17, Campanian) and the Scollard and the Frenchman Formations (both *n* = 15, late Maastrichtian) (Fig. 2B). A rank diversity versus absolute diversity plot (Fig. 2B) illustrates an exponential decrease in all diversity metrics (except families represented), indicating low evenness (high dominance) in the known diversity between formations. After the five most diverse formations have been accounted for, there is a low abundance of named taxa in the remaining formations.

Table 2:
Number of dinosaur occurrences (broken into skeletal occurrences, track site, and egg sites) in Canadian provinces. Numbers in parentheses indicate percentage of the total across Canada for the respective category. Data derived from the Paleobiology Database with minor modifications (see Methods).

Region	Skeletal occurrences	Track sites	Egg sites
Canada	499	76	3
Alberta	476 (96.0)	29 (38.2)	3 (100)
Saskatchewan	10 (2.0)	0 (0)	0 (0)
Nova Scotia	6 (1.2)	5 (6.3)	0 (0)
British Columbia	3 (0.6)	32 (40.5)	0 (0)
Yukon	2 (0.4)	10 (12.7)	0 (0)
Northwest Territories	1 (0.2)	0 (0)	0 (0)
Nunavut	1 (0.2)	0 (0)	0 (0)

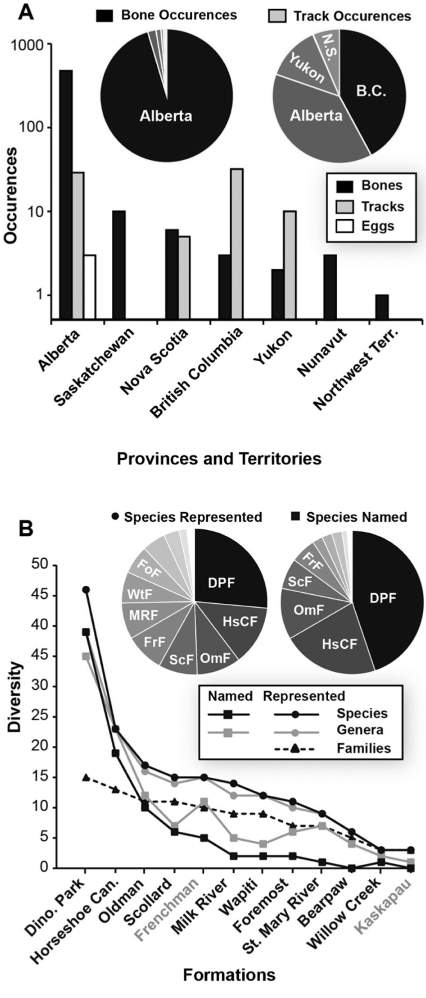

Figure 2:
A) Distribution of dinosaur body fossils, tracks and egg sites between Canadian provinces. Data mainly derived from the Paleobiology Database. B) Rank diversity versus absolute diversity plot illustrating the diversity metrics for all dinosaur formations with three or more taxa. Formations in grey are outside Alberta. Black, grey, and dotted lines indicate species, genera, and families, respectively. Circles indicate known or represented taxa, and squares indicate named taxa. Abbreviations: DPF, Dinosaur Park Formation; FoF, Foremost Formation; FrF, Frenchman Formation; HsCF, Horseshoe Canyon Formation; MRF, Milk River Formation; OmF, Oldman Formation; ScF, Scollard Formation; and WtF, Wapiti Formation.

Table 3:
Number of dinosaur occurrences (skeletal occurrences only) in formations with three or more species. Numbers in parentheses indicate percentage of the total. Data derived from the Paleobiology Database.

Formation	Skeletal occurrences
Total	348
Dinosaur Park	255 (73.3)
Horseshoe Canyon	38 (10.9)
Scollard	13 (3.7)
Foremost	10 (2.9)
St. Mary River	10 (2.9)
Frenchman	8 (2.3)
Wapiti	7 (2.0)
Milk River	3 (0.8)
Kaskapau	3 (0.8)
Willow Creek	1 (0.3)
Oldman	0 (0)
Bearpaw	0 (0)

Table 4:
Diversity metrics of all Canadian formations with three or more known dinosaur taxa. Formations are ranked in decreasing diversity. Fam. Rep. = Families represented, Gen. Rep. = Genera represented, Gen. Nam. = Genera named, Sp. Rep = Species represented, Sp. Nam. = Species named, End. Sp. = Endemic species. The Dinosaur Park Formation exposed in Saskatchewan is excluded because it is a subset of the diversity of the Dinosaur Park Formation exposed in Alberta.

Formation	Age	Fam. Rep.	Gen. Rep.	Gen. Nam.	Sp. Rep.	Sp. Nam.	End. Sp.
Dinosaur Park	Campanian	15	39	35	46	37	33
Horseshoe Canyon	late Camp./early Maas.	13	23	23	23	19	14
Oldman	Campanian	11	16	12	17	10	6
Scollard	late Maastrichtian	11	14	7	15	4	0
Frenchman	late Maastrichtian	10	15	11	15	5	1
Milk River	Santonian	9	12	5	14	2	2
Wapiti	late Camp./early Maas.	9	12	4	12	2	0
Foremost	Campanian	7	10	6	11	2	2
St. Mary River	late Camp./early Maas.	7	9	7	9	1	0
Bearpaw	Campanian	5	6	4	6	0	0
Willow Creek	late Maastrichtian	3	3	2	3	1	0
Kaskapau	Turonian	3	3	1	3	0	0

Diversity metrics

Of the different metrics of formational diversity, four (genera represented, named genera, species represented, and named species) are highly correlated, with pairwise r^2 values between all metrics being greater than 0.9 (Figs. 2B and 3A). This indicates that these metrics capture similar patterns of relative diversity between the formations, but predominantly reflects that most dinosaur genera are monospecific (which is related to taxonomic practices of dinosaur systematists). Most highly correlated are named species to named genera ($r^2 = 0.95$) as well as species represented to genera represented ($r^2 = 0.99$), indicating that 95% and 99%, respectively, of species diversity is explained by generic diversity. Slopes for pairwise regression of all four metrics are between 0.96 and 1.16, indicating near one-to-one correlations (Fig. 3A).

Conversely, the diversity patterns suggested by the number of families represented in each formation shows a much more even pattern between formations and a relatively low correlation with both generic ($r^2 = 0.84$, 0.71) and species ($r^2 = 0.78$, 0.61) diversity (Fig. 3B). Furthermore, correlations between family diversity and the generic and species metrics are better described by exponential relationships than linear ones (Fig. 3B) based on Akaike weights. Linear relationships might reasonably describe the link between family and species/genus diversity in low diversity (i.e., low-sampled) formations, with slopes much higher than 1.00 (e. g., 2.32, 2.26), but this relationship breaks down once higher diversity is known (> 10 families or > 20 genera/species; Fig. 3B). This pattern indicates a disconnect between diversity at the family level and diversity at the genus and species levels.

The slope of the rank diversity versus absolute diversity plots (Fig. 2B) reveals the evenness of the different diversity metrics between the formations. All generic and species metrics have high slopes (–2.5 to –2.1), indicating high dominance and low evenness (these diversity metrics continue to increase with increased sampling), whereas the family diversity metric has a relatively lower slope (–0.99), indicating high evenness (this metric is established in low samples and does not increase rapidly with higher sampling).

Although inconsistencies exist between the diversity data set presented here and the occurrence data derived from the PBDB (e. g., no occurrences in the Oldman and Bearpaw formations), all diversity metrics are highly correlated with the number of dinosaur occurrences (Fig. 4), with r^2 values between 0.622 and 0.760.

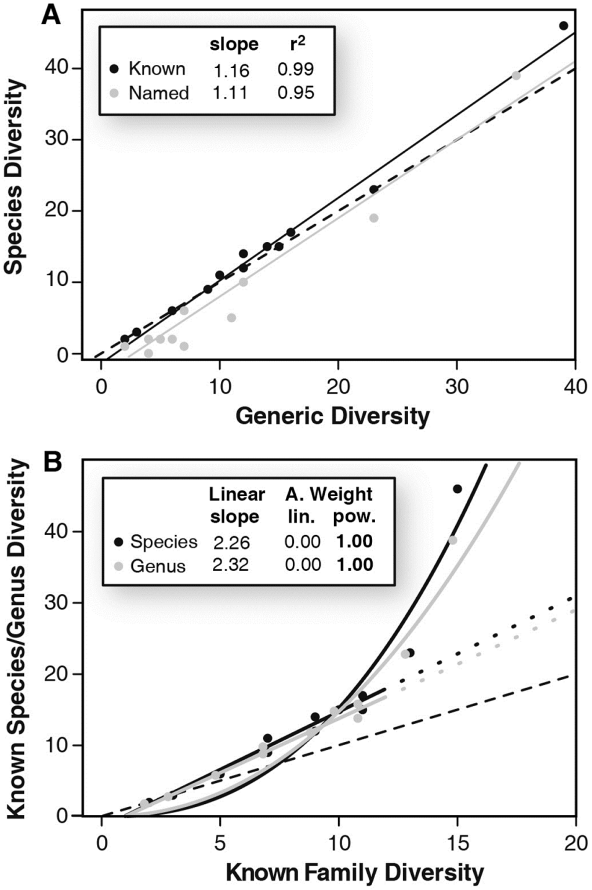

Figure 3:
Correlations of the different diversity metrics for Canadian dinosaur-bearing formations. A) Species diversity as a function of genus diversity for both known (black) and named genera/species (grey). Solid lines show best-fitting (linear) functions. B) Known species (black) and genus (grey) diversity as a function of family diversity. Curved lines show best-fitting (power) functions. Straight lines indicate the best linear fit when the two highest sampled formations are excluded (solid) and the loss of linearity as diversity increases (dotted). In both graphs, the dashed line indicates a perfect one-to-one linear correlation (slope = 1.00, intercept = 0,0).

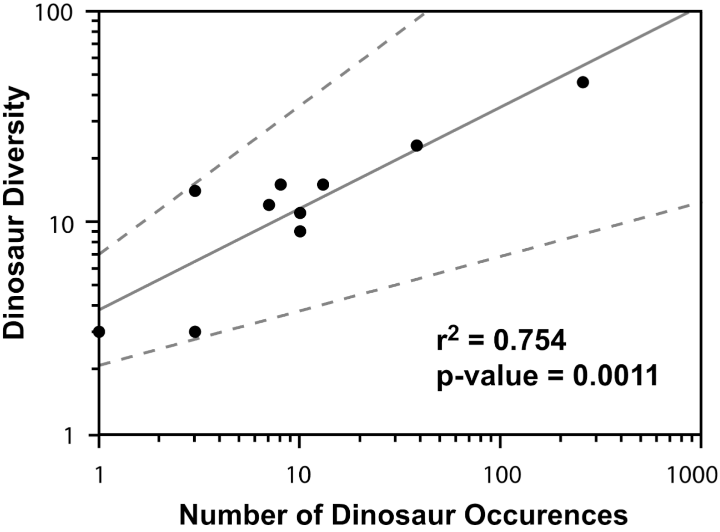

Figure 4:
Correlation between sampling intensity (number of dinosaur occurrences as derived from the Paleobiology Database) and species diversity (derived from our dataset) for all Canadian formations with three or more dinosaur species. Dashed lines indicate 95% confidence interval.

Holotypes

The number and location of Canadian dinosaur holotypes reflects the pattern of collection intensity and historical timing (Fig. 5). The CMN has the most valid holotypes (31, or half of all Canadian dinosaur holotypes), followed by the ROM (11), TMP (9), and AMNH (8). The NHM(UK), UALVP, and RSM each house only a single holotype. The high numbers of holotypes at the CMN, and to the lesser degree the AMNH and ROM, represent, in part, a "first-on-site" phenomenon for the Dinosaur Park and Horseshoe Canyon Formations, whereby the first institution to collect from a formation often ends up finding the most new taxa because most specimens discovered represent a new taxon. The number of holotypes at the TMP represents the more recent discoveries of other dinosaurs, often derived from different formations.

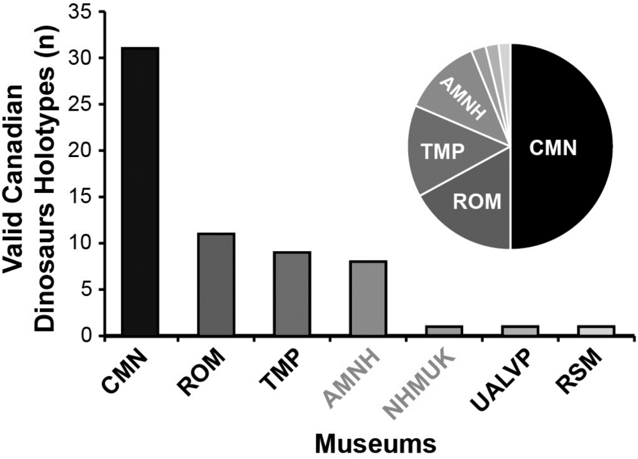

Figure 5:
Distribution of holotypes of Canadian dinosaurs in museum collections. Text in grey indicates museums outside of Canada.

Discussion

It is important to note that although the assemblage data are presented here at the formation scale (as is common practice in dinosaur palaeontology; e. g., Barrett *et al.* 2009), these often do not represent ecologically cohesive units, but rather time-averaged collections that might sample multiple faunas or communities. Recent work has shown that there are distinct taxonomic turnovers, and therefore biostratigraphic faunal zonation, within several formations that have both large samples and biostratigraphic data for analysis (Ryan & Evans 2005; Ryan *et al.* 2012a; Mallon *et al.* 2013; Eberth *et al.* 2013). Recent high-resolution biostratigraphic work on the Dinosaur Park Formation has revealed distinct faunal zonation within a deposition timeframe of less than 1.5 million years (Ryan & Evans 2005; Mallon *et al.* 2013). Faunal zones are also present within the Horseshoe Canyon Formation (Russell & Chamney 1967; Eberth *et al.* 2013), which represents approximately 4.5 million years of deposition. Therefore, taxa co-occurring in the same formation should not be assumed to be contemporaneous. These turnovers are also likely to be present in other more poorly sampled formations, particularly those that represent more than one million years of deposition, such as the Oldman Formation.

Dinosaur diversity

The majority of described Canadian dinosaur taxa are derived from a few well-sampled formations (i.e., Dinosaur Park, Horseshoe Canyon, Scollard, and Oldman), all of which have extensive outcrops along the Red Deer River Valley of Alberta. This river valley cuts through Late Cretaceous outcrop of Maastrichtian to Campanian age and has been the focus of much of the historic and current dinosaur field expeditions (Sternberg 1917; Sternberg 1950b; Russell 1966; Russell 1967b; Russell & Chamney 1967; Spalding 1999; Currie 2005a). As a result, nearly three-quarters (72%) of the named dinosaur species found in Canada have been discovered in this river valley. The intense sampling within the Red Deer River Valley has resulted in these formations representing some of the best-sampled and best-understood dinosaur assemblages in the world (Currie & Koppelhus 2005; Eberth *et al.* 2013). However, it also highlights how little is known about the diversity of the remaining dinosaur bearing formations in Alberta as well as the rest of Canada.

The apparent differences in the diversity of dinosaur assemblages (Fig. 2B) is almost certainly because of a combination of human meditated (e. g., sampling and research-intensity effects), taphonomic, and palaeobiological factors (for a review, see Upchurch *et al.* 2011). The most diverse formations are those with the highest abundance of fossil material (e. g., Dinosaur Park and Horseshoe Canyon) and, as a result, are characterised by longer and more intense collection histories (Fig. 4). Those with lower-diversity assemblages are often characterised by both less abundant and less well-preserved remains, which have, in part, resulted in less intense sampling.

Recent research has begun to specifically target less-fossiliferous, less-extensively exposed, and more difficult to access formations, which often represent either temporal or geographic areas outside of the well-sampled Red Deer River Valley. Within Alberta, these field surveys have concentrated on the Milk River and South Saskatchewan River Valleys of southern Alberta and the Grande Prairie region in the north. Recent multi-year collecting efforts have also been undertaken in the Frenchman River Valley of Southern Saskatchewan and in the subarctic and high arctic of Canada's northern territories. This fieldwork has resulted in the discovery of multiple new occurrences and new taxa (Nunez-Betelu *et al.* 2005; Ryan & Russell 2005; Ryan 2007; Arbour & Graves 2008; Currie *et al.* 2008; Larson 2008; Fanti & Miyashita 2009; Brown *et al.* 2011, 2013b; Evans *et al.* 2012, 2013; Ryan *et al.* 2012a, b; Larson & Currie 2013), and is improving our understanding of dinosaur diversity and biogeography in these poorly sampled areas and time periods within Canada. Despite this work, our knowledge of Canadian dinosaur diversity remains heavily biased towards the Late Cretaceous, with very few Triassic, Jurassic, and Early Cretaceous occurrences, and still relies heavily on deposits exposed in a small area of southern Alberta.

The high correlations, and slopes of approximately 1, between the generic and species diversity metrics indicate that generic diversity is a reasonable proxy for species diversity, at least for Late Cretaceous formations of Alberta (Fig. 3A). This result is not surprising because the vast majority of dinosaur genera are monospecific (Dodson 1990), a taxonomic practice that is common among dinosaur systematists. Although not the ideal scope for evolutionary studies (Brooks & McLennan 2002), the genus level is often used as a metric for dinosaur diversity (Dodson 1990; Wang & Dodson 2006; Benton 2008; Barrett *et al.* 2009) and its utility in this regard is verified by these results. The most practical of the diversity metrics (genera represented and species represented) have a slope of 1.16. This value is very similar to, but slightly above 1.00 and, because of the very high correlation ($r^2 = 0.99$) between the metrics, the lower and upper 95% confidence intervals of the slope (1.08 and 1.25) do not include 1.00. This suggests a slightly greater than one-to-one correlation between generic and species diversities, with a slope equal to that of the average number of species per genus of previous global dinosaur diversity analyses (1.1–1.2; Dodson 1990; Wang & Dodson 2006; Benton 2008, 2010) and reflects multiple species being present within single genera in the highly diverse Dinosaur Park Formation (specifically the large ornithischian taxa). As such, although generic diversity is a reasonable proxy for species diversity in most situations, this relationship can start to break down in highly diverse, heavily sampled formations, especially those that preserved faunal turnover events at the species level (Ryan & Evans 2005; Ryan *et al.* 2012a; Mallon *et al.* 2013). In contrast to the similarity in diversity patterns suggested by genera- and species-level metrics, the family-level metric does not correlate with generic or species diversity at high diversity. Family diversity, therefore, is not a good indicator of dinosaur diversity in well-sampled formations, although it might be appropriate for diversity studies at larger temporal and taxonomic scales (Kemp 1999; but see Brooks & McLennan 2002).

Patterns of discovery of new taxa

Comparison of the updated occurrence list to that of Ryan and Russell (2001) provides some interesting information on patterns of dinosaur discovery. All taxa named since 2001 can be characterised in two ways, either taxonomically (Ceratopsia: 57% of new taxa, with 43% being Ceratopsidae and 14% being Leptoceratopsidae) or by size class (small bodied [< ~100 kg] taxa: 50% of new taxa) (Fig. 6). Moreover, these two categories represent different aspects of the species-discovery curve, with ceratopsian discoveries often occurring in the early phase of discovery (some of the first taxa discovered in a formation) and small taxa more often found in the later phase (some of the most recent taxa found in well-sampled formations). Brown *et al.* (2013a) noted differences in both species discovery and description rates between large (> 60 kg) and small (< 60 kg) size classes in the Dinosaur Park Formation and suggested these might be present in other formations with similar presentational regimes.

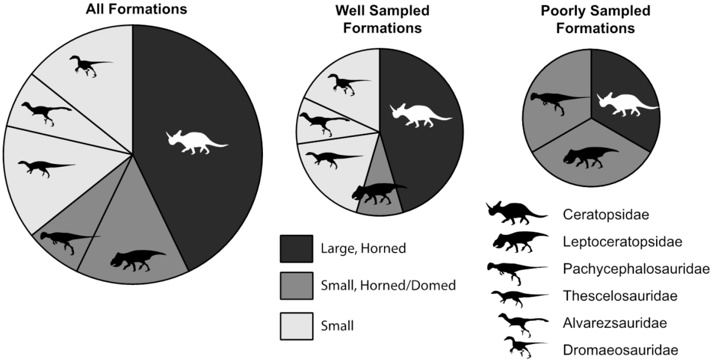

Figure 6:
Relative proportion of newly named dinosaur species (since 2001) at the family level as well as between well (Dinosaur Park, Oldman, Horseshoe Canyon, and Frenchman) and more poorly sampled formations (Milk River and Foremost). All newly named taxa belong to Ceratopsia or a size class of less than ~100kg. Ceratopsia and Pachycephalosauridae dominate dinosaur discoveries in poorly sampled formations, whereas small (and not taphonomically robust) taxa are found in the well-sampled formations.

Although exceptions exist (e. g., *Unescoceratops koppelhusae*, Dinosaur Park Formation), the majority of new ceratopsian discoveries often represent some of the first named taxa in either newly or poorly sampled formations (e. g., *Xenoceratops foremostensis*, Foremost Formation; *Gryphoceratops morrisoni*, Milk River Formation; and *Pachyrhinosaurus lakustai*, Wapiti Formation) or in poorly sampled stratigraphic intervals of otherwise reasonably well-known formations (e. g., *Albertaceratops nesmoi* and *Coronosaurus brinkmani*, both Oldman Formation; *Vagaceratops irvinensis*, Dinosaur Park Formation; and *Eotriceratops xerinsularis*, Horseshoe Canyon Formation). The early discovery and description of ceratopsian taxa can likely be at tributed to two distinct aspects of their fossil record. First, the majority of these taxa can be diagnosed by the ornamentation and morphology of isolated parietals, which are easily identified in the field, robust, and resistant to weathering. This first aspect is also shared with pachycephalosaurids, which might also explain their discovery and description in the early phase of the taxonomic sampling of formations (e. g., *Stegoceras validum* and '*Stegoceras*' *brevis*, both Dinosaur Park Formation; *Colepiocephale lambei*, Foremost Formation; and *Acrotholus audeti*, Milk River Formation) (Evans *et al.* 2013). Second, centrosaurine ceratopsids are frequently preserved in high-abundance, monodominant bone beds, probably accounting for their early discovery. The combination of high local abundance, resistance to taphonomic destruction, and highly diagnostic morphology often results in these animals being some of the first dinosaurs discovered and diagnosed in a formation or horizon. Additionally, partially because of this unique fossil record, ceratopsians (particularly centrosaurines) have experienced greater research activity recently compared to other ornithischians (Ryan *et al.* 2010b), helping to explain the recent increase in their diversity (Sampson & Loewen 2010).

The increased rate of description of small-bodied taxa (< ~100 kg) since 2001 represents the opposite trend to that described above. Small taxa are most often described in the latter phase of discovery in well-sampled formations (e. g., *Hesperonychus elizabethae* and *Unescoceratops koppelhusae*, both Dinosaur Park Formation; *Albertonykus borealis* and *Atrociraptor marshalli*, both Horseshoe Canyon Formation; and *Albertadromeus syntarsus*, Oldman Formation). Exceptions to this pattern do exist (e. g., *Gryphoceratops morrisoni* or *Acrotholus audeti*), but these taxa are among those diagnosable to species level based on robust isolated elements.

This delayed recognition of small taxa can be explained by a combination of taphonomic and collection biases. The extent of these biases has been illustrated by Brown *et al.* (2013a, b), using the Dinosaur Park Formation as a model and shows that small dinosaurs (< ~60 kg) are less likely to be complete and/or articulated and also take significantly longer to be found and described than large dinosaurs. This is likely a combination of smaller skeletons being more prone to chemical and physical weathering, carnivory, and scavenging, thereby reducing their probability and quality of fossilisation. Relative to large material, smaller material can also be more difficult to discover and identify in the field. The results indicate that the diversity of all formations (including those that are already highly sampled) will likely increase with continued sampling and that the new taxa will be dominated by small-bodied animals. A large number of taxa are also likely awaiting discovery in poorly sampled formations. In both cases, recognition of this diversity awaits discovery of further diagnostic material.

Provinciality and endemicity

Recent discussions (Lehman 1987, 1997, 2001; Sampson *et al.* 2010; Vavrek & Larsson 2010; Brown & Druckenmiller 2011; Gates *et al.* 2012) have concentrated on issues of provinciality and/or endemicity of dinosaur faunas in the Late Cretaceous of North America, with many authors suggesting that Campanian taxa (particularly ornithischians) are endemic to regions of Laramidia. Analysis of the occurrence data set (see Appendix) reveals that the majority of ornithischian taxa that can be confidently identified to species level occur within only a single formation. At face value, this would suggest a high degree of formational endemicity within dinosaur species caused by restricted geographic ranges and temporal occurrences. However, it is still unclear in most cases how much of this endemicity is because of restricted geographic range and how much is because of a lack of, or poor sampling in, contemporaneous formations.

Recent work has demonstrated turnover in ornithischian taxa, and likely entire faunas, within single formations (Ryan & Evans 2005; Ryan *et al.* 2012a; Mallon *et al.* 2013; Eberth *et al.* 2013). In light of this, the non-persistence of single dinosaur species in a geographically consistent but temporally successive series of formations should not be surprising (this explains the majority of the formational endemicity), but the question of endemicity is more about geographic range than temporal longevity.

Whether these taxa are limited in their geographic range is often a more difficult question to answer because the geographic coverage of outcrop of any particular temporal interval is sporadic. Recent research has revealed that multiple Campanian ornithischian species (e. g., *Centrosaurus apertus, Chasmosaurus russelli, Vagaceratops irvinensis,* and *Lambeosaurus magnicristatus*) have geographic ranges spanning from Dinosaur Provincial Park to the Milk River area of southern Alberta (~180 km) and sometimes as far east as Saskatchewan (Holmes *et al.* 2001; Evans 2007; Ryan *et al.* 2010c; Tokaryk *et al.* 2012; Evans *et al.* in press). Furthermore, at least one taxon, *Centrosaurus apertus*, is represented by both articulated and bone-bed material in both the Dinosaur Park and Oldman Formations (Ryan *et al.* 2010c). The apparent wide geographic ranges and long temporal durations of certain theropod tooth morphotypes, based on isolated teeth, has been documented and suggests that these small theropods might be less spatially and temporally restricted than their ornithischian counterparts (Baszio 1997b; Fiorillo & Gangloff 2000; Sankey 2001; Weishampel *et al.* 2004; Fanti & Miyashita 2009). However, recent work by Larson and Currie (2013) has shown that at least some isolated small-theropod teeth with previously reported large temporal spans can be differentiated between formations using morphometric analysis. This indicates that these and other distinct theropod taxa unique to particular formations likely exist, but have not yet been diagnosed because of a lack of non-dental material. Interestingly, these differences in teeth might not occur just in time-successive formations, but also in penecontemporaneous formations, suggesting a reduced range of these tooth morphotypes both spatially and temporally.

A more complete understanding of the patterns of provinciality or endemicity of both ornithischian and theropod taxa requires greater and more even sampling of formations as well as the discovery and description of more diagnostic material. Until this can be achieved, many of the patterns cannot be confidently differentiated from those predicted because of inadequate or unequal sampling (Vavrek & Larsson 2010).

Future directions

An improved knowledge of the chronostratigraphy and intraformational biostratigraphy of southern Alberta combined with long-term, well-supported field programs will enable researchers to investigate new and established regions of the province. This will no doubt lead to significant new fossil finds that can be used to better understand dinosaur diversity. Recent discoveries of new ceratopsians within the lower (regressive) part of Belly River Group

(Ryan 2007; Ryan *et al.* 2012b), where the remains of few dinosaur taxa have been identified below the family-level, likely foreshadow the recovery of new faunas comprising distinct species of other contemporaneous groups, such as hadrosaurids, ankylosaurs, tyrannosaurs, and ornithomimids.

The most exciting future finds will likely be centred on poorly known areas outside of southern Alberta, where the richness of the fossil record is not yet understood. The Canadian Arctic is now more accessible, with extensive Mesozoic outcrops ranging from the Triassic through the latest Cretaceous. Dinosaur remains have been discovered on Bylot Island (Kanguk Formation), Axel Heiberg Island (Kanguk Formation), and potentially Cameron Island (Heiberg Formation) in the high latitude Canadian Arctic Archipelago as well as in the Yukon (Bonnet Plume Formation) and central Northwest Territories (Summit Creek Formation) (Fig. 1; Evans *et al.* 2012). Huge potential for future discoveries exists as climate change makes remote arctic areas more accessible and lengthens the summer field season. We anticipate future discoveries here in the near future. British Columbia represents a geomorphologically complex area that includes terrestrial and near-shore Mesozoic deposits that should produce dinosaurs. Work in the interior of the province (Arbour & Graves 2008), Vancouver Island (Ludvigsen 1996), and near Tumbler Ridge (Rylaarsdam *et al.* 2006) will surely reveal a greatly expanded dinosaur skeletal record for this province within the next decade.

With the exception of the Triassic–Early Jurassic of Nova Scotia, the eastern half of the country has produced no dinosaur fossils. This is because of a dearth of Mesozoic terrestrial strata in the region of the Canadian Shield and southern Ontario (Fig. 1). However, rocks of the Early Cretaceous Mattagami Formation that outcrop in the Moose River Basin (James Bay Lowlands) have produced excellent macroplant fossils deposited in a terrestrial depositional setting (Hopkins & Sweet 1976; Norris *et al.* 1976), suggesting that there is potential for the first Cretaceous dinosaurs to be discovered in the Eastern provinces.

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Literature cited

Arbour V.M., Burns M.E. & Sissons R.L. (2009). A redescription of the ankylosaurid dinosaur *Dyoplosaurus acutosquameus* Parks, 1924 (Ornithischia: Ankylosauria) and a revision of the genus. *J. Vertebr. Paleontol.*, 29, 1117–1135.

Arbour V.M. & Graves M.C. (2008). An ornithischian dinosaur from the Sustut Basin, north-central British Columbia, Canada. *Can. J. Earth Sci.*, 45, 457–463.

Barrett P.M., McGowan A.J. & Page V. (2009). Dinosaur diversity and the rock record. *Proc. Roy. Soc. Lond. Ser. B*, 276, 2667–2674.

Baszio S. (1997a). Palaeo-ecology of dinosaur assemblages throughout the Late Cretaceous of South Alberta, Canada. *Cour. Forschungsinst.*, 196, 1–31.

Baszio S. (1997b). Systematic palaeontology of isolated dinosaur teeth from the Latest Cretaceous of South Alberta, Canada. *Cour. Forschungsinst.*, 196, 33–77.

Beland P. & Russell D.A. (1978). Paleoecology of Dinosaur Provincial Park (Cretaceous), Alberta, interpreted from the distribution of articulated vertebrate remains. *Can. J. Earth Sci.*, 16, 250–255.

Bell P.R., Sissons R.L., Burns M.E., Fanti F. & Currie P.J. (In press). New hadrosaurine material from the upper Campanian Wapiti Formation, west-central Alberta. In: *The Hadrosaurs: Proceedings of the International Hadrosaur Symposium* (eds. Eberth DA & Evans DC). Indiana University Press Bloomington.

Benton M.J. (2008). How to find a dinosaur, and the role of synonymy in biodiversity studies. *Palaeobiol.*, 34, 516–533.

Benton M.J. (2010). Naming dinosaur species: the performance of prolific authors. *J. Vertebr. Paleontol.*, 30, 1478–1485.

Braman D.R. (ed.) (2007). *Ceratopsian Symposium Short Papers, Abstracts, and Programs*. Royal Tyrrell Museum, Drumheller, Alberta.

Braman D.R., Eberth D.A., Evans D.C. & Taylor W. (eds.) (2011). *Hadrosaur Symposium Abstract Volume*. Royal Tyrrell Museum, Drumheller, Alberta.

Braman D.R., Therrien F., Koppelhus E.B. & Taylor W. (2005). Dinosaur Park Symposium short papers, abstracts and program. In: *Dinosaur Park Symposium*. Royal Tyrrell Museum Drumheller, Alberta, p. 152.

Briggs D.E. G. & Fortey R.A. (2005). Wonderful strife: systematics, stem groups, and the phylogenetic signal of the Cambrian radiation. *Palaeobiol.*, 31, 94–112.

Brinkman D.B., Russell A.P., Eberth D.A. & Peng J. (2004). Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 213, 295–313.

Brooks D.R. & McLennan D.A. (2002). *The Nature of Diversity: an Evolutionary Voyage of Discovery*. University of Chicago Press, Chicago.

Brown B. (1912). A crested dinosaur from the Edmonton Cretaceous. *Trans. Zool. Soc. Lond.*, 11, 131–139.

Brown B. (1913). A new trachodont dinosaur, *Hypacrosaurus*, from the Edmonton Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.*, 32, 395–406.

Brown B. (1914a). A complete skull of *Monoclonius* for the Belly River Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.*, 33, 539–548.

Brown B. (1914b). *Anchiceratops*, a new genus of horned dinosaurs from the Edmonton Cretaceous of Alberta. With discussion of the origin of the ceratopsian crest and the brain casts of *Anchiceratops* and *Trachodon*. *Bull. Am. Mus. Nat. Hist.*, 33, 539–548.

Brown B. (1914c). *Corythosaurus casuarius*, a new crested dinosaur from the Belly River Cretaceous, with provisional classification of the family Trachodontidae. *Bull. Am. Mus. Nat. Hist.*, 33, 559–565.

Brown B. (1914d). *Leptoceratops*, a new genus of Ceratopsia from the Edmonton Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.*, 33, 567–580.

Brown B. (1916). A new crested trachodont dinosaur *Prosaurolophus maximus*. *Bull. Am. Mus. Nat. Hist.*, 35, 701–708.

Brown B. (1917). A complete skeleton of the horned dinosaur *Monoclonius*, and description of a second skeleton showing skin impressions. *Bull. Am. Mus. Nat. Hist.*, 37, 281–306.

Brown B. & Kaisen P.C. (1908) The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. *Bull. Am. Mus. Nat. Hist.*, 24, 187–201.

Brown B. & Schlaikjer E.M. (1943). A study of the troodont dinosaurs with the description of a new genus and four new species. *Bull. Am. Mus. Nat. Hist.*, 82, 115–150.

Brown C.M., Boyd C.A. & Russell A.P. (2011). A new basal ornithopod dinosaur (Frenchman Formation, Saskatchewan, Canada), and implications for late Maastrichtian ornithischian diversity in North America. *Zool. J. Linn. Soc.*, 163, 1157–1198.

Brown C.M., Campione N.E., Giacomini H.C., O'Brien L.J., Vavrek M.J. & Evans D.C. (In press). Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: a comment on Codron *et al.* (2012). *Biol. Lett.*, doi:10.1098/rsbl.2012.0582.

Brown C.M. & Druckenmiller P.S. (2011). Basal ornithopod (Dinosauria: Ornithischia) teeth from the Prince Creek Formation (early Maastrichtian) of Alaska. *Can. J. Earth Sci.*, 48, 1342–1354.

Brown C.M., Evans D.C., Campione N.E., O'Brien L.J. & Eberth D.A. (2013a). Evidence for taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial alluvial-paralic system. *Palaeogeogr., Palaeoclimatol., Palaeontol.*, 372, 108–122.

Brown C.M., Russell A.P., Evans D.C. & Ryan M.J. (2013b). New data on the diversity and abundance of small-bodied ornithopods (Dinosauria: Ornithischia) from the Belly River Group (Campanian) of Alberta. *J. Vertebr. Paleontol.*, 33, 495–520.

Campione N.E., Brink K.S., Freedman E.A., McGarrity C.T. & Evans D.C. (2013). '*Glishades ericksoni*', an indeterminate juvenile hadrosaurid from the Two Medicine Formation of Montana: implications for hadrosauroid diversity in the latest Cretaceous (Campanian-Maastrichtian) of western North America. *Palaeobiodivers. Palaeoenviron.*, 93, 65–75.

Campione N.E. & Evans D.C. (2011). Cranial growth and variation in Edmontosaurs (Dinosauria: Hadrosauridae): implications for latest Cretaceous megaherbivore diversity in North America. *PLoS ONE*, 6, e25186.

Carpenter K. (1982). Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and a description of a new species of theropod. *Contrib. Geology, Univ. Wyom.*, 20, 123–134.

Carpenter K. (2004). Redescription of *Ankylosaurus magniventris* Brown 1908 (Ankylosauridae) from the Upper Cretaceous of the Western Interior of North America. *Can. J. Earth Sci.*, 41, 961–986.

Chinnery B. (2004). Description of *Prenoceratops pieganensis* gen et. sp. nov. (Dinosauria: Neoceratopsia) from the Two Medicine Formation of Montana. *J. Vertebr. Paleontol.*, 24, 572–590.

Cope E.D. (1876a). Descriptions of some vertebrate remains from the Fort Union beds of Montana. *Proc. Acad. Nat. Sci. Phila.*, 28, 248–261.

Cope E.D. (1876b). On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. *Proc. Acad. Nat. Sci. Phila.*, 28, 340–359.

Cracraft J. (1971). Caenagnathiformes: cretaceous birds convergent in jaw mechanism to dicynodont reptiles. *J. Palaeontol.*, 45, 805–809.

Currie P.J. (1987). Theropods of the Judith River Formation of Dinosaur Provincial Park, Alberta, Canada. In: *Fourth Symposium on Mesozoic Terrestrial Ecosystems.* (eds. Currie PJ & Koster EH). Occasional Paper of the Royal Tyrrell Museum of Palaeontology 3 Drumheller, 52–60.

Currie P.J. (2005a). History of research. In: *Dinosaur Provincial Park: Spectacular Ancient Ecosystem Revealed* (eds. Currie PJ & Koppelhus EB). Indiana University Press Indianapolis, 3–33.

Currie P.J. (2005b). Theropods, including birds. In: *Dinosaur Provincial Park: a Spectacular Ancient Ecosystem Revealed* (eds. Currie PJ & Koppelhus EB). Indiana University Press Indianapolis, 367–397.

Currie P.J., Hurum J.H. & Sabath K. (2003). Skull structure and evolution in tyrannosaurid dinosaurs. *Acta Palaeontol. Pol.*, 48, 227–234.

Currie P.J. & Koppelhus E.B. (eds.) (2005). *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*. Bloomington: Indiana University Press, Bloomington, Indian.

Currie P.J., Langston J.W. & Tanke D.H. (2008). A new species of *Pachyrhinosaurus* (Dinosauria, Ceratopsidae) from the Upper Cretaceous of Alberta, Canada. In: *A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta* (eds. Currie PJ, Langston JW & Tanke DH). NRC Research Press Ottawa, 1–108.

Currie P.J., Nadon G.C. & Lockley M.G. (1991). Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. *Can. J. Earth Sci.*, 28, 102–115.

Currie P.J., Rigby J.K.J. & Sloan R.E. (1990). Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: *Dinosaur Systematics: Approaches and Perspectives* (eds. Carpenter K & Currie PJ). Cambridge University Press Cambridge, 107–125.

Currie P.J. & Varricchio D.J. (2004). A new dromaeosaurid from the Horseshoe Canyon Formation (upper Cretaceous) of Alberta, Canada. In: *Feathered Dinosaurs* (eds. Currie PJ, Koppelhus EB, Shugar MA & Wright JL). Indiana University Press Bloomington, 112–132.

Dodson P. (1971). Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 10, 21–74.

Dodson P. (1990). Counting dinosaurs: how many kinds were there? *Proc. Natl. Acad. Sci. USA*, 87, 7908–7612.

Eberth D.A., Braman D.R. & Tokaryk T.T. (1990). Stratigraphy, sedimentology and vertebrate palaeontology of the Judith River Formation (Campanian) near Muddy Lake, west-central Saskatchewan. *Bull. Can. Petrol. Geol.*, 38, 387–406.

Eberth D.A., Evans D.C., Brinkman D., Therrien F., Tanke D.H. & Russell L.S. (2013). Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climate influence. *Can. J. Earth Sci.*, 50, 701–726.

Evans D.C. (2007). *Ontogeny and Evolution of Lambeosaurine Dinosaurs (Ornithischia: Hadrosauridae)*. Ph.D. dissertation. University of Toronto, Toronto, Canada.

Evans D.C., McGarrity C.T. & Ryan M.J. (In press). A new skull of *Prosaurolophus maximus* from southeastern Alberta, and the spacio-temporal distribution of faunal zones in the Dinosaur Park Formation. In: *The Hadrosaurs: Proceedings of the International Hadrosaur Symposium* (eds. Eberth DA & Evans DC). Indiana University Press Bloomington.

Evans D.C., Schott R.K., Larson D.W., Brown C.M. & Ryan M.J. (2013). The oldest North American pachycephalosaurid and the hidden diversity of small-bodied ornithischian dinosaurs. *Nature Commun.*, 4, 1828.

Evans D.C., Vavrek M.J., Braman D.R., Campione N.E., Dececchi T.A., Zazula G.D. & Sues H.D. (2012). Vertebrate fossils (Dinosauria) from the Bonnet Plume Formation, Yukon Territory, Canada. *Can. J. Earth Sci.*, 49, 396–411.

Falcon-Lang H.J. (2006). A history of research at the Joggins Fossil Cliffs of Nova Scotia, Canada, the world's finest Pennsylvanian section. *Proc. Geol. Assoc.*, 117, 377–392.

Falcon-Lang H.J. & Calder J.H. (2004). Feature: UNESCO World Heritage and the Joggins cliffs of Nova Scotia. *Geol. Today*, 20, 139–143.

Fanti F. & Miyashita T. (2009). A high latitude vertebrate fossil assemblage from the Late Cretaceous of west-central Alberta, Canada: evidence for dinosaur nesting and vertebrate latitudinal gradient. *Palaeogeogr., Palaeoclimatol., Palaeontol.*, 275, 37–53.

Farke A.A., Ryan M.J., Barrett P.M., Tanke D.H., Braman D.R., Loewen M.A. & Graham M.R. (2011). A new centrosaurine from the Late Cretaceous of Alberta, Canada, and the evolution of parietal ornamentation in horned dinosaurs. *Acta Palaeontol. Pol.*, 56, 691–702.

Fedak T.J. (2006). *Description and Evolutionary Significance of the Sauropodomorph Dinosaurs from the Early Jurassic (Hettangian) McCoy Brook Formation*. Ph.D. dissertation. Dalhousie University, Halifax, Canada.

Fiorillo A.R. & Gangloff R.A. (2000). Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on arctic dinosaur palaeoecology. *J. Vertebr. Paleontol.*, 20, 675–682.

Forster C.A. (1996). New information on the skull of *Triceratops*. *J. Vertebr. Paleontol.*, 16, 246–258.

Galton P.M. & Sues H.-D. (1983). New data on pachycephalosaurid dinosaurs (Reptilia: Ornithischia) from North America. *Can. J. Earth Sci.*, 20, 462–472.

Gates T.A., Prieto-Márquez A. & Zanno L.E. (2012). Mountain building triggered Late Cretaceous North American megaherbivore dinosaur radiation. *PLoS ONE*, 7, e42135.

Gilmore C.W. (1923). A new species of *Corythosaurus* with notes on other Belly River Dinosauria. *Can. Field Nat.*, 37, 46–52.

Gilmore C.W. (1924a). A new coelurid dinosaur from the Belly River Cretaceous of Alberta. *Can. Dept. Mines (Geol. Surv. Can.) Bull.*, 38, 1–12.

Gilmore C.W. (1924b). A new species of *Laosaurus*, an ornithischian dinosaur from the Cretaceous of Alberta *Proc. Trans. Roy. Soc. Can.*, 18, 1–7.

Gilmore C.W. (1930). On dinosaurian reptiles from the Two Medicine Formation of Montana. *US Natl. Mus., Proc.*, 77, 1–39.

Holmes R.B., Forster C.A., Ryan M.J. & Shepherd K.M. (2001). A new species of *Chasmosaurus* (Dinosauria: Ceratopsia) from the Dinosaur Park Formation of southern Alberta. *Can. J. Earth Sci.*, 38, 1423–1438.

Hopkins W.S. & Sweet A.R. (1976). Miospores and megaspores from the lower Cretaceous Mattagami Formation of Ontario. *Geol. Surv. Can. Bull.*, 256, 55–71.

Horner J.R. & Currie P.J. (1994). Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In: *Dinosaur Eggs and Babies* (eds. Carpenter K, Hirsch KF & Horner JR). Cambridge University Press New York, 312–336.

Irmis R.B. (2007). Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *J. Vertebr. Paleontol.*, 27, 350–361.

Kemp T. (1999). *Fossils and Evolution*. Oxford University Press, Oxford.

Lambe L.M. (1902). New genera and species from the Belly River series (mid-Cretaceous). *Contrib. Can. Palaeontol., Geol. Surv. Can.*, 3, 25–81.

Lambe L.M. (1910). Note on the parietal crest of *Centrosaurus apertus* and a new proposed generic name for *Stereocephalus tutus*. *Ottawa Nat.*, 24, 149–151.

Lambe L.M. (1913). A new genus and species of Ceratopsia from the Belly River Formation of Alberta. *Ottawa Nat.*, 27, 109–116.

Lambe L.M. (1914a). On a new genus and species of carnivorous dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Stephanosaurus marginatus* from the same horizon. *Ottawa Nat.*, 28, 145–155.

Lambe L.M. (1914b). On *Gryposaurus notabilis*, a new genus and species of trachodont dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Chasmosaurus belli*. *Ottawa Nat.*, 27, 145–160.

Lambe L.M. (1915). On *Eoceratops canadensis*, gen. nov., with remarks on other genera of Cretaceous horned dinosaurs. *Can. Geol. Surv., Mus. Bull. No. 12, Geol. Sect.*, 24, 1–49.

Lambe L.M. (1917). A new genus and species of crestless hadrosaur from the Edmonton Formation of Alberta. *Ottawa Nat.*, 31, 65–73.

Lambe L.M. (1918). The Cretaceous genus *Stegoceras*, typifying a new family referred provisionally to the Stegosauria. *Trans. Roy. Soc. Can.*, 12, 23–36.

Lambe L.M. (1919). Description of a new genus and species (*Panoplosaurus mirus*) of armored dinosaur from the Belly River Beds of Alberta. *Trans. Roy. Soc. Can. Ser.*, 3, 39–50.

Langston W. (1965). *Pre-Cenozoic Vertebrate Palaeontology in Alberta: its Past and Future*. University of Alberta Department of Geology Bulletin.

Langston W., Jr. (1975). The ceratopsian dinosaurs and associated lower vertebrates from the St. Mary River formation (Maestrichtian) at Scabby Butte, southern Alberta. *Can. J. Earth Sci.*, 12, 1576–1608.

Larson D.W. (2008). Diversity and variation of theropod dinosaur teeth from the uppermost Santonian Milk River Formation (Upper Cretaceous), Alberta: a quantitative method supporting identification of the oldest dinosaur tooth assemblage in Canada. *Can. J. Earth Sci.*, 45, 1455–1468.

Larson D.W., Campione N.E., Brown C.M., Evans D.C. & Ryan M.J. (In press). Hadrosauroid material from the Santonian Milk River Formation of southern Alberta, Canada. In: *Proceedings of the International Hadrosaur Symposium* (eds. Evans DC & Eberth DA). Indiana University Press Bloomington.

Larson D.W. & Currie P.J. (2013). Multivariate analyses of small theropod dinosaur teeth and implications for palaeoecological turnover through time. *PLoS ONE*, 8, e54329.

Lehman T.M. (1987). Late Maastrichtian palaeoenvironments and dinosaur biogeography in the western interior of North America. *Palaeogeogr., Palaeoclimatol., Palaeontol.*, 60, 187–217.

Lehman T.M. (1997). Late Campanian dinosaur biogeography in the Western Interior of North America. In: *Dinofest International: Proceedings of a Symposium Sponsored by Arizona State University* (eds. Wolberg DL, Stump E & Rosenberg GD). Academy of Natural Sciences Philadelphia, 223–240.

Lehman T.M. (2001). Late Cretaceous dinosaur provinciality. In: *Mesozoic Vertebrate Life* (eds. Tanke DH, Carpenter K & Skrepnick MW). Indiana University Press Bloomington, 310–328.

Leidy J. (1856). Notices of remains of extinct Reptiles and Fishes, discovered by Dr. F. V. Hayden in the Bad Lands of the Judith River, Nebraska Territory. *Proc. Acad. Nat. Sci. Phila.*, 8, 72–73.

Longrich N.R. (2008). A new, large ornithomimid from Cretaceous Dinosaur Park Formation of Alberta, Canada; implications for the study of dissociated dinosaur remains. *Palaeontol.*, 51, 983–997.

Longrich N.R. & Currie P.J. (2009a). A microraptorine (Dinosauria–Dromaeosauridae) from the Late Cretaceous of North America. *Proc. Natl. Acad. Sci. USA*, 106, 5002–5007.

Longrich N.R. & Currie P.J. (2009b). *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretac. Res.*, 30, 239–252.

Ludvigsen R. (1996). Ancient saurians: Cretaceous reptiles of Vancouver Island. In: *Life in Stone: a Natural History of British Columbia's Fossils* (ed. Ludvigsen R). UBC Press Vancouver, 156–166.

Makovicky P.J. (2001). A *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsia) braincase from the Horseshoe Canyon. In: *Mesozoic Vertebrate Life* (eds. Tanke DH & Carpenter K). Indiana University Press Bloomington, 243–262.

Makovicky P.J. (2010). A redescription of the *Montanoceratops cerorhynchus* holotype, with a review of referred material. In: *New Perspectives on Horned Dinosaurs: the Royal Tyrrell Museum Ceratopsian Symposium* (eds. Ryan MJ, Chinnery-Allgeier BJ & Eberth DA). Indian University Press Bloomington, 68–82.

Mallon J.C., Evans D.C., Ryan M.J. & Anderson J.S. (2013). Megaherbivorous dinosaur turnover in the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 350–352, 124–138.

Marsh O.C. (1881). Principal characters of American Jurassic dinosaurs. Part IV. Spinal cord, pelvis and limbs of *Stegosaurus*. *Am. J. Sci.*, *Ser. 3*, 21, 167–170.

Marsh O.C. (1889). Notice of new American dinosaurs. *Am. J. Sci.*, *Ser. 3*, 37, 334–336.

Marsh O.C. (1890). Description of new dinosaurian reptiles. *Am. J. Sci.*, 39, 81–86.

Marsh O.C. (1892). *Notice of New Reptiles from the Laramie Formation*. Yale University.

Matthew W.D. & Brown B. (1922). The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.*, 46, 357–385.

McCrea R.T. & Buckley L.G. (2010). First results from a new dinosaur excavation from northeastern British Columbia. *BC Palaeontol. All. Bull.*, 54, 3–10.

Miyashita T., Currie P.J. & Chinnery-Allgeier B.J. (2010). First basal neoceratopsian from the Oldman Formation (Belly River Group), southern Alberta. In: *New Perspectives on Horned Dinosaurs: the Royal Tyrrell Museum Ceratopsian Symposium* (eds. Ryan MJ, Chinnery-Allgeier BJ & Eberth DA). Indiana University Press Bloomington, 83–90.

Morris S.C. (1992). Burgess Shale-type faunas in the context of the 'Cambrian explosion': a review. *J. Geol. Soc.*, 149, 631–636.

Narbonne G.M. (2005). The Ediacara biota: neoproterozoic origin of animals and their ecosystems. *Annu. Rev. Earth Planet. Sci.*, 33, 421–442.

Nesbitt S.J., Irmis R.B. & Parker W.G. (2007). A critical re-evaluation of the Late Triassic dinosaur taxa of North America. *J. Syst. Palaeontol.*, 5, 209–243.

Norris G., Telford P.G. & Vos M.A. (1976). An Albian microflora from the Mattagami Formation, James Bay Lowlands, Ontario. *Can. J. Earth Sci.*, 13, 400–403.

Nunez-Betelu L.M., Hills L.V. & Currie P.J. (2005). The first hadrosaur from the Late Cretaceous of Axel Heiburg Island, Canadian Arctic archipelago. In: *Dinosaur Park Symposium: Short Papers, Abstracts, and Program* (eds. Braman DR, Therrien F, Koppelhus EB & Taylor W). Special Publication of the Royal Tyrrell Museum Drumheller, 69–72.

Olsen P.E., Shubin N. & Anders M.H. (1987). New Early Jurassic tetrapod assemblages constrain Triassic-Jurassic tetrapod extinction event. *Science*, 237, 1025–1029.

Osborn H.F. (1905). *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bull. Am. Mus. Nat. Hist.*, 21, 259–265.

Osborn H.F. (1917). Skeletal adaptations of Ornitholestes, Struthiomimus, Tyrannosaurus. *Bull. Am. Mus. Nat. Hist.*, 35, 733–771.

Parks W.A. (1920). *The osteology of the trachodont dinosaur* Kritosaurus incurvimanus. University of Toronto Studies, Geological Series, 11, Toronto.

Parks W.A. (1922). Parasaurolophus walkeri*, a new genus and species of crested trachodont dinosaur*. University of Toronto Studies, Geological Series, 13, Toronto.

Parks W.A. (1923). Corythosaurus intermedius*, a new species of trachodont Dinosaur*. University of Toronto Studies, Geological Series, 15, Toronto.

Parks W.A. (1925). Arrhinoceratops brachyops*, a new genus and species of Ceratopsia from the Edmonton Formation of Alberta*. University of Toronto Studies, Geological Series, 19, Toronto.

Parks W.A. (1926). Thescelosaurus warreni*, a new species of orthopodous dinosaur from the Edmonton formation of Alberta*. University Toronto Studies, Geological Series, 21, Toronto.

Parks W.A. (1928). Struthiomimus samueli*, a new species of Orithomimidae from the Belly River Formation of Alberta*. University of Toronto Studies, Geological Series, 26, Toronto.

Parks W.A. (1931). *A new genus and two new species of trachodont dinosaurs from the Belly River Formation of Alberta*. University of Toronto Studies, Geological Series, 31, Toronto.

Parks W.A. (1933). *New species of dinosaurs and turtles from the Upper Cretaceous formations of Alberta*. University of Toronto Studies, Geological Series, 34, Toronto.

Parks W.A. (1935). *New species of trachodont dinosaurs from the Cretaceous formations of Alberta with notes on other species*. University of Toronto Studies, Geological Series, 37, Toronto.

Russell D.A. (1967a). A census of dinosaur specimens collected in western Canada. *Natl. Mus. Can. Nat. Hist. Pap.* 36, 1–13.

Russell D.A. (1967b). The Dinosaurs of Canada. *Can. Geogr. J.*, 75, 44–51.

Russell D.A. (1972). Ostrich dinosaurs from the Late Cretaceous of western Canada. *Can. J. Earth Sci.*, 9, 375–402.

Russell D.A. (1977). *A Vanished World: the Dinosaurs of Western Canada*. National Museum of Natural Sciences, Ottawa, Canada.

Russell D.A. (1984). *A Check List of the Families and Genera of North American Dinosaurs*. National Museums of Canada, National Museum of Natural Sciences, Ottawa, Canada.

Russell D.A. (1990). Mesozoic vertebrates of Arctic Canada. In: *Canada's Missing Dimension: Science and History in the Canadian Arctic Islands* (ed. Harington CR). Canadian Museum of Nature Ottawa, Canada, 81–89.

Russell D.A. & Chamney T.P. (1967). Notes of the biostratigraphy of dinosaurian and microfossil faunas in the Edmonton Formation (Cretaceous), Alberta. *Natl. Mus. Can., Nat. Hist. Pap.*, 35, 1–22.

Russell L.S. (1935). Fauna of the upper Milk River beds, Southern Alberta. *Trans. Roy. Soc. Can.* 4, 115–128.

Russell L.S. (1949). The relationships of the Alberta Cretaceous dinosaur *"Laosaurus" minimus* Gilmore. *J. Paleontol.*, 23, 518–520.

Russell L.S. (1966). Dinosaur hunting in western Canada. *Roy. Ont. Mus. Life Sci. Contrib.*, 70, 1–37.

Ryan M., Eberth D.A., Brinkman D., Currie P.J. & Tanke D.H. (2010a). A new *Pachycephalosaurus*-like ceratopsid from the upper Dinosaur Park Formation (Late Campanian) of Southern Alberta, Canada. In: *New Perspectives on Horned Dinosaurs: the Royal Tyrrell Museum Ceratopsian Symposium* (eds. Ryan M, Chinnery-Algeier BJ & Eberth DA). Indiana University Press Bloomington, 141–155.

Ryan M., Evans D.C., Currie P.J., Brown C.M. & Brinkman D. (2012). New leptoceratopsids from the Upper Cretaceous of Alberta, Canada. *Cretac. Res.*, 35, 69–80.

Ryan M.J. (2007). A new basal centrosaurine ceratopsid from the Oldman Formation, Southeastern Alberta. *J. Palaeontol.*, 81, 376–396.

Ryan M.J., Chinnery-Allgeier B.J. & Eberth D.A. (eds.) (2010b). *New Perspectives on Horned Dinosaurs: the Tyrrell Museum Ceratopsian Symposium*. Indiana University Press, Bloomington.

Ryan M.J. & Evans D.C. (2005). Ornithischian dinosaurs. In: *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed* (eds. Currie PJ & Koppelhus EB). Indiana University Press Indianapolis, 312–348.

Ryan M.J., Evans D.C., Brown C.M., Scott E. & Chiba K. (2010c). Palaeobiogeographic range of *Centrosaurus apertus* (Ornithischia: Ceratopsidae), with implications for Late Cretaceous dinosaur provinciality and evolution. *J. Vertebr. Paleonotol.*, 28, 154A–155A.

Ryan M.J., Evans D.C., Currie P.J., Brown C.M. & Brinkman D. (2012a). New leptoceratopsids from the Upper Cretaceous of Alberta, Canada. *Cretac. Res.*, 35, 69–80.

Ryan M.J., Evans D.C. & Shepherd K.M. (2012b). A new ceratopsid from the Foremost Formation (middle Campanian) of Alberta. *Can. J. Earth Sci.*, 49, 1251–1262.

Ryan M.J. & Russell A.P. (2001). Dinosaurs of Alberta (exclusive of Aves). In: *Mesozoic Vertebrate Life* (eds. Tanke DH, Carpenter K & Skrepnick MW). Indiana University Press Bloomington, 279–297.

Ryan M.J. & Russell A.P. (2005). A new centrosaurine ceratopsid from the Oldman Formation of Alberta and its implications for centrosaurine taxonomy and systematics. *Can. J. Earth Sci.*, 42, 1369–1387.

Rylaarsdam J.R., Varban B.L., Plint A.G., Buckley L.G. & McCrea R.T. (2006). Middle Turonian dinosaur palaeoenvironments in the Upper Cretaceous Kaskapau Formation, northeast British Columbia. *Can. J. Earth Sci.*, 43, 631–652.

Sampson S. & Currie P.J. (1996). On the trail of Cretaceous dinosaurs. In: *Life in Stone: a Natural History of British Columbia's Fossils* (ed. Ludvigsen R). UBC Press Vancouver, 143–155.

Sampson S.D. & Loewen M.A. (2010). Unraveling a radiation: a review of the diversity, stratigraphic distribution, biogeography, and evolution of horned dinosaurs (Ornithischia: Ceratopsidae). In: *New Perspectives on Horned Dinosaurs: the Royal Tyrrell Museum Ceratopsian Symposium* (eds. Ryan M, Chinnery-Allgeier BJ & Eberth DA). Indiana University Press Bloomington, 405–427.

Sampson S.D., Loewen M.A., Farke A.A., Roberts E.M., Forster C.A., Smith J.A. & Titus A.L. (2010). New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. *PLoS ONE*, 5, e12292.

Sankey J., Brinkman D., Guenther M. & Currie P.J. (2002). Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. *J. Palaeontol.*, 76, 751–763.

Sankey J.T. (2001). Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. *J. Palaeontol.*, 75, 208–215.

Schott R.K., Evans D.C. & Williamson T.E. (2009). The anatomy and systematics of *Colepiocephale lambei* (Dinosauria: Pachycephalosauridae). *J. Vertebr. Paleontol.*, 29, 771–786.

Schultze H.P. & Cloutier R. (eds.) (1996). *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Friedrich Pfeil, Munich.

Shubin N., Olsen P.E. & Sues H.D. (1994). Early Jurassic small tetrapods from the McCoy Brook Formation of Nova Scotia, Canada. In: *In the Shadow of the Dinosaurs* (eds. Fraser NC & Sues HD). Cambridge University Press, New York, 242–250.

Spalding D.A.E. (1999). *Into the Dinosaurs' Graveyard: Canadian Digs and Discoveries*. Doubleday Canada, Toronto.

Sternberg C.H. (1917). *Hunting Dinosaurs in the Bad Lands of the Red Deer River, Alberta, Canada: a Sequel to The life of a Fossil Hunter*. CH Sternberg, Lawrence, Kansas.

Sternberg C.M. (1926). A new species of *Thespesius* from the Lance Formation of Saskatchewan. *Can. Geol. Surv. Bull.*, 44, 73–84.

Sternberg C.M. (1928). A new armored dinosaur from the Edmonton Formation of Alberta. *Trans. Roy. Soc. Can.*, 3, 93–106.

Sternberg C.M. (1932). Two new theropod dinosaurs from the Belly River Formation of Canada. *Can. Field Nat.*, 46, 99–105.

Sternberg C.M. (1933). A new *Ornithomimus* with complete abdominal cuirass. *Can. Field Nat.*, 47, 79–83.

Sternberg C.M. (1935). Hooded hadrosaurs of the Belly River Series of the Upper Cretaceous. *Can. Dept. Mines Bull., Geol. Ser.*, 77, 1–37.

Sternberg C.M. (1937). Classification of *Thescelosaurus*: a description of a new species. *Proc. Geol. Soc. Am.*, 1936, 375.

Sternberg C.M. (1940a). Ceratopsidae from Alberta. *J. Palaeontol.*, 14, 468–480.

Sternberg C.M. (1940b). *Thescelosaurus edmontonensis*, n. sp., and classification of the Hypsilophodontidae. *J.Palaeontol.*, 14, 481–494.

Sternberg C.M. (1950a). *Pachyrhinosaurus canadensis*, representing a new family of the Ceratopsia, from southern Alberta. *Natl. Mus. Can., Bull.*, 118, 109–120.

Sternberg C.M. (1950b). Steveville west of the 4th Meridian, with notes on fossil localities. *Geol. Surv. Can. Map*, *969A.*

Sternberg C.M. (1953). A new hadrosaur from the Oldman Formation of Alberta: discussion of nomenclature. *Natl. Mus. Can. Bull.*, 128, 274–286.

Sternberg C.M. (1966). *Canadian Dinosaurs*. National Museum of Canada Geological Series No. 64, Bulletin 103, Ottawa.

Sternberg R.M. (1940c). A toothless bird from the Cretaceous of Alberta. *J. Palaeontol.*, 14, 81–85.

Sues H.-D. (1978). A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta Canada. *Zool. J. Linn. Soc.*, 62, 381–300.

Sues H.-D. (1997). On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. *J. Vertebr. Paleontol.*, 17, 698–716.

Sullivan R.M. (2003). Revision of the dinosaur *Stegoceras* Lambe (Ornithischia, Pachycephalosauridae). *J. Vertebr. Paleontol.*, 23, 181–207.

Tokaryk T., Ryan M.J. & Evans D.C. (2012). No environmental partitioning of Ceratopsidae within the lower Dinosaur Park Formation (Campanian) faunal zone of western Canada. *J. Vertebr. Paleontol.*, 30 (online suppl.), 184.

Tokaryk T.T. (1986). Ceratopsian dinosaurs from the Frenchman Formation (Upper Cretaceous) of Saskatchewan. *Can. Field Nat.* 100, 192–196.

Tokaryk T.T. & Bryant H.N. (2004). The fauna from the *Tyrannosaurus rex* excavation, Frenchman Formation (Late Maastrichtian), Saskatchewan. In: *Summary of Investigations 2004, Volume 1*. Saskatchewan Geological Survey, Saskatchewan Industry Resources, Misc. Rep, 1–12.

Tokaryk T.T. & Harington C.R. (1992). *Baptornis* sp. (Aves: Hesperornithiformes) from the Judith River Formation (Campanian) of Saskatchewan, Canada. *J. Palaeontol.*, 66, 1010–1012.

Tyson H. (1981). The structure and relationships of the horned dinosaur *Arrhinoceratops* Parks (Ornithischia: Ceratopsidae). *Can. J. Earth Sci.*, 18, 1241–1247.

Upchurch P., Mannion P.D., Benson R.B.J., Butler R.J. & Carrano M.T. (2011). Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. *Geol. Soc., Lond., Spec. Publ.*, 358, 209–240.

Vavrek M.J. & Larsson H.C.E. (2010). Low beta diversity of Maastrichtian dinosaurs of North America. *Proc. Natl. Acad. Sci. USA*, 107, 8265–8268.

Wang S.C. & Dodson P. (2006). Estimating the diversity of dinosaurs. *Proc. Natl. Acad. Sci. USA*, 103, 13601–13605.

Weishampel D.B., Barrett P.M., Coria R.A., Le Loeuff J., Xu X., Zhao X., Sahni A., Gomani E.M.P. & Noto C.R. (2004). Dinosaur distribution. In: *The Dinosauria* (eds. Weishampel DB, Dodson P & Osmolska H). University of California Press Berkeley, 517–608.

Wu X.-C., Brinkman D.B., Eberth D.A. & Braman D.R. (2007). A new ceratopsid dinosaur (Ornithischia) from the uppermost Horseshoe Canyon Formation (upper Maastrichtian), Alberta, Canada. *Can. J. Earth Sci.*, 44, 1243–1265.

Appendix

Abbreviations: Hg&s, holotype of genus and species; Hs, holotype of species; and Lg&s, lectotype of genus and species.

Taxon	Reference specimen	Other material	Reference
Alberta			
Milk River Formation			
Hadrosauridae			
Hadrosauridae indet.	TMP 2007.035.0012 (frontal)	isolated material	Larson et al. (in press)
Pachycephalosauridae			
Pachycephalosauridae n. gen et. sp.	TMP 2008.045.0001$^{\text{Hg\&s}}$ (frontoparietal dome)	frontoparietal domes, teeth	Evans *et al.* (2013)
Ankylosauridae			
Ankylosauridae indet.	MR-4:55 (Baszio UofA number) (tooth)	teeth	Baszio (1997)
Nodosauridae			
Nodosauridae indet.	MR-4:130 (Baszio UofA number) tooth	teeth	Baszio (1997)
Leptoceratopsidae			
Gryphoceratops Ryan *et al.*, 2012			
Gryphoceratops morrisoni Ryan *et al.* 2012	ROM 56635$^{\text{Hg\&s}}$ (dentary)	teeth	Ryan *et al.* (2012)
Ceratopsidae			
Ceratopsidae indet.	TMP 1991.054.0017 (tooth)	teeth; femur; Russell (1935: plate V-2)	Russell (1935)
Tyrannosauridae			
Tyrannosauridae indet.	UALVP 48415 (tooth)	teeth	Larson (2008)
Ornithomimidae			
Ornithomimidae indet.	TMP 1991.105.0006 (caudal vertebra)	phalanges, metatarsal; manual phalanx; Russell (1935, Pl 2, Fig. 10)	Russell (1935)
Dromaeosauridae			
Milk River Saurornitholestinae gen. et sp. Larson & Currie 2013	UALVP 47980 (tooth)	teeth	Larson & Currie (2013)
Milk River Dromaeosauridae gen. et sp. Larson & Currie 2013	UALVP 48460 (tooth)	teeth	Larson & Currie (2013)
Milk River Dromaeosaurinae gen. et sp. Larson & Currie 2013	UALVP 48422 (tooth)	teeth	Larson & Currie (2013)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Aquilan cf. *Richardoestesia gilmorei* Larson & Currie 2013	UALVP 47985 (tooth)	teeth	Larson & Currie (2013)
?Aquilan cf. *Richardoestesia isosceles* Larson & Currie 2013	UALVP 48279 (tooth)	teeth	Larson & Currie (2013)
Zapsalis Cope 1876			
Milk River cf. *Zapsalis* sp. Larson & Currie 2013	UALVP 48431 (tooth)	teeth	Larson & Currie (2013)
Paronychodon Cope 1876			
cf. *Paronychodon lacustris* Cope 1876	UALVP 48365 (tooth)	teeth	Larson (2008)

Taxon	Reference specimen	Other material	Reference
Foremost Formation			
Hadrosauridae			
Hadrosauridae indet.	TMP 1996.081.0001 (tooth)	teeth, partial skeleton	Ryan & Russell (2001)
Pachycephalosauridae			
Colepiocephale Sullivan 2003			
Colepiocephale lambei (Sternberg 1945)	CMN 8818$^{Hg\&s}$ (frontoparietal dome)	frontoparietal domes	Schott *et al.* (2009)
Ankylosauridae			
Ankylosauridae indet.	TMP 1980.013.0040 (tooth)		Brinkman *et al.* (2004)
Nodosauridae			
Nodosauridae indet.	TMP 1996.007.0017 (tooth)	teeth	Brinkman *et al.* (2004)
Ceratopsidae			
Centrosaurinae			
Xenoceratops Ryan *et al.* 2012			
Xenoceratops foremostensis Ryan *et al.* 2012	CMN 53283$^{Hg\&s}$ (partial parietal)	parietal and squamosal fragments	Ryan *et al.* (2012)
Tyrannosauridae			
Tyrannosauridae indet.	TMP 1988.086.0004 (tooth)	teeth	Brinkman *et al.* (2004)
Dromaeosauridae			
Saurornitholestes Sues 1978			
Saurornitholestes sp.	TMP 1988.086.0029 (tooth)	teeth	Brinkman *et al.* (2004)
Theropoda incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Richardoestesia sp.	TMP 1988.086.0044 (tooth)	teeth	Brinkman *et al.* (2004)
Richardoestesia n. sp. Baszio 1997	uncatalogued TMP teeth		Baszio (1997), Sankey et al. (2002)
Paronychodon Cope 1876			
Paronychodon sp.	uncatalogued TMP teeth	teeth	Brinkman *et al.* (2004)
Oldman Formation			
Thescelosauridae			
Orodrominae			
Orodrominae indet.	TMP 2008.045.0002 (postcranial skeleton)	teeth, isolated elements	Brown *et al.* (2013)
Orodrominae n. gen. et sp. Brown *et al.* in press	TMP 2009.037.0044$^{Hg\&s}$ (partial skeleton)	NA	Brown *et al.* (2013)

Taxon	Reference specimen	Other material	Reference
Oldman Formation			
Tyrannosauridae			
Daspletosaurus Russell 1970			
Daspletosaurus torosus Russell 1970	CMN 8506$^{Hg\&s}$ (partial skeleton)		Russell (1970)
Troodontidae			
Troodontidae indet.	TMP 1989.077.005 (tooth)	teeth	Larson & Currie (2013)
Dromaeosauridae			
Dromaeosaurus Matthew & Brown 1922			
Dromaeosaurus albertensis Matthew & Brown 1922	TMP 1999.055.0328 (tooth)	teeth	Larson & Currie (2013)
Saurornitholestes Sues 1978			
Saurornitholestes langstoni Sues 1978	TMP 1994.144.0105 (tooth)	teeth, partial skeleton	Larson & Currie (2013)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Oldman cf. *Richardoestesia gilmorei* Larson & Currie 2013	TMP 1986.171.0061 (tooth)	teeth	Larson & Currie (2013)
Richardoestesia isosceles Sankey 2001	TMP 1986.159.0062 (tooth)	teeth	Larson & Currie (2013)
Paronychodon Cope 1876			
Paronychodon sp.	TMP 1992.077.0006 (teeth)	teeth	Larson & Currie (2013)
Dinosaur Park Formation			
Hadrosauridae			
Hadrosaurinae			
Gryposaurus Lambe 1914			
Gryposaurus notabilis Lambe 1914			
(=*Gryposaurus incurvimanus* Parks 1920)	CMN 2278$^{Hg\&s}$ (skull & postcrania)	skulls & associated postcrania	Lambe (1914), Prieto-Marquez (2010)
Prosaurolophus Brown 1916			
Prosaurolophus maximus Brown 1916	AMNH 5836$^{Hg\&s}$ (skull)	skeletons	Brown (1916)
Lambeosaurinae			
Corythosaurus Brown 1914b			
(= *Tetragonosaurus erectofrons* Park 1931)			
[can't be assigned to species]			
Corythosaurus casuarius Brown 1914b			
(= *Corythosaurus bicristatus* Park 1935			
Corythosaurus brevicristatus Park 1935)	AMNH 5240$^{Hg\&s}$ (skeleton)	skulls & associated postcrania	Brown (1914)
Corythosaurus intermedius Parks 1923			
(= *Corythosaurus excavatus* Gilmore 1923)	ROM 776^{Hs} (skull)	skulls & skeletons	Parks (1923)

Taxon	Reference specimen	Other material	Reference
Oldman Formation			
Tyrannosauridae			
Daspletosaurus Russell 1970			
Daspletosaurus torosus Russell 1970	CMN 8506$^{Hg\&s}$ (partial skeleton)		Russell (1970)
Troodontidae			
Troodontidae indet.	TMP 1989.077.005 (tooth)	teeth	Larson & Currie (2013)
Dromaeosauridae			
Dromaeosaurus Matthew & Brown 1922			
Dromaeosaurus albertensis Matthew & Brown 1922	TMP 1999.055.0328 (tooth)	teeth	Larson & Currie (2013)
Saurornitholestes Sues 1978			
Saurornitholestes langstoni Sues 1978	TMP 1994.144.0105 (tooth)	teeth, partial skeleton	Larson & Currie (2013)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Oldman cf. *Richardoestesia gilmorei* Larson & Currie 2013	TMP 1986.171.0061 (tooth)	teeth	Larson & Currie (2013)
Richardoestesia isosceles Sankey 2001	TMP 1986.159.0062 (tooth)	teeth	Larson & Currie (2013)
Paronychodon Cope 1876			
Paronychodon sp.	TMP 1992.077.0006 (teeth)	teeth	Larson & Currie (2013)
Dinosaur Park Formation			
Hadrosauridae			
Hadrosaurinae			
Gryposaurus Lambe 1914			
Gryposaurus notabilis Lambe 1914			
(=*Gryposaurus incurvimanus* Parks 1920)	CMN 2278$^{Hg\&s}$ (skull & postcrania)	skulls & associated postcrania	Lambe (1914), Prieto-Marquez (2010)
Prosaurolophus Brown 1916			
Prosaurolophus maximus Brown 1916	AMNH 5836$^{Hg\&s}$ (skull)	skeletons	Brown (1916)
Lambeosaurinae			
Corythosaurus Brown 1914b			
(= *Tetragonosaurus erectofrons* Park 1931)			
[can't be assigned to species]			
Corythosaurus casuarius Brown 1914b			
(= *Corythosaurus bicristatus* Park 1935			
Corythosaurus brevicristatus Park 1935)	AMNH 5240$^{Hg\&s}$ (skeleton)	skulls & associated postcrania	Brown (1914)
Corythosaurus intermedius Parks 1923			
(= *Corythosaurus excavatus* Gilmore 1923)	ROM 776^{Hs} (skull)	skulls & skeletons	Parks (1923)

Taxon	Reference specimen	Other material	Reference
Dinosaur Park Formation			
Lambeosaurus Parks 1923			
(= *Tetragonosaurus praeceps* Parks 1931)			
[can't be assigned to species]			
Lambeosaurus lambei Parks 1923	CMN 2869$^{\mathrm{Lg\&s}}$ (skull)	skulls & skeletons	Parks (1923)
Lambeosaurus clavinitialis Sternberg 1935	CMN 8703$^{\mathrm{Hs}}$ (skeleton)	skull & skeletons	Sternberg (1935)
(= *Corythosaurus frontalis* Parks 1935)			
Lambeosaurus magnicristatus Sternberg 1935	CMN 8705$^{\mathrm{Hs}}$ (skull)	skulls & associated postcrania	Sternberg (1935)
Parasaurolophus Parks 1922			
Parasaurolophus walkeri Parks 1922	ROM 768$^{\mathrm{Hg\&s}}$ (skeleton)	fragmentary skulls, skeleton	Parks (1922)
Thescelosauridae			
Orodrominae			
Orodrominae incertae sedis	TMP 2002.012.0135 (frontal)	teeth, isolated elements	Brown *et al.* (2013)
Pachycephalosauridae			
Stegoceras Lambe 1902			
Stegoceras validum Lambe 1902			
(= *Ornatotholus browni* Galton & Sues 1983)	CMN 515$^{\mathrm{Hg\&s}}$ (frontoparietal dome)	teeth, frontoparietal domes, partial skeleton	Lambe (1902)
Stegoceras breve Lambe 1918	CMN 1423$^{\mathrm{Hs}}$ (frontoparietal dome)	frontoparietal domes	Lambe (1918)
Hanssuessia Sullivan 2003			
Hanssuessia sternbergi (Brown & Schlaikjer 1943)	CMN 8817$^{\mathrm{Hg\&s}}$ (frontoparietal dome)	frontoparietal domes	Sullivan (2003)
Pachycephalosaurus Brown & Schlaikjer 1943 **			
?*Pachycephalosaurus wyomingensis* (Gilmore 1930)			
(=*Troodon wyomingensis* Gilmore 1930)	BMNH R8646 (frontoparietal dome)	NA	Ryan & Evans (2005)
Pachycephalosauridae nov. sp.	TMP 2002.012.0063 (squamosal)		Ryan & Evans (2005)
Ankylosauridae			
Euoplocephalus Lambe 1910			
Euoplocephalus tutus Lambe 1902			
(=*Stereocephalus tutus* Lambe 1902)	CMN 210$^{\mathrm{Hg\&s}}$ (partial skull)	teeth, skulls, skeletons	Lambe (1902)
Dyoplosaurus Parks 1924			
Dyoplosaurus acutosquameus Parks 1924	ROM 784$^{\mathrm{Hg\&s}}$ (partial skeleton)		Arbour *et al.* (2009)
Nodosauridae			
Edmontonia Sternberg 1928			
Edmontonia rugosidens Gilmore 1930			
(=*Palaeosincus rugoisidens* Gilmore 1930)	AMNH 5665 (partial skeleton)	teeth, skeletons, isolated elements	Gilmore (1930)

Taxon	Reference specimen	Other material	Reference
Dinosaur Park Formation			
Panoplosaurus Lambe 1919			
Panoplosaurus mirus Lambe 1919	CMN 2759$^{Hg\&s}$ (skull & partial skeleton)	teeth, skeleton, isolated elements	Lambe (1919)
Leptoceratopsidae			
Unescoceratops Ryan *et al*. 2012			
Unescoceratops koppelhusae Ryan *et al*. 2012	TMP 1995.012.0006$^{Hg\&s}$ (dentary)	isolated elements	Ryan *et al*. (2012)
Ceratopsidae			
Centrosaurinae			
Centrosaurus Lambe 1904			
(= *Monoclonius* Cope 1876)			
Centrosaurus apertus Lambe 1902			
(= *Monoclonius dawsoni* Lambe 1902			
Monoclonius flexus Brown 1914			
Monoclonius cutleri Brown 1917			
Monoclonius nasicornus Brown 1917			
Centrosaurus longirostris Sternberg 1940)	CMN 971$^{Hg\&s}$ (parietal)	skeletons, bone beds, isolated elements	Lambe (1902)
Styracosaurus Lambe 1913			
Styracosaurus albertensis Lambe 1913	CMN 344$^{Hg\&s}$ (skull and skeleton)	skeletons, bone beds, isolated elements	Lambe (1913)
***Spinops* Farke *et al*. 2010			
***Spinops sternbergorum* Farke *et al*. 2010	NHMUK R 16307$^{Hg\&s}$ (parietal)	partial skull and parietal	Farke *et al*. (2010)
Pachyrhinosaurini			
Pachyrhinosaurini indet.	TMP 2002.076.0001 (partial skeleton)		Ryan *et al*. (2010)
Chasmosaurinae			
Anchiceratops Brown 1914			
Anchiceratops sp.	CMN 9813	frill	Langston (1959)
Chasmosaurus Lambe 1914a			
(=*Protorosaurus* Lambe 1914b			
Eoceratops Lambe 1915)			
Chasmosaurus belli (Lambe 1914a)			
(=*Monoclonius belli* Lambe 1902)	CMN 491$^{Hg\&s}$ (skull)	skulls, skeletons, isolated elements	Lambe (1902)
Chasmosaurus russelli Sternberg 1940b			
(includes *C. canadensis* Lambe 1902			
(=*Monoclonius canadensis* Lambe 1902)			
Eoceratops canadensis Lambe 1915			
=*Mojoceratops perifania* Longrich 2010			
& *C. kaiseni* Brown 1933)	CMN 8800^{Hs} (skull)	skulls, skeletons, isolated elements	Sternberg (1940b)

Taxon	Reference specimen	Other material	Reference
Dinosaur Park Formation			
Vagaceratops Sampson *et al.* 2010			
Vagaceratops irvinensis (Holmes *et al.* 2001)			
(= *Chasmosaurus irvinensis* Holmes *et al.* 2001)	CMN 41357^{Hs} (skeleton, partial skull)	skull, parietal	Holmes *et al.* (2001)
Ornithomimidae			
Dromiceiomimus Russell 1972			
Dromiceiomimus samueli (Parks 1928)			
(=*Struthiomimus samueli* Parks 1928)	ROM 840^{Hs} (partial skeleton)		Parks (1928)
Ornithomimus Marsh 1890b			
Ornithomimus edmontonicus Sternberg 1933	CMN 12441	skulls, skeletons, isolated elements	Sternberg (1933)
Struthiomimus Osborn 1916			
Struthiomimus altus (Lambe 1902)			
(=*Ornithomimus altus* Lambe 1902)	CMN 930$^{Hg\&s}$ (skeleton)	skulls, skeletons, isolated elements	Lambe (1902)
Ornithomimidae indet. - large ornithomimid	ROM 41844 (manual ungual)	isolated elements	Longrich (2008)
Tyrannosauridae			
Gorgosaurus Lambe 1914			
Gorgosaurus libratus Lambe 1914b	CMN 2120$^{Hg\&s}$ (skull & skeleton)	skulls, skeletons, isolated elements	Lambe (1914)
Daspletosaurus Russell 1970			
Daspletosaurus sp.	FMNH PR 308 (partial skeleton)	skulls, skeletons, isolated elements	Currie (2005)
Avimimidae			
Avimimus Kurzanov 1981			
Avimimus sp.	TMP 1998.008.0028 (metatarsal)	isolated elements	Currie (2005)
Caenagnathidae			
Caenagnathus Sternberg 1940			
Caenagnathus collinsi Sternberg 1940	CMN 8776$^{Hg\&s}$ (lower jaw)		Sternberg (1940)
Caenagnathus sternbergi Cracraft 1971	CMN 2690^{Hs} (lower jaw)	lower jaws	Cracraft (1971)
Chirostenotes Gilmore 1924a			
Chirostenotes pergracilis Gilmore 1924a	CMN 2367$^{Hg\&s}$ (partial skeleton)	partial skeletons	Gilmore (1924a)
Elmisaurus Currie 1989			
Elmisaurus elegans (Parks 1933)	ROM 781^{Hs} (metatarsus)	metatarsal	Parks (1933)
Troodontidae			
Troodon Leidy 1856			
Troodon inequalis Sternberg 1932	NMC 8539^{Hs} (partial skeleton)	teeth, isolated elements	Sternberg (1932)
Pectinodon Carpenter 1982			
Dinosaur Park cf. *Pectinodon* sp.		teeth	Larson & Currie (2013)

Taxon	Reference specimen	Other material	Reference
Dinosaur Park Formation			
Dromaeosauridae			
Dromaeosaurus Matthew & Brown 1922			
Dromaeosaurus albertensis Matthew & Brown 1922	AMNH 5356$^{Hg\&s}$ (partial skull & postcranial)	skull, skeleton, isolated elements	Matthew & Brown (1922)
Zapsalis Cope 1876			
Zapsalis abradens Cope 1876	TMP 1984.163.0080 (tooth)	teeth	Larson & Currie (2013)
Saurornitholestes Sues 1978			
Saurornitholestes langstoni Sues 1978	TMP 1974.010.0005$^{Hg\&s}$ (partial skeleton)	partial skeletons, isolated elements	Sues (1978)
Microraptorinae			
Hesperonychus Longrich & Currie 2009			
Hesperonychus elizabethae Longrich & Currie 2009	UALVP 48778$^{Hg\&s}$ (pelvis)	isolated elements	Longrich & Currie (2009)
Therizinosauroidea			
?Therizinosauroidea indet.	CMN 12349 (frontal)	ungual, pedal elements	Currie (1987)
Theropoda incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Richardoestesia gilmorei Currie, Rigby & Sloan 1990	CMN 343$^{Hg\&s}$ (paired dentaries)	teeth	Currie *et al.* (1990)
Richardoestesia isosceles Sankey 2001	TMP 1996.142.0019 (tooth)	teeth	Sankey (2001)
Paronychodon Cope 1876			
cf. *Paronychodon lacustris* Cope 1876	TMP 1986.060.0114 (tooth)	teeth	Currie (2005)
Bearpaw Formation			
Hadrosauridae			
Hadrosaurinae			
Prosaurolophus Brown 1916			
Prosaurolophus sp.	TMP 1983.064.0003 (partial skeleton)	partial skeleton	Campione *et al.* (2013)
Nodosauridae			
Edmontonia Gilmore 1930			
Edmontonia sp.	TMP 1983.064.0091 (scute)		
Pachycephalosauridae			
Stegoceras Lambe 1902			
Stegoceras sp.	TMP 1990.108.0001 (frontoparietal dome)		
Ceratopsidae			
Ceratopsidae indet.	TMP 1991.036.0416 (phalanx)		
Ornithomimidae			
Ornithomimidae indet.	TMP 1978.028.0016 (metatarsal)	isolated elements	

Taxon	Reference specimen	Other material	Reference
Horseshoe Canyon Formation			
Thescelosauridae			
Thescelosaurinae			
Parksosaurus Sternberg 1937			
Parksosaurus warreni (Parks 1926)			
(=*Thescelosaurus warreni* Parks 1926)	ROM 804$^{\mathrm{Hg\&s}}$ (skull & skeleton)		Parks (1937)
Hadrosauridae			
Hadrosaurinae			
Edmontosaurus Lambe 1920			
Edmontosaurus regalis Lambe 1917			
(=*Thespesius edmontoni* Gilmore 1924)	CMN 2288$^{\mathrm{Hg\&s}}$ (skull & skeleton)	skeletons, bone bed material	Lambe (1917), Campione & Evans (2011)
Saurolophus Brown 1912			
Saurolophus osborni Brown 1912	AMNH 5220$^{\mathrm{Hg\&s}}$ (skeleton)	skulls, skeleton, & isolated material	Brown (1912)
Lambeosaurinae			
Hypacrosaurus Brown 1913			
Hypacrosaurus altispinus Brown 1913			
(= *Cheneosaurus tolmanensis* Lambe 1917)	AMNH 5204$^{\mathrm{Hg\&s}}$ (postcrania)	skulls, associated postcrania, isolated elements	Brown (1913)
Pachycephalosauridae			
Prenocephale Lambe 1902			
Prenocephale edmontonense Brown & Schlaikjer 1943			
(=*Troodon edmontonense* Brown & Schlaikjer 1943)	CMN 8830$^{\mathrm{Hs}}$ (frontoparietal dome)	isolated elements	Brown & Schlaikjer (1943)
Ankylosauridae			
Euoplocephalus Lambe 1910			
Euoplocephalus tutus (Lambe 1902)			
(=*Stereocephalus tutus* Lambe 1902)	AMNH 5266 (partial skeleton)	teeth, skulls, skeletons, isolated elements	
Nodosauridae			
Edmontonia Sternberg 1928			
Edmontonia longiceps Sternberg 1928	CMN 8531$^{\mathrm{Hg\&s}}$ (skull & partial skeleton)	teeth, skulls, skeleton?, isolated elements	Lambe (1928)
Leptoceratopsidae			
Montanoceratops Sternberg 1951			
Montanoceratops sp.	AMNH 5244 (partial skull)		Makovicky (2001)

Taxon	Reference specimen	Other material	Reference
Horseshoe Canyon Formation			
Ceratopsidae			
Centrosaurinae			
Pachyrhinosaurus Sternberg 1950			
Pachyrhinosaurus canadensis Sternberg 1950	CMN 8867$^{Hg\&s}$ (skull)	skulls, skeletons, isolated elements	Sternberg (1950)
Chasmosaurinae			
Anchiceratops Brown 1914			
Anchiceratops ornatus Brown 1914	AMNH 5251$^{Hg\&s}$ (skull)	skulls, skeleton, isolated elements	Brown (1914)
Arrhinoceratops Parks 1925			
Arrhinoceratops brachyops Parks 1925	ROM 796$^{Hg\&s}$ (skull)		Parks (1925)
Eotriceratops Wu *et al.* 2007			
Eotriceratops xerinsularis Wu *et al.* 2007	TMP 2005.057.0007$^{Hg\&s}$ (partial skeleton)		Wu *et al.* (2007)
Ornithomimidae			
Dromiceiomimus Russell 1972			
Dromiceiomimus brevitertius Parks 1926 (=*Struthiomimus brevitertius* Park 1926 including *S. ingens* Parks 1933)	ROM 797$^{Hg\&s}$ (post crania)		Russell (1972)
Ornithomimus Marsh 1890			
Ornithomimus edmontonicus Sternberg 1933	CMN 8632^{Hs} (skeleton)	partial skeletons	Sternberg (1933)
Struthiomimus Osborn 1917			
Struthiomimus altus Lambe 1902 (= *Ornithomimus altus* Lambe 1902)	AMNH 5257 (partial skeleton)	partial skeletons	Russell (1972)
Tyrannosauridae			
Daspletosaurus Russell 1970			
Daspletosaurus undescribed species	TMP 1986.064.0001 (partial skeleton)		
Albertosaurus Osborn 1905			
Albertosaurus sarcophagus Osborn 1905	CMN 5600$^{Hg\&s}$ (skull)	skeletons, bone bed, isolated elements	Osborn (1905)
Caenagnathidae			
Epichirostenotes Sullivan 2011			
Epichirostenotes curriei Sullivan 2011	ROM 43250$^{Hg\&s}$ (partial skeleton)		Sues (1997)
Troodontidae			
Troodon Leidy 1856			
Horseshoe Canyon cf. *Troodon* sp.	TMP 1997.044.0004 (teeth)	teeth	Larson & Currie (2013)

Taxon	Reference specimen	Other material	Reference
Horseshoe Canyon Formation			
Dromaeosauridae			
Horseshoe Canyon Dromaeosaurinae gen. et sp.	TMP 2003.045.0060 (teeth)	teeth	Larson & Currie (2013)
Atrociraptor Currie & Varricchio 2004			
Atrociraptor marshalli Currie & Varricchio 2004	TMP 1995.166.0001$^{Hg\&s}$ (partial skull)	teeth	Currie & Varricchio (2004)
Alvarezsauridae			
Albertonykus Longrich & Currie 2009			
Albertonykus borealis Longrich & Currie 2009	TMP 2001.045.0091$^{Hg\&s}$ (ulna)	isolated elements	Longrich & Currie (2009)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Horseshoe Canyon cf. *Richardoestesia gilmorei*	TMP 1994.028.0001 (teeth)	teeth	Larson & Currie (2013)
Paronychodon Cope 1876			
cf. *Paronychodon lacustris* Cope 1876	TMP 1041 (tooth) (Baszio 1997 number)	teeth	Larson & Currie (2013)
Scollard Formation			
Thescelosauridae			
Thescelosaurus Gilmore 1913			
Thescelosaurus neglectus Glimore 1913 (=*Thescelosaurus edmontonensis* Sternberg 1940)	CMN 8537^{Hs} (skull & skeleton)	teeth	Sternberg (1940)
Hadrosauridae indet.	TMP 1986.207.0022 (vertebrae)	teeth, isolated elements	Russell (1987)
Ankylosauridae			
Ankylosauridae indet.	TMP 1986.207.0026 (scutes)	scutes, teeth	Ryan & Russell (2001)
Ankylosaurus Brown 1908			
Ankylosaurus magniventris Brown 1908	AMNH 5214 (skull and skeleton)	scutes, teeth	Carpenter (2004)
Pachycephalosauridae			
Pachycephalosauridae indet.	TMP 2011.011.0421 (frontoparietal dome)		
Leptoceratopsidae			
Leptoceratops Brown 1914c			
Leptoceratops gracilis Brown 1914c	AMNH 5205$^{Hg\&s}$ (partial skeleton)	teeth, skeletons, isolated material	Brown (1914c)
Ceratopsidae			
Chasmosaurinae			
Triceratops Marsh 1889			
Triceratops sp.	CMN 8862 (partial skull)	teeth, isolated elements	Forster (1996)

Taxon	Reference specimen	Other material	Reference
Scollard Formation			
Ornithomimidae			
Ornithomimidae indet.	TMP 1993.104.0001 (partial skeleton)	isolated elements	
Tyrannosauridae			
Tyrannosaurus Osborn 1905			
Tyrannosaurus rex Osborn 1905	TMP 1987.012.0014 (partial skeleton)	skeletons, isolated elements	Currie (2003)
Caenagnathidae			
?Caenagnathidae n. sp.		isolated elements	
Troodontidae			
Troodon Leidy 1856			
cf. *Troodon* Leidy 1856	TMP 1994.106.0001 (tooth)	teeth	
Dromaeosauridae			
Dromaeosauridae indet(?)	TMP 1981.001.0001 (manus)		
Dromaeosaurus Matthew & Brown 1992			
cf. *Dromaeosaurus albertensis* Matthew & Brown 1922	TMP 1981.031.0099 (tooth)	teeth	Baszio (1997)
Saurornitholestes Sues 1978			
cf. *Saurornitholestes langstoni* Sues 1978	TMP 1987.016.0018 (tooth)	teeth	Baszio (1997)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
cf. *Richardoestesia gilmorei* Currie, Rigby & Sloan 1990	UofA 859 (tooth)	teeth	Baszio (1997)
cf. *Richardoestesia isosceles* Sankey 2001	UofA 1129 (tooth)	teeth	Baszio (1997)
Paronychodon Cope 1876			
Paronychodon-like sensu Currie, Rigby & Sloan 1990	UofA 1219 (tooth)	teeth	Baszio (1997)
Allison Formation			
Thescelosauridae			
Orodrominae			
Orodrominae indet.	CMN 9483		Gilmore (1924), Russell (1949)
St. Mary River Formation			
Hadrosauridae indet.	TMP 1997.066.0001 (partial skeleton) teeth(?), isolated elements, footprints		Currie *et al.* (1991)
Edmontosaurus Lambe 1917			
Edmontosaurus sp.	CMN 10661 (squamosal)	isolated elements	Langston (1975)

Taxon	Reference specimen	Other material	Reference
St. Mary River Formation			
Ceratopsidae			
Pachyrhinosaurus Sternberg, 1950			
Pachyrhinosaurus canadensis Sternberg 1950	CMN 9485 (skull)	bone bed elements	Langston (1975)
Anchiceratops Brown 1940			
Anchiceratops sp.	CMN 9829 (frill)		Langston (1975)
Nodosauridae			
Edmontonia Sternberg 1928			
Edmontonia cf. *longiceps* Sternberg 1928	CMN 21864 (tooth)	NA	Langston (1975)
Ornithomimidae indet.	CMN 10653 (metatarsal)	NA	Langston (1975)
Tyrannosauridae indet.	CMN 9589 (tooth)	teeth	Langston (1975)
Albertosaurus Osborn 1905			
Albertosaurus sp.	TMP 1987.085.0010 (tooth)		
Deinonychosauria indet. (*Saurornithoides*-like)	CMN 10674 (tooth)		Langston (1975)
Troodontidae			
Troodon Leidy 1856			
Troodon indet.	CMN 10649 (tooth)		Langston (1975)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Richardoestesia sp.	TMP 1998.052.0002 (tooth)		
Willow Creek Formation			
Hadrosauridae indet.	TMP 1981.006.0003 (ischium)	teeth	Ryan & Russell (2001)
Leptoceratopsidae			
Prenoceratops Chinnery 2004			
Prenoceratops sp.	TMP 1982.011.0001 (partial skeleton)		Makovicky (2010)
Tyrannosauridae			
Tyrannosaurus Osborn 1905			
Tyrannosaurus rex	TMP 1981.006.0001 (skull & partial skeleton)	isolated elements	Currie (2003)
Clearwater Formation			
Ankylosauria			
Nodosauridae	TMP 2011.033.0001 (partial skeleton)	NA	

Taxon	Reference specimen	Other material	Reference
Wapiti Formation			
Hypsilophodontidae			
Hypsilophodontidae indet.	TMP 2004.093.0005 (tooth)		Fanti & Miyashita (2009)
Hadrosauridae indet.	UALVP 50636.01 (tooth)	teeth, isolated elements	Fanti & Miyashita (2009)
Ceratopsidae			
Centrosaurinae			
Pachyrhinosaurus Sternberg 1950			
Pachyrhinosaurus lakustae Currie *et al.* 2008	TMP 1986.055.0258$^{\mathrm{Hs}}$ (skull)	bone beds	Currie *et al.* (2008)
Pachycephalosauridae			
Pachycephalosauridae indet.	TMP 2004.093.0001 (tooth)	NA	Fanti & Miyashita (2009)
Ankylosauridae			
Ankylosauridae indet.	TMP 2004.023.0009 (tooth)	tooth	Fanti & Miyashita (2009)
Ornithomimidae indet.	TMP 1989.053.0035 (vertebrae)	isolated elements	Ryan & Russell (2001)
Tyrannosauridae			
Tyrannosauridae indet.	UALVP 50641.01 (tooth)	isolated teeth & elements	Fanti & Miyashita (2009)
Dromaeosauridae			
Dromaeosauridae indet.	UALVP 50640.01 (tooth)	NA	Fanti & Miyashita (2009)
Saurornitholestes Sues 1978			
Saurornitholestes sp.	TMP 1989.055.1523 (tooth)	teeth, frontal, isolated elements	Fanti & Miyashita (2009)
Troodontidae			
Troodontidae indet.	TMP 2004.023.0003 (teeth)	teeth	Fanti & Miyashita (2009)
Theropod incertae sedis			
Paronychodon Cope 1876			
Paronychodon sp.	UAVLP 48815 (tooth)	NA	Fanti & Miyashita (2009)
Richardoestesia Currie, Rigby & Sloan 1990			
Richardoestesia gilmorei Currie, Rigby & Sloan 1990	TMP 2004.093.0003 (tooth)	NA	Fanti & Miyashita (2009)
British Columbia			
Brothers Peak Formation			
Ornithischia			
Cerapoda			
Cerapoda indet.	RBCM.EH.2006.019 (partial skeleton)	NA	Arbour & Graves (2008)

Taxon	Reference specimen	Other material	Reference
uncertain formation			
Ornithischia			
Ornithopoda indet.	pedal ungual	NA	Sampson & Currie (1996)
Theropoda indet.	tooth	NA	Ludvigsen (1996)
Kaskapau Formation			
Hadrosauridae			
Hadrosauridae indet.	jaw with teeth	associated and isolated material	McCrea & Buckley (2010)
Tyrannosauridae			
Tyrannosauridae indet.	tooth	teeth	McCrea & Buckley (2010)
Dromaeosauridae			
Saurornitholestes Sues 1978			
Saurornitholestes sp.	tooth		McCrea & Buckley (2010)
Saskatchewan			
Frenchman Formation			
Thescelosauridae			
Thescelosaurus Gilmore, 1913			
Thescelosaurus assiniboiensis Brown *et al.* 2011	RSM P 1225.1^{Hs} (partial skeleton)		Brown *et al.* (2011)
Hadrosauridae			
Hadrosaurinae			
Edmontosaurus Lambe 1920			
Edmontosaurus annectens Marsh 1892			
(= *Edmontosaurus saskatchewanensis* Sternberg 1926)	CMN 8509 (skull, partial skeleton)		Sternberg (1926), Campione & Evans (2011)
Pachycephalosauridae			
Pachycephalosauridae indet.	RSM P2943.5 (tooth)		Tokaryk & Bryant (2004)
Ceratopsidae			
Chasmosaurinae			
Triceratops Marsh 1889			
Triceratops horridus Marsh 1889	RSM P2525.1	skulls	Tokaryk (1986)
Torosaurus March 1881			
cf. *Torosaurus*	EM 16.1 (frill)		Tyson (1981)
Ankylosauridae			
Ankylosaurus Brown 1908			
cf. *Ankylosaurus magniventris*	RSM P99.1 (scute)	scute	Burns (2009)

Taxon	Reference specimen	Other material	Reference
Frenchman Formation			
Tyrannosauridae			
Tyrannosauridae indet.			
Tyrannosaurus Osborn 1905			
Tyrannosaurus rex Osborn 1905	RSM P2523.8 (skeleton)	isolated material	Tokaryk & Bryant (2004)
Ornithomimidae			
Ornithomimus Marsh 1890			
Ornithomimus sp.			
Struthiomimus Lambe 1902			
Struthiomimus sedens (Marsh 1892)	RSM 2904.1		
Caenagnathidae			
Chirostenotes Gilmore 1924			
Chirostenotes sp.			
Troodontidae			
Troodontidae indet.		teeth	Buckley (2009)
Dromaeosauridae			
Dromaeosauridae indet(?)			
Dromaeosaurus Matthew & Brown 1992			
cf. *Dromaeosaurus* sp.	PSM P2523.116 (tooth)	teeth	Tokaryk & Bryant (2004)
Saurornitholestes Sues 1978			
Saurornitholestes sp.		teeth	Buckley (2009)
Theropod incertae sedis			
Richardoestesia Currie, Rigby & Sloan 1990			
Richardoestesia sp.		teeth	Buckley (2009)
Paronychodon Cope 1876			
cf. *Paronychodon* sp.		teeth	Buckley (2009)
Dinosaur Park Formation (Saskatchewan)			
Hadrosauridae			
Lambeosaurinae			
Lambeosaurinae indet.			Tokaryk & Harington (1992)

Taxon	Reference specimen	Other material	Reference
Dinosaur Park Formation (Saskatchewan)			
Ceratopsidae			
Centrosaurinae			
Centrosaurus Lambe 1904			
(= *Monoclonius* Cope 1876)			
Centrosaurus apertus Lambe 1902			
(= *Monoclonius dawsoni* Lambe 1902			
Monoclonius flexus Brown 1914			
Monoclonius cutleri Brown 1917			
Monoclonius nasicornus Brown 1917			
Centrosaurus longirostris Sternberg 1940)	RSM P2105.1 (orbital horn core)		Tokaryk *et al.* (1990)
Chasmosaurinae			
Chasmosaurus Lambe 1914			
Chasmosaurus indet.	RSM P1990.6 (orbital horn core)		Tokaryk *et al.* (1990), Tokaryk & Harington (1992)
Ornithomimidae			
Ornithomimidae indet.			Tokaryk *et al.* (1990)
Dromaeosauridae			
Saurornitholestes Sues 1978			
Saurornitholestes langstoni Sues 1978			Tokaryk *et al.* (1990)
Troodontidae			
Troodon Leidy 1856			
Troodon formosus Leidy 1856			Tokaryk *et al.* (1990)
Tyrannosauridae			
Albertosaurus Osborn 1905			
Albertosaurus sp.			Tokaryk *et al.* (1990)
Nunavut			
Kanguk Formation			
Hadrosauridae			
Hadrosauridae indet.	TMP 1997.04.0002 (centrum)		Russell (1990), Núñez-Betelu *et al.* (2005)
Tyrannosaurid			
Tyrannosaurid indet.			Evans *et al.* (2012)
Heiberg Formation			
Archosauriformes indet.			
Arctosaurus Adams 1875			
Arctosaurus osborni Adams 1875	NMI 62 1971$^{\mathrm{Hg\&s}}$ (cervical vertebra)		Nesbitt *et al.* (2007)

Taxon	Reference specimen	Other material	Reference
Yukon			
Bonnet Plume Formation			
Ornithischia			
Ornithischia indet.	YG 380.2 (pedal phalanx)		Evans *et al.* (2012)
Ornithopoda			
Ornithopoda indet.	YG 380.1 (humerus)		Evans *et al.* (2012)
Hadrosauridae			
Hadrosauridae indet.	UA 19363 (vertebra, metacarpal, rib)		Russell (1984)
Northwest Territories			
Summit Creek Formation			
Ceratopsia			
Ceratopsia indet.	CMN 38507 (distal quadrate)		Russell (1984)
Nova Scotia			
Wolfville Formation			
?Ornithischia indet.	NSM 004 GF 012.001 (maxilla)		Irmis *et al.* (2007)
McCoy Brook Formation			
Sauropodomorpha			
Anchisauridae			
Prosauropod gen. et sp. nov	FGM998GF13-2 (partial skeleton)	multiple skeletons	Fedak (2006), Olsen *et al.* (1987)
Procompsognathidae			
Procompsognathidae indet.			Olsen *et al.* (1987)
Fabrosauridae			
Fabrosauridae indet.	MCZ 9119 (tooth)	teeth and postcrania	Shubin *et al.* (1995), Olsen *et al.* (1987)
cf. *Scutellosaurus*			Olsen *et al.* (1987)

III. Functional morphology, conservation, and ecology

Evolutionary morphology of the lissamphibian braincase

Hillary C. Maddin

Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA

Current address: Department of Earth Sciences, 2125 Herzberg Building, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6, Canada; E-mail: hillary.maddin@carleton.ca

Abstract

The study of the evolutionary morphology of the skull has led to the hypothesis that subunits within the skull behave as internally integrated complexes that vary independently of surrounding subunits (i.e., the modular-skull hypothesis). One such hypothesised module is the braincase. A practical application of this property of the braincase has been in the field of systematics, where braincase morphology has been shown to vary in a phylogenetically informative way. The conservation of this property across a broad taxonomic spectrum suggests that the utility of braincase morphology in addressing evolutionary questions applies to tetrapods in general. One group that may benefit from such application is Batrachia (frogs and salamanders), where uncertainty in aspects of their evolutionary history remains. As a first step towards exploring this potential, the morphology of the braincases of the early diverging frog and salamander species *Ascaphus truei* and *Hynobius naevius*, respectively, is described on the basis of microcomputed tomography and complementary histological sections. The antotic region is found to be variable in its contribution to the foramina enclosing the trigeminal and facial nerves in *A. truei* and *H. naevius,* an area that has been shown to be informative at the family level in caecilians. Comparison between *A. truei* and *H. naevius* reveals strong conservation of the morphology and composition of the braincase and these observations can be extended to caecilians as well. Discussion of the composition of the braincase in a broad phylogenetic context, including relevant fossil taxa, reveals lissamphibian braincase mor-

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BIS Verlag, Oldenburg, Germany.

phology is most consistent with transformations documented in the temnospondyl lineage. Extension of this approach to a broader phylogenetic sampling of batrachian species has the potential to refine taxonomic identifications of fossil specimens, thereby increasing the utility of isolated remains in microvertebrate assemblages and providing improved resolution of taxonomic data points to better understand the evolutionary history of lissamphibians.

Introduction

The craniate skull is composed of tissues of diverse developmental origin (Couly *et al.* 1993) that are integrated via complex morphogenetic processes. Understanding how various factors internal and external to the organism influence the skull to produce novel morphology or, equally as interesting, convergent morphology has been the subject of intense study for over a century (e. g., Darwin 1859). It is becoming increasingly apparent that different regions of the skull behave as internally integrated units that vary somewhat independently of surrounding units because of the interactions of distinct intrinsic properties and the presence of localised constraints (i.e., cranial modularity; Hallgrímsson *et al.* 2004; Goswami 2007; Klingenberg 2008). The braincase is one such region of the skull that is strongly influenced by early developmental constraints in addition to being somewhat buffered from the influence of external factors (Shea 1985; Lieberman *et al.* 2000). That the morphology of the braincase varies independently of the other regions of the skull is supported by a growing body of literature that identifies the braincase as a discrete module within the skull (Cheverud 1996; Hallgrímsson *et al.* 2004, 2007; Goswami 2007).

One practical application of braincase modularity has been in the field of phylogenetics. Recent studies in certain groups of mammals have demonstrated the superior performance of the morphology of the braincase (in contrast to other units of the skull such as the face, cranial vault, and lower jaw) to yield phylogenetic hypotheses congruent with those based on molecular data (Cardini & Elton 2008; Goswami & Polly 2010). Morphological data derived from the braincase is, therefore, of great utility to phylogeneticists when molecular data are sparse or lacking, such as when examining the fossil record. This property of the braincase has been recently shown to apply to caecilian amphibians (Maddin *et al.* 2012b), thereby extending the utility of the braincase to morphology-based phylogenetics of non-amniote tetrapods as well. The potential for the braincase to address phylogenetic questions among the other non-amniote tetrapod groups, frogs and salamanders, remains to be explored in full.

The goal of the current study is to initiate an effort towards documenting variation in braincase morphology in frogs and salamanders, with the aim of revealing new phylogenetically informative data within these groups. As a first step towards this goal, detailed descriptions of the adult morphology of the braincase based on microcomputed tomography (µCT) are provided for the relatively early diverging frog and salamander species, *Ascaphus truei* and *Hynobius naevius*, respectively. Various aspects of the morphology and development of these taxa have been provided previously (e. g., *A. truei*: de Villiers 1934; Pusey 1943; Altig 1969; Reiss 1997; *H. naevius*: Tsusaki 1922; Fox 1959; Carroll & Holmes 1980); however, these studies typically focus on one system at a time (e. g., chondrocranium, dermal skull, nervous system, or musculature) and little comparison across lissamphibian groups is made. By combining µCT techniques with traditional histological data, new information about the three-dimensional osteological morphology of the braincase and its associated soft-tissue structures is obtained, and useful visual data are generated that will facilitate future comparative analyses.

As relatively early diverging representatives of the frog and salamander lineages, analysis of the morphology of the braincases of *A. truei* and *H. naevius* might provide meaningful data for comparisons with various fossil lissamphibians and putative Palaeozoic-aged sister taxa. A more complete understanding of the form and composition of the braincase of representative extant taxa permits discussion in a broad evolutionary context and sheds light on our understanding of lissamphibian phylogeny and evolution, topics that remain the focus of on-going study (Bolt 1991; Trueb & Cloutier 1991; Hedges & Maxson 1993; Milner 1993; Reiss 1996; Laurin & Reisz 1997; Schoch & Milner 2004; Marjanovic & Laurin 2007; Ruta & Coates 2007; Pyron 2011; Fong *et al.* 2012; Maddin & Anderson 2012).

Institutional abbreviations: FMNH, Field Museum of Natural History, Chicago, IL; MVZ, Museum of Vertebrate Zoology, University of California Berkeley, Berkeley, CA; UAMZ, University of Alberta Museum of Zoology, Edmonton, AB; and UMMZ, University of Michigan Museum of Zoology, Ann Arbor, MI.

Materials and methods

Specimens

A dried skull of an adult specimen of the ascaphid frog *A. truei* (UMMZ 152263; skull length 12 mm) and an alcohol-preserved, whole specimen of the hynobiid salamander *H. naevius* (UAMZ 3635; skull length 7 mm) were obtained for study. The specimens were subjected to µCT at the University of Calgary (Calgary, Alberta). The scans of *A. truei* and *H. naevius* were performed on a SkyScan 1173 scanner at 80 kVp and 60 µA with a voxel resolution of 21.5 μm^3 and 12.1 μm^3, respectively.

Histological slides of mature individuals of *A. truei* and *Salamandrella keyserlingii* (another hynobiid salamander) were also available for study. These slides are currently curated by D. Wake at the MVZ. Slide-book numbers are S-720 and S-533 for *A. truei* and *S. keyserlingii*, respectively.

Visualisation of microcomputed tomography

All scan data were down-sampled to a maximum of 512 pixels in any orientation, rendered as 8-bit grey scale TIFFs using the batch processing function in Photoshop CS2, and imported into Amira v4 and v5 (Visage Imaging; San Diego, CA) as a series of stacked images. The elements of the braincase were isolated by labelling structures using the LabelFields module and visualised by applying the SurfaceGen and SurfaceView modules to the labelled data. The morphology of the braincase and stapes is described here based on the three-dimensional SurfaceView models generated from the µCT data sets. Linear and angular measurements were taken using the 3D-line and 3D-angle measurement tools, respectively, in Amira v5.

Phylogenetic interpretations

Patterns of braincase evolution were inferred using the phylogenetic hypothesis of extinct and extant amphibians of Maddin *et al.* (2012a). The 50% majority-rule consensus tree of Maddin *et al.* (2012a) was used as a backbone for the optimisation of braincase element character states (presence/absence) to visualise the locations of transformations in the evolution of the non-amniote braincase. The program MacClade v4.08a OSX was used and both the ACCTRAN and DELTRAN optimisation criteria were selected and compared. The results are discussed below as they pertain to competing hypotheses of lissamphibian phylogeny.

Results

General morphology of the batrachian braincase

The general morphology of the osseous braincase of frogs and salamanders is similar. The ossifications comprising the braincase of batrachians are reduced in comparison to the plesiomorphic non-amniote tetrapod condition. Ossifications of the anterior region of the braincase include only the sphenethmoid (Noble 1931), which is often referred to as the orbitosphenoid because of its general restriction to the orbital (Francis 1934; de Beer 1937; Rose 2003; ethmoid of Gaupp 1896–1904). The orbitosphenoid of batrachians is variable in size, ranging from a very small, crescent-shaped bone in some frogs to a more robust, rectangular bone in some salamanders (Parker 1876, 1881; Duellman & Trueb 1994). This differs from the condition seen in caecilians in which the element termed the sphenethmoid is a robust, composite element enclosing the forebrain anteriorly and laterally. In many frogs, the orbitosphenoids are fused ventrally into one unit (Parker 1881; Gaupp 1896–1904), whereas the orbitosphenoids remain paired in salamanders (Francis 1934; Trueb 1993).

The posterior region of the braincase is composed of the otic-occipital complex. This complex includes the otic capsules and the occipital surface with the paired occipital condyles. The otic capsule is generally a single element in adult frogs and salamanders; however, the composite nature of this ossification is sometimes apparent as a median suture or incomplete ossification, separating it into anterior and posterior units. The exoccipital is typically indistinguishably fused to the otic capsule and forms the occipital condyle. The supraoccipital, basioccipital, and basisphenoid are considered to be lost in batrachians (Duellman & Trueb 1994; Müller 2006) as well as in lissamphibians in general.

The parasphenoid forms the floor of the braincase. Anteriorly, the parasphenoid is elongate and slightly concave dorsally. It makes contact with the ventral margin of the orbitosphenoid in the orbital region. Posteriorly, the parasphenoid expands laterally, cupping the otic capsules from below. In batrachians, the parasphenoid remains distinct from the otic capsule ossifications, in contrast to the condition seen in caecilians where it fuses indistinguishably with the otic capsules to form the composite os basale (Duellman & Trueb 1994).

Morphology of the braincase of *Ascaphus truei*

The orbitosphenoid is a small element in *A. truei* (Fig. 1A and E). The anterior margin of the orbitosphenoid is strongly rounded and the posterior margin is deeply incised by the anterior margin of the optic foramen, resulting in an overall crescent-like shape (Fig. 1E). The dorsal and ventral posterior apices of the crescent are blunt and would be continuous with the unossified portions of the orbital and trabecular cartilages, respectively. Dorsally, the orbitosphenoid contacts the medial surface of the lateral-most edge of the frontoparietal (Fig. 1A). Ventrally, the orbitosphenoid rests on the lateral margins of the parasphenoid (Fig. 1B).

In dorsal view, the entire otic-occipital complex is the shape of a rounded rectangle that is roughly twice as wide laterally as it is long (Fig. 1A). Contours on the dorsal surface of the otic capsules correspond to the anterior and posterior semicircular canals of the enclosed inner ear. These canals can be seen to be oriented orthogonally to one another, and together they are angled from the long axis of the skull by about 45º (Fig. 1A). A zone of weak ossification within the otic capsule is visible in dorsal and ventral views as a disruption of the lateral outline in the location of the midpoint of the horizontal semicircular canal (Fig. 1A, B, and E). This gap is completed by cartilage.

Two osseous processes extend anteriorly from the anterodorsal margin of the otic capsule (Fig. 1E and F). Both end in roughened surfaces that are continuous with cartilage, the taenia marginalis dorsally and the ascending process of the palatoquadrate cartilage ventrally (Reiss 1997). The space between these processes corresponds to the posterior margin of the prootic foramen, which serves to transmit the maxillary-mandibular trunk of the trigeminal nerve (Fig. 2A). The ophthalmic branch of the trigeminal exits the brain cav ity ventral to the ascending process through a foramen bounded posteriorly by the otic capsule (Fig. 2B). A thin sheet of bone that is continuous with the dorsal surface of the posterior portion of the otic capsule extends medially (Fig. 1D). It approaches its bilateral counterpart near the midline of the skull. The posterior margin of this sheet forms the dorsolateral margin of the foramen magnum. Ventral to this sheet, the occipital condyle protrudes posteriorly.

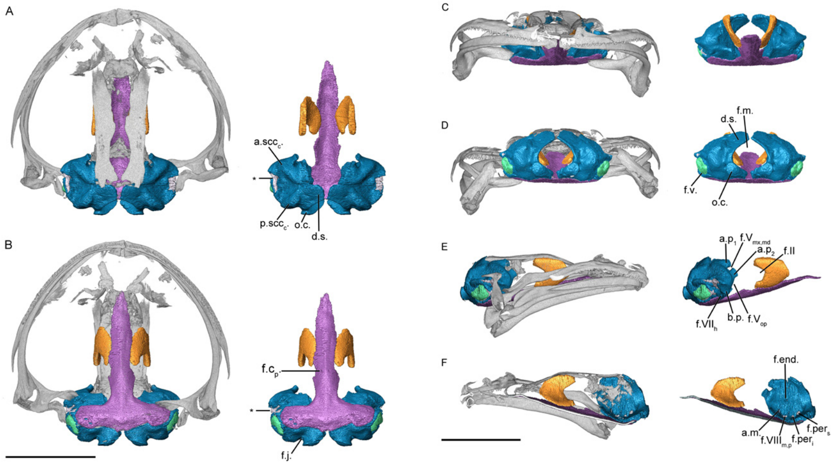

Figure 1:
Microcomputed-tomography volume renderings of the complete skull (left) and isolated elements of the braincase (right) of the frog *Ascaphus truei* (UMMZ 152263). A small orbitosphenoid (orange) forms the anterolateral walls of the braincase and the otic-occipital complex (blue) is located posteriorly. A zone of weak ossification (asterisk) is located in the middle of the lateral surface of the otic capsule. The middle-ear ossicle (green), the operculum, fills the entire fenestra vestibuli and the parasphenoid (purple) forms the floor of the brain cavity. An inner-ear endocast (grey) was generated to help visualise features of the otic capsule (e. g., zone of weak ossification or foramina). Views: A, dorsal; B, ventral; C, anterior; D, posterior; E; right lateral; and F, right medial. Abbreviations: a.m., auditory meatus; a.p$_1$, anterior process 1 of the otic capsule (connects to taenia marginalis); a.p$_2$, anterior process 2 of the otic capsule (connects to ascending process of the palatoquadrate); a.scc$_c$., contour of the anterior semicircular canal; b.p., facet for receipt of the basal process of the palatoquadrate; d.s., dorsal surface of the otic-occipital complex; f.c$_p$, foramen for the palatal branch of the carotid artery; f.end., endolymphatic foramen; f.j., jugular foramen; f.m., foramen magnum; f.per$_i$, inferior perilymphatic foramen; f.per$_s$, superior perilymphatic foramen; f.v., foramen vestibuli; f.II, optic foramen; f.V$_{mx,md}$, foramen for the maxillary-mandibular trunk of the trigeminal nerve; f.V$_{op}$, foramen for the ophthalmic branch of the trigeminal nerve; f.VII$_h$, foramen for the hyomandibular ramus of the facial nerve; f.VIII$_{m,d}$, foramen for the medial and posterior branches of the vestibulocochlear nerve; o.c., occipital condyle; and p.scc$_c$., contour of the posterior semicircular canal. Scale bars equal 5 mm.

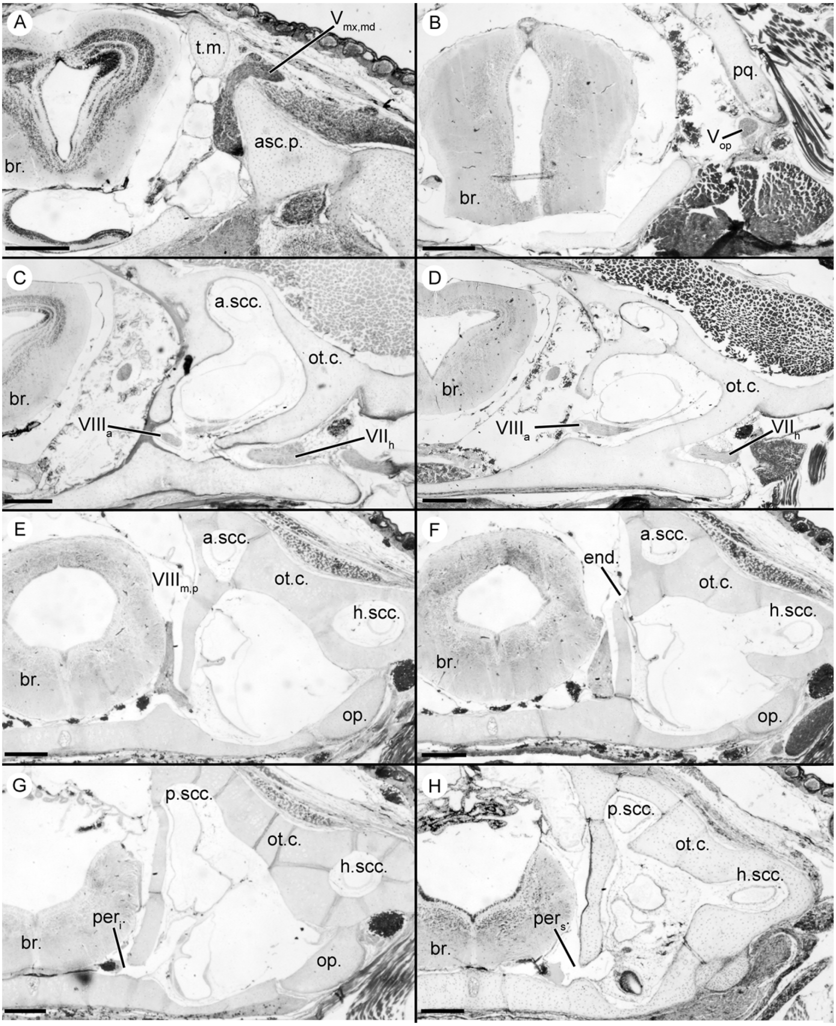

Figure 2:
Transverse histological sections of the frog *Ascaphus truei* (MVZ slide book S-720), passing through the skull in an anterior to posterior direction (A→H). A, the maxillary-mandibular trunk of the trigeminal passes through the foramen bounded by the two anterior processes of the otic capsule and parts of the chondrocranium (depicted here). B, the ophthalmic branch of the trigeminal nerve passes ventrally between the palatoquadrate and the parasphenoid. C, the anterior branch of the vestibulocochlear nerve passes through the auditory *(continued overleaf)*

(continued from overleaf) meatus to the inner ear. D, the hyomandibular ramus of the facial nerve continues laterally and exits the braincase. E, the medial and posterior branches of the vestibulocochlear nerve enter the inner ear just posterior to the anterior branch. F, the endolymphatic duct enters the brain cavity dorsal to the vestibulocochlear nerve branches. G, the inferior perilymphatic sac enters the brain cavity in the posterior region of the otic capsule. H, the superior perilymphatic sac enters the brain cavity posterior to the inferior sac. Abbreviations: a.scc., anterior semicircular canal; asc.p, ascending process of the palatoquadrate; br., brain; h.scc., horizontal semicircular canal; op., operculum; ot.c., otic capsule; p.scc., posterior semicircular canal; per_{i}., inferior perilymphatic sac; per_{s}., superior perilymphatic sac; pq., palatoquadrate; t.m., taenia marginalis; $V_{mx,md}$, maxillary-mandibular trunk of the trigeminal nerve; V_{op}, ophthalmic branch of the trigeminal nerve; VII_{h}, hyomandibular ramus of the facial nerve; $VIII_{a}$, anterior branch of the vestibulocochlear nerve; $VIII_{m,p}$, and medial and posterior branches of the vestibulocochlear nerve. Scale bars equal 300 μm.

In lateral view, the otic capsule is circular in outline (Fig. 1E). The zone of weak ossification present near the midpoint of the otic capsule exposes a portion of the horizontal semicircular canal. In lateral view, the dorsal portion of the otic capsule is bounded by the contours corresponding to the anterior and posterior semicircular canals. Between them, the surface is inclined dorsomedially. The squamosals do not form a close contact with the dorsal surface of the otic capsules and overlap by the parietals is restricted to a small anterior region medial to the anterior semicircular canal (Fig. 1A).

The anterior half of the ventral portion of the otic capsule bears a roughened facet for receiving the palatobasal process of the palatoquadrate (Fig. 1E; Reiss 1997). Posterior and ventral to this facet is a small foramen that serves to transmit the hyomandibular ramus of the facial nerve (Figs. 1E and 2C). The posterior half of the ventral portion of the otic capsule is occupied by the slightly anteroposteriorly ovoid fenestra vestibuli (Fig. 1E). The occipital condyle projects slightly beyond the posterior margin of the otic capsule in lateral view. The jugular foramen, which occurs in the base of the condyle, is not visible in lateral view (Fig. 1E).

In posterior view, the otic-occipital complex is somewhat kidney-shaped in outline, with a slightly convex dorsal margin (Fig. 1D). The fenestra vestibuli is visible at the lateral margins of the complex. A roughly circular foramen magnum is located centrally on the occipital surface, the diameter of which is roughly one-third of the width of the entire complex in posterior view (Fig. 1D). The paired occipital condyles occupy the ventrolateral corners of the foramen magnum.

The medial surface of the otic capsule is relatively well ossified (Fig. 1F). An arc of five foramina pierces the ventral margin of the medial wall of the otic capsule. The anterior-most foramen leads to a short anterolaterally directed canal termed the auditory meatus (Reiss 1997). A foramen opening to the inner ear pierces the posterior wall of the auditory meatus (Fig. 1F). This foramen transmits the anterior branch of the auditory nerve to the ampullae of the anterior and horizontal semicircular canals as well as to the utricular macula (Fig. 2C). The meatus continues laterally, carrying the hyomandibular ramus of the facial nerve, and eventually exits at the small foramen located on the lateral surface of the otic capsule just posterior to the articular facet for the basal process of the palatoquadrate (Fig. 2D).

The next foramen, located posterior to the opening of the auditory meatus, is large (Fig. 1F). Its location corresponds to that of a pair of foramina identified as transmitting the medial and posterior branches of the auditory nerve (Fig. 2E; de Villiers 1934). A small process extends ventrally from the dorsal margin of this foramen, suggesting that division of this large foramen by an osseous boundary is incomplete in this individual (Fig. 1F). Dorsal to this foramen is a small foramen located at roughly the centre point of the otic capsule. It serves to transmit the endolymphatic sac to the brain cavity (Fig. 2F). The posterior-most foramina are the superior and inferior perilymphatic foramina, which transmit the perilymphatic sacs into the brain cavity (Fig. 2G and H).

The parasphenoid is a very thin sheet of bone that forms the floor of the brain cavity (Fig. 1B). Anteriorly, the parasphenoid is long, narrow, and slightly concave dorsally, resulting in a somewhat trough-like form (Fig. 1C) before tapering to a blunt point. The parasphenoid expands slightly laterally posterior to the contact with the orbitosphenoids in the area ventral to the optic foramen. In this region, a pair of small foramina also pierces the parasphenoid (Fig. 1B). These foramina transmit the palatal branches of the internal carotid artery. Discrete foramina serving as the entrance point for the carotid arteries are not present in *A. truei*. Instead, the carotids enter the brain cavity just anterior to the otic-occipital complex in an area bounded by the otic capsules dorsally and parasphenoid ventrally. Below the otic capsules, the parasphenoid expands abruptly, cupping the otic capsules from below (Fig. 1B). This results in a T-shaped outline of the parasphenoid in *A. truei*. The muscle attachment site for the hypaxial muscles of the neck (e. g., subvertebralis; Carroll & Holmes 1980) contours the ventral surface of the posterior portion of the parasphenoid.

A single, disc-like middle-ear ossicle is present in *A. truei* (Fig. 1E). This has been identified as the operculum (de Villiers 1934); however, it remains possible this ossicle could actually be a stapes lacking a columellar process. The ossicle is somewhat ovoid in outline, filling the fenestra vestibuli. A roughened patch on the posterodorsal region of the lateral surface indicates the location of the insertion point of a slip of the m. levator scapulae superior (the "opercularis" muscle of some authors; see Monath 1965) onto this ossicle (Fig. 1E; de Villiers 1934). No process or foramen is present on the ossicle.

Morphology of the braincase of *Hynobius naevius*

The orbitosphenoid is an anteroposteriorly elongate, rectangular element in *H. naevius* (Fig. 3E). The orbitosphenoid is inclined slightly dorsolaterally away from the midline (Fig. 3C). The anterior margin of the orbitosphenoid is straight and nearly vertically oriented. The posterior margin is deeply incised by the anterior margin of the optic foramen (Fig. 3E and F). Dorsal and ventral to the optic foramen, the posterior margin terminates in roughened surfaces that continue in cartilage similar to the condition seen in *A. truei*. These are the orbital and trabecular cartilages, respectively. Dorsally, the orbitosphenoid contacts the medial surface of the lateral-most edge of the frontal anteriorly and of the parietal posteriorly (Fig. 3A). Ventrally, the orbitosphenoid rests on the lateral margins of the anterior portion of the parasphenoid (Fig. 3B). The anterior region of the ventral margin of the orbitosphenoid curves towards the midline, creating a medially directed, pointed process (Fig. 3A).

The otic-occipital complex is in the shape of a rounded rectangle with its long axis oriented transversely (Fig. 3A). In dorsal view, the otic-occipital complex is roughly two-thirds as long anteroposteriorly as it is wide laterally (Fig. 3A). The dorsal surface of the otic capsules is weakly contoured by the anterior and posterior semicircular canals of the enclosed inner ear. These canals are oriented at a wider angle than those in *A. truei* (possibly indicative of a functional difference between taxa), at roughly 104º to one another. The anterior and posterior canals are oriented at angles of 40º and 36º, respectively, from the long axis of the skull. The anterior canal also delimits the anterior margin of the contact point for the squamosal bone (Fig. 3A). Medial to the squamosal, the parietal covers the anteromedial portion of the otic-occipital complex. Medial to the anterior semicircular canal is a thin sheet of bone that receives a ventrally curved, pointed flange of the parietal (Fig. 3E). A more robust, anteriorly directed process extends from the ventral margin of the otic capsule and is continuous with the posterior trabecular cartilage (Fig. 3E and F). Between these processes is the posterior margin of the prootic foramen, which serves to transmit the entire trigeminal nerve (Fig. 3F).

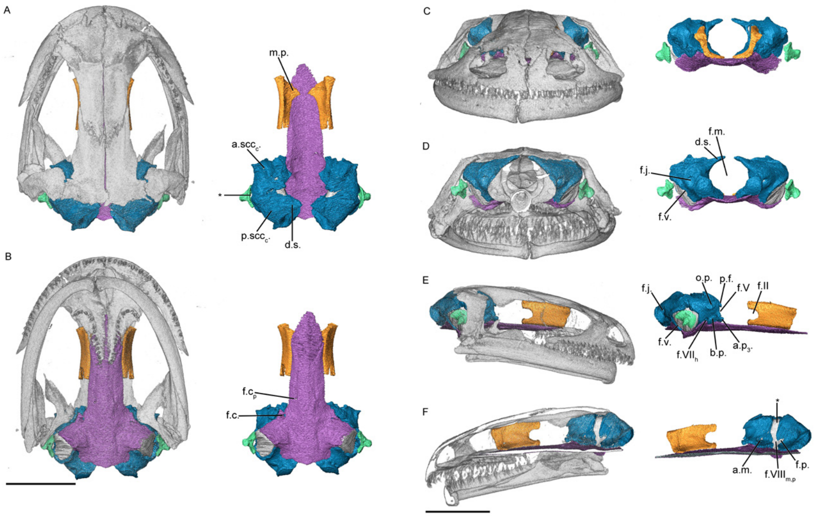

Figure 3:
Microcomputed-tomography volume renderings of the complete skull (left) and isolated elements of the braincase (right) of the salamander *Hynobius naevius* (UAMZ 3635). A rectangular orbitosphenoid (orange) forms the anterolateral walls of the braincase and the otic-occipital complex (blue) is located posteriorly. A vertical zone of weak ossification (asterisk) is located on the medial surface of the otic capsule. The middle-ear ossicle (green), the stapes, fills the anterior half of the fenestra vestibuli (the operculum is cartilage and fills the posterior half) and the parasphenoid (purple) forms the floor of the brain cavity. An inner-ear endocast (grey) was generated to help visualise features of the otic capsule (e. g., zone of weak ossification or foramina). Abbreviations: a.m., auditory meatus; a.p$_3$., anterior process 3 of the otic capsule (connects with the trabecular cartilage); a.scc$_c$., contour of the anterior semicircular canal; b.p., facet for receipt of the basal process of the palatoquadrate; d.s., dorsal surface of the otic-occipital complex; f.c., foramen for the carotid artery; f.c$_p$, foramen for the palatal branch of the carotid artery; f.j., jugular foramen; f.m., foramen magnum; f.v., foramen vestibuli; f.II, optic foramen; f.V, foramen for the trigeminal nerve; f.VII$_h$, foramen for the hyomandibular ramus of the facial nerve; f.VIII$_{m,d}$, foramen for the medial and posterior branches of the vestibulocochlear nerve; m.p., medial process of the sphenethmoid; o.p., facet for receipt of the otic process of the palatoquadrate; p.f., flange for receipt of the parietal; and p.scc$_c$., contour of the posterior semicircular canal. Scale bars equal 2 mm.

A zone of poor ossification of the otic capsule typical of even mature lissamphibians is visible in dorsal view as a disruption of the medial outline at roughly the midpoint location of the otic capsule (Fig. 3F). This zone divides the medial wall of the otic capsule into anterior and posterior halves. A small gap is also present on the lateral margin in the area of the horizontal semicircular canal. These gaps are completed by cartilage. A thin sheet of bone continuous with the dorsal surface of the posterior half of the otic capsule extends medially (Fig. 3C and D) similar to that seen in *A. truei*. It approaches its bilateral counterpart near the midline of the skull. The posterior margin of this sheet forms the dorsolateral margin of the foramen magnum.

In lateral view, the dorsal portion of the otic capsule is bounded by the contours of the anterior and posterior semicircular canals (Fig. 3E). Between them, the surface is only slightly inclined dorsomedially. The anterior half of the ventral portion of the otic capsule bears a pair of roughened facets (Fig. 3E). The dorsal facet is directed towards the medial surface of the squamosal and contacts the otic process of the palatoquadrate cartilage. The ventral facet is directed towards a trough in the pterygoid that is filled by the basal process cartilage of the palatoquadrate as seen in the histology of the closely related taxon *Salamandrella keyserlingii* (Fig. 4A; Rose 2003). Posterior to the ventral facet is a small foramen that serves to transmit the hyomandibular ramus of the facial nerve (Figs. 3E and 4B). The remainder of the ventral portion of the otic capsule is occupied by the large, somewhat diamond-shaped fenestra vestibuli (Fig. 3E). The occipital condyle is large and projects well beyond the posterior margin of the otic capsule in lateral view. The jugular foramen in the base of the condyle is visible in lateral view (Fig. 3E).

In posterior view, the otic-occipital complex is trapezoidal in outline, with the dorsal side longer than the ventral side (Fig. 3D). The fenestra vestibuli is visible at the lateral margins of the complex. A roughly circular foramen magnum is located centrally on the occipital surface, the diameter of which is about one-third of the width of the entire complex in posterior view (Fig. 3D). The large occipital condyles occupy the ventrolateral corners of the foramen magnum. The jugular foramina are visible in posterior view.

The medial surface of the otic capsule is relatively well ossified except for the vertical line of weak ossification (Fig. 3F). Only a single foramen is closed completely by bone on the medial surface of the otic capsule; three others are partially or completely formed by the cartilage filling the zone of poor ossification. The single foramen completed by osseous margins is the foramen within the auditory meatus that serves to transmit the anterior branch of the auditory nerve to the inner ear (Fig. 3F). The auditory meatus continues laterally, transmitting the hyomandibular ramus of the facial nerve to the external surface of the braincase via the foramen located just posterior to the articular facet for the basal process of the palatoquadrate (Fig. 3E).

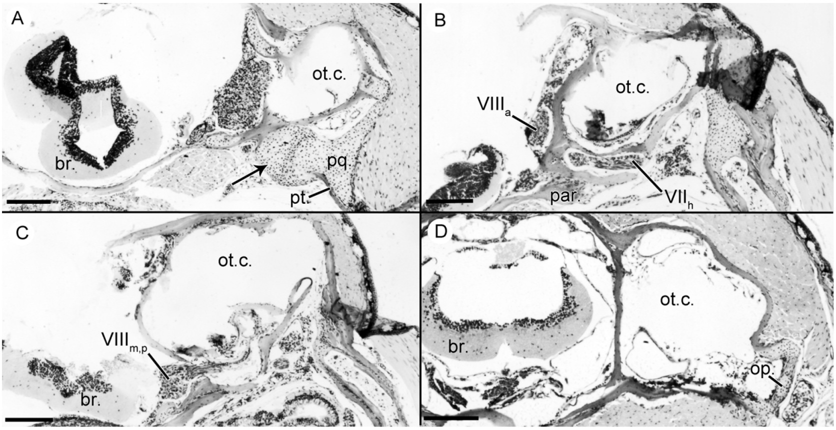

Figure 4:
Transverse histological sections of the hynobiid salamander *Salamandrella keyserlingii* (MVZ slide book S-533), passing through the skull in an anterior to posterior direction (A→D). A, the cartilage (arrow) residing within the osseous facet that receives the basal process of the palatoquadrate. B, the anterior branch of the vestibulocochlear nerve and hyomandibular ramus of the facial nerve passing through the auditory meatus. The opening for the vestibulocochlear nerve to the inner ear is not visible in this section. C, the medial and posterior branches of the vestibulocochlear nerve passing into the inner ear. D, the cartilaginous operculum occupies the posterior portion of the fenestra vestibuli. Abbreviations: br., brain; op., operculum; ot.c., otic capsule; par., parasphenoid; pq., palatoquadrate; pt., pterygoid; VII$_h$, hyomandibular ramus of the facial nerve; VIII$_a$, anterior branch of the vestibulocochlear nerve; and VIII$_{m,p}$, medial and posterior branches of the vestibulocochlear nerve. Scale bars equal 300 μm.

The rest of the foramina posterior to the opening of the auditory meatus are located partially or completely within the zone of poor ossification. Partial anterior and posterior osseous margins of a foramen are located on either side of the gap. With the remaining margins completed in cartilage, the anterior foramen transmits the medial and posterior branches of the auditory nerve to the inner ear (Fig. 4C). The posterior partially ossified foramen is the perilymphatic foramen, which serves to transmit the perilymphatic sac to the brain cavity. A fourth foramen, the endolymphatic foramen, is enclosed completely by cartilage in the zone of poor ossification just dorsal to the foramen for the medial and posterior branches of the auditory nerve.

The parasphenoid is a very thin sheet of bone that forms the floor of the brain cavity (Fig. 3B). Anteriorly, the parasphenoid is long, narrow, and slightly concave dorsally. Its anterior tip is pointed and the region is underlain by the paired vomers (Fig. 3B). At the level of the otic capsules, the parasphenoid expands laterally, forming a diamond-shaped posterior portion in contrast to the T-shaped parasphenoid of *A. truei*. A pair of foramina pierces the parasphenoid near the lateral edges just ventral to the foramen transmitting the hyomandibular ramus of the facial nerve in the otic-occipital complex (Fig. 3B). These foramina transmit the internal carotid arteries to the brain cavity. Anteriorly, the palatal branches of the carotids pass out through a pair of small foramina in the parasphenoid anterior to the otic-occipital complex (Fig. 3B). Below the otic capsules, the parasphenoid cups the otic capsule, completing the braincase floor in *H. naevius*. The muscle attachment site for the hypaxial muscles of the neck gently contours the ventral surface of the posterior portion of the parasphenoid.

A single, ossified middle-ear ossicle is present in *H. naevius*; however, unlike the single ossicle in *A. truei*, the ossicle in *H. naevius* is more certainly identified as the stapes. It is noteworthy that the complement of ossicles in the middle ear of salamanders is highly variable, which has led to difficulty in assessing their homology (see Kingsbury & Reed 1909; Monath 1965). The presence of a columellar process on the ossicle in *H. naevius* and the presence of a large gap presumably filled by the operculum supports the identification of the osseous ossicle in *H. naevius* as the stapes and not as an operculum or fused stapes-operculum. The footplate of the stapes of *H. naevius* is half-moon shaped, occupying only the dorsal to anterodorsal portion of the fenestra vestibuli (Fig. 3E). In *S. keyserlingii*, the remainder of the fenestra vestibuli is filled with the cartilaginous operculum (Fig. 4D). An operculum is also present in *H. naevius* (Monath 1965); however, it is cartilaginous and so is not detected in the µCT data. A robust columellar process is present and directed towards the medial surface of the squamosal.

Phylogenetic interpretations

Optimisation of braincase bone presence/absence was conducted on the hypothesised evolutionary relationships presented in Maddin *et al.* (2012a) to explore possible patterns of braincase evolution in non-amniote tetrapods. DELTRAN and ACCTRAN options were largely unambiguous with few exceptions. The location of basisphenoid loss is unambiguously resolved as occurring on the stem of the clade uniting lissamphibians and their closest stem-group relatives. Under the DELTRAN option, basioccipital loss occurs at the base of the clade including *Tersomius-Micropholis* and relatives, whereas, under the ACCTRAN option, the loss occurs one node deeper. This difference is because Branchiosauridae and Micromelerpetontidae are scored as unknown for this character and the different optimisations infer different states for the missing entries of these taxa (i.e., absent under DELTRAN, but present under ACCTRAN). The locations of the independent losses of the supraoccipital among members of the lepospondyl plus stem-amniote *Limnoscelis* clade also differ slightly between the two optimisations. Appearance of the supraoccipital on the stem of this clade, however, is unambiguously resolved.

Discussion

Conservation of the lissamphibian braincase

The above descriptions and analysis emphasise the conserved nature of the batrachian braincase in terms of its structure and composition. Comparison with previous work on the braincase of caecilians (Maddin 2011; Maddin *et al.* 2012b) further demonstrates a broad conservation of most of these aspects across lissamphibians in general.

The anterior ossification, variably termed the orbitosphenoid or sphenethmoid in lissamphibians (Noble 1931; Francis 1934; Ramaswami 1941), is typically restricted to the region anterior to the optic foramen (Fig. 5). In lissamphibians, the orbitosphenoid represents an ossification that initiates in the preoptic root of the orbital cartilage (i.e., the pila preoptica) and spreads posteriorly (Rose 2003; Dulcey Cala *et al.* 2009). In most salamanders, this ossification encloses the optic foramen completely (Francis 1934; Rose 2003). In caecilians, the ossification in this region termed the sphenethmoid includes additional ossifications such as the anterior wall, nasal septum, and dorsomedial process, all of which are located anterior to the optic foramen. This is in contrast to the structure termed the orbitosphenoid or sphenethmoid in amniote taxa (de Beer 1926) such as reptiles. When present, the orbitosphenoid of amniotes arises via ossification of the cartilages posterior to the optic foramen (de Beer 1926; Shaner 1926; Bellairs 1949), namely the posterior portion of the orbital cartilage, the pila metoptica, and pila antotica (Bellairs 1949). Referring to these bones, which arise from different regions of the chondrocranium, with the same name gives an inaccurate impression of homology from both topological and developmental perspectives. Whereas it is not appropriate to propose new names for these elements at this time given the lack of a complete understanding of morphological and developmental variation in these ossifications in both the lissamphibian and reptile clades, the term orbitosphenoid should be used with caution in a broadly comparative context. The key point here, however, is that in this area of variably ossifying parts of the chondrocranium, all lissamphibians possess an ossification in this conserved position and that this ossification appears to differ from the similarly-named ossification of amniotes.

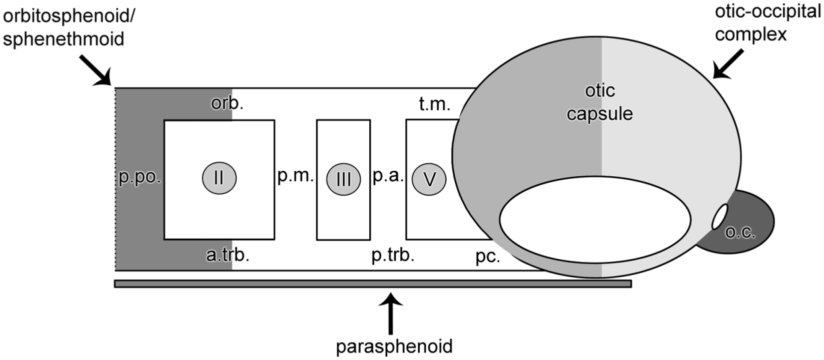

Figure 5:
Schematic illustration of the generalised lissamphibian braincase, depicting the composition and developmental origin of the components. The orbitosphenoid is derived from the ossification of the chondrocranium anterior to the optic foramen. The otic-occipital complex is composed of the prootic (middle grey) and opisthotic (light grey) ossifications, making up the otic capsule and the exoccipital (dark grey) of the occiput. The parasphenoid forms the floor of the brain cavity. All three groups possess this conserved *Bauplan*; however, caecilians additionally incorporate ossifications of the taenia marginalis, pila antotica, and posterior trabecular cartilages as well as the parasphenoid into the otic-occipital complex, forming the os basale ossification.

The posterior portion of the braincase, the otic-occipital complex, is also strongly conserved among batrachians in terms of its structure and composition. This conservation can be extended to caecilians as well with only slight modification (discussed below). In plesiomorphic, non-amniote tetrapods, the otic capsule is formed by the prootic (anteriorly) and the opisthotic (posteriorly) ossifications (Romer 1962). These bones are typically indistinguishably fused in adults, making the otic capsule a composite structure (de Beer 1937; Romer 1962). All developmental studies of lissamphibian taxa support the identification of distinct ossifications comprising the osseous otic capsule (e. g., frogs: *Ascaphus* [Altig 1969], *Hyla* [de Sá 1988], and *Hamptophyrne* [de Sá & Trueb 1991]; salamanders: *Ambystoma* [Bonebrake & Brandon 1971], *Eurycea* [Rose 1995], and *Siren* [Reilly & Altig 1996]; caecilians: *Hypogeophis* [Müller 2006], *Gegeneophis* [Müller *et al.* 2005], and *Dermophis* [Wake & Hanken 1982]) and, therefore, support the retention of the plesiomorphic condition including discrete prootic and opisthotic ossifications. Interestingly, the prootic itself has been observed to also be composite, being composed of a dorsal pterotic and ventral prootic ossification (Worthington & Wake 1971). In the batrachian taxa examined here, remnants of a suture dividing the otic capsule into anterior and posterior halves is present.

In many studies of modern lissamphibian anatomy, the posterior ossification is termed the exoccipital rather than the opisthotic (Duellman & Trueb 1994). This naming convention likely stems from the lack of observed discrete opisthotic and exoccipital ossifications as well as from aspects of the development of this region. The exoccipital is an ossification of the cartilaginous occipital arch (de Beer 1937; Romer 1962). At early stages in development, the occipital arch is separated from the otic capsule by the metotic fissure (de Beer 1937; Fox 1959; Schmalhausen 1968). During development, the cartilage of the occipital arch fuses to that of the otic capsule, thereby closing the metotic fissure. The closure of this fissure completes the jugular foramen and encloses the glossopharyngeal and vagus nerves (de Beer 1937). Despite this closure, the ossifications of the posterior otic capsule (opisthotic) and occipital arch (exoccipital) remain discrete in the Palaeozoic non-amniote tetrapods, separated by a suture that forms along the metotic fissure (e. g., *Acheloma*; Maddin *et al.* 2010). By contrast, there is no sutural trace of the fissure in any known extant lissamphibian. Additionally, only a single centre of ossification forms the occiput and the posterior part of the otic capsule, so it appears that only a prootic and exoccipital ossification are present in many species (e. g., frogs: *Acris* [Maglia *et al.* 2007] and *Hyla* [de Sá 1988]; salamanders: *Notophthalmus* [Reilly 1986] and *Eurycea* [Rose 1995]; caecilians: *Dermophis* [Wake & Hanken 1982] and *Gegeneophis* [Müller *et al.* 2005]). In these cases, the posterior ossification initiates in the condyle, like the exoccipital, and subsequently spreads anteriorly to cover the posterior part of the otic capsule. No separate opisthotic ossification centre is observed in these taxa.

However, developmental evidence supports the presence of a discrete opisthotic in some species. Several studies of early development report the presence of a discrete centre of ossification in the occipital arch (the exoccipital) and its subsequent fusion to an ossification in the posterior otic capsule (opisthotic) (e. g., frogs: *Ascaphus* [Altig 1969]; salamanders: *Ambystoma* [Bonebrake & Brandon 1971] and *Siren* [Reilly & Altig 1996]), supporting the retention of the plesiomorphic osseous composition of the otic-occipital complex in these species.

Is an opisthotic ossification present or absent, or both, in lissamphibians? The answer to this question relies partly on the criteria used to define the element. A topological definition can identify any ossification of the posterior otic capsule between the prootic and metotic fissure as an opisthotic. By contrast, a developmental definition might require an ossification centre discrete from the exoccipital to be present to consider an opisthotic as being present. In lissamphibians, it might be difficult to definitively detect a separate ossification centre in the posterior otic-capsule region given the close proximity of the opisthotic ossification to the exoccipital and the synchronised spreading of their ossifications (Altig 1969; Bonebrake & Brandon 1971). Therefore, failure of the opisthotic and exoccipital ossification centres to be differentiated from one another does not preclude the presence of an opisthotic and does not necessarily violate a developmental definition of its presence. Finer resolution of developmental series and histological analysis of the ossifying opisthotic and exoccipital regions would help resolve the homology of the posterior otic ossification. Until this time, given the uncertainty in the developmental data, the posterior ossification observed in adult batrachians could be more accurately referred to as the opisthotic-exoccipital (Carroll & Holmes 1980; Carroll 2007).

Where the braincase of caecilians differs from the above-described conserved structure of the batrachian braincase is in the addition of two neighbouring regions, rather than through deviations from the conserved batrachian *Bauplan*. First, caecilians incorporate ossifications of the taenia marginalis, parachordal cartilage, and pila antotica to the anterior surface of the prootic. This ossified region has been termed the pleurosphenoid (Carroll 2007; Jenkins *et al.* 2007), but might be more generally referred to as the antotic ossification to prevent an impression of homology with the reptilian pleurosphenoid (Rieppel 1976), something that is unclear at this time. Second, caecilians fuse the otic-occipital complex to the margins of the underlying parasphenoid, forming the composite os basale element. The otic-occipital complex portion of the os basale is consistent in its composition with that of batrachians. An anterior prootic ossification forms within the anterior otic capsule and a posterior exoccipital ossification forms within the occipital condyle and spreads anteriorly to cover the posterior otic capsule (Wake & Hanken 1982; Müller *et al.* 2005; Müller 2006). An opisthotic has not been named in a caecilian because of the similar apparent lack of a discrete ossification centre within the posterior part of the otic capsule (Wake & Hanken 1982; Müller *et al.* 2005; Müller 2006).

Implications for braincase evolution and lissamphibian phylogeny

The overall similarity of braincase structure and composition exhibited by members of the three lissamphibian groups is undeniable and invokes hypotheses of shared evolutionary transitions. This is relevant in light of ongoing debate concerning the nature of the relationships among the three living groups and the various fossil lineages of non-amniote tetrapods (Milner 1993; Laurin & Reisz 1997; Ruta & Coates 2007; Anderson *et al.* 2008; Pyron 2011; Fong *et al.* 2012). The composition of the lissamphibian braincase is characterised by the absence of several elements, namely the basisphenoid, basioccipital, and supraoccipital (Schoch & Milner 2004; Müller 2006). In lissamphibians, the portions of the chondrocranium that give rise to the basisphenoid and basioccipital appear to be absent and, in caecilians, the tectum synoticum, which gives rise to the supraoccipital, is also absent (de Beer 1937). In contrast to the pattern of loss of elements of the dermal skull, which is highly homoplastic across tetrapods, the pattern of loss of elements of the braincase does not vary to the same degree. In fact, it appears that the basisphenoid and basioccipital ossifications are lost only once among non-amniote tetrapods in positions along the stem of the lissamphibian clade and that the supraoccipital ossification might appear only once on the stem of the lepospondyl-amniote clade, although it is lost again several times (Fig. 6).

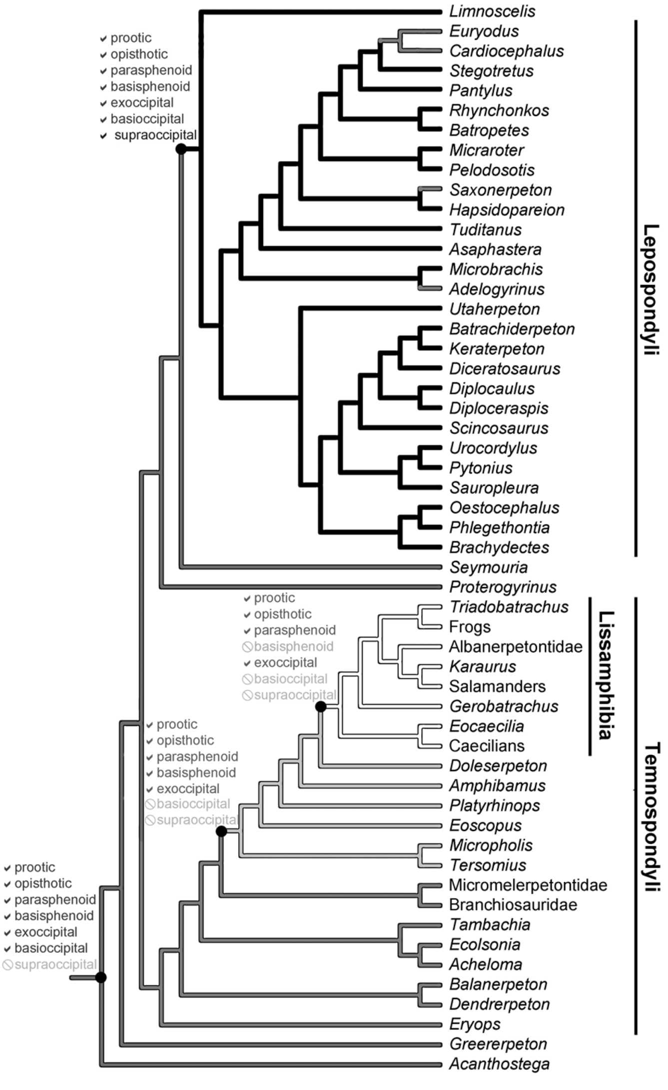

Figure 6:
Visualisation of the transformation of braincase bone composition across non-amniote tetrapod phylogeny. The plesiomorphic complement (six elements; middle-grey branches) includes all bones except for the supraoccipital. Gain of the supraoccipital on the stem of *(continued overleaf)*

(continued from overleaf) of the lepospondyl-amniote clade completes the full complement (seven elements; black branches) of bones seen among non-amniote tetrapods (some losses occur among lepospondyls, thereby reversing the complement to the plesiomorphic condition; middle-grey tips).The basioccipital is lost once within dissorophoids, reducing the complement to five elements (light-grey branches). The basisphenoid is lost on the lissamphibian stem, reducing the complement of braincase bones to the minimum amount seen among non-amniote tetrapods (four elements; white branches). The DELTRAN optimisation displayed was performed in MacClade v4.08a using the 50% majority-rule consensus tree of Maddin *et al.* (2012a).

When present, the basisphenoid ossification is often difficult to distinguish from that of the parasphenoid because of the fusion of the elements into the composite parabasisphenoid (or basiparasphenoid) complex. The basisphenoid part of this complex is formed by the ossification of the anterior portion of the basal plate (parachordals; Romer 1962) surrounding the hypophysis of the brain. There is no elaboration of the basal plate in lissamphibians into a skeletal structure surrounding the hypophysis (i.e., no sella turcica). The basioccipital, when present, is a ventral, median ossification of the occipital arch (Romer 1962). In lissamphibians, this region is not chondrified (de Beer 1937) and the paired lateral cartilages that are the precursors of the exoccipitals are the only structures making up the occipital arch (de Beer 1937).

Interestingly, as has been pointed out previously by Schoch and Milner (2004), only the temnospondyl lineage captures transitions consistent with an evolutionary reduction of these ossifications. By contrast, lepospondyls, the alternatively hypothesised relatives of some or all lissamphibians (Laurin & Reisz 1997; Marjanovic & Laurin 2007; Anderson *et al.* 2008), possess heavily ossified basisphenoid and basioccipital regions of the braincase (Carroll 1998a, b; Wellstead 1998). Included here are lysorophian lepospondyls, such as *Brachydectes*, and aïstopod lepospondyls, such as *Phlegethontia*, that are superficially similar in morphology to batrachians (Carroll 1998a; Wellstead 1998; Anderson 2002) as well as the microsaurs that share a number of similarities with caecilians (Carroll 1998b). In these taxa, a common pattern of dermal bone reduction/loss to that seen in lissamphibians is not paralleled by a common pattern of braincase bone reduction. Rather, these taxa display some of the more well ossified conditions of the braincase seen among non-amniote tetrapods. If lissamphibians are more closely related to lepospondyls, the similarities with temnospondyls must be interpreted as homoplasy. Similarly, a paraphyletic topology additionally requires similarities between lissamphibian groups to be interpreted as homoplasy (Fong *et al.* 2012). Together, the conservation of braincase structure and composition, along with the evolutionary transformations consistent with patterns of temnospondyl evolution, supports the growing consensus of a monophyletic Lissamphibia derived from the temnospondyl lineage.

Applications of morphological variation of the braincase

It is well known that the anterior central nervous system (i.e., the brain and cranial nerves) is strongly conserved in terms of its development, structure, and organisation across all craniates (Romer 1962). It is therefore not surprising that comparisons of representatives of the three lissamphibian groups reveal conserved positional relationships between the trigeminal and hyomandibular rami of the facial nerves as they emerge from the braincase (Figs. 1E and 3E). This high level of conservation provides the basis for the establishment of the homology of osteological correlates of these soft-tissue structures and permits one to make meaningful comparisons of them and their potential variation across taxa. In this case, the osteological correlates are the foramina that serve to transmit the cranial nerves.

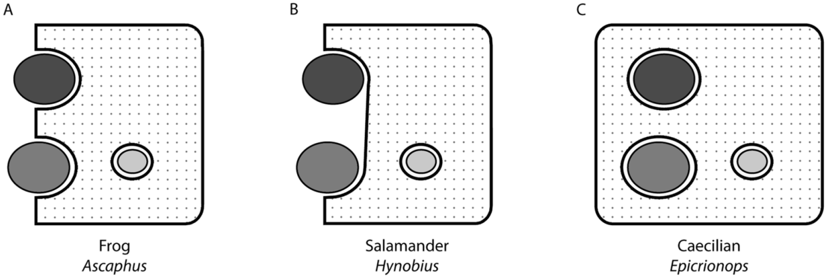

Figure 7:
Schematic illustrations depicting the variation in the osseous contributions to the trigeminal and hyomandibular ramus of the facial-nerve foramina in representatives of the three groups of lissamphibians. Maxillary-mandibular trunk of the trigeminal nerve (dark grey), ophthalmic branch of the trigeminal nerve (middle grey), and hyomandibular ramus of the facial nerve (light grey). A–B, in both of batrachian species *Ascaphus truei* and *Hynobius naevius*, the trigeminal foramina/foramen is bounded by bone (stippled region) posteriorly only. C, in the caecilian depicted here (based on *Epicrionops bicolor* FMNH 152310; see Maddin 2011), all foramina are completed by bone.

Among the lissamphibians examined here, there is variation in the way the anterior part of the otic-occipital complex contributes to the margins of the various foramina (Fig. 7). In *A. truei*, an osseous process connected to the palatoquadrate cartilage separates the two trunks of the trigeminal nerve (Fig. 7A), whereas the two trunks exit the braincase through a common foramen in *H. naevius* (Fig. 7B). Previous work on caecilians (Fig. 7C) revealed that the patterns by which the osseous part of the braincase contributed to the foramina of these nerves varied within the group in a phylogenetically informative way (Maddin 2011; Maddin *et al.* 2012b). The presence of variation between *A. truei* and *H. naevius* suggests that this approach to revealing new phylogenetic information could apply to frogs and salamanders as well.

An important use of new phylogenetic data from the lissamphibian braincase involves the fossil record. Although lissamphibian fossils are fairly common, the scarcity of low taxonomic level diagnostic features in the elements often leads to poor taxonomic resolution of many specimens (e. g., Holman & Harrison 2002; Venczel & Csiki 2003; Skutschas & Gubin 2012). Frog and salamander remains are commonly preserved in microvertebrate sites (e. g., Prasad & Sahni 1987; Brinkman 1990; Evans & Milner 1993; Rocek & Nessov 1993; Khajuria & Prasad 1998; Borsuk-Bialynicka *et al.* 1999) and as articulated skeletons (e. g., Franzen 1985; Wang & Gao 1999; Gao & Chen 2004). The isolated elements found at microvertebrate sites are typically well preserved in three dimensions, permitting detailed analysis of their morphology. The potential for the braincase to yield taxonomically diagnostic features could increase the utility of commonly preserved isolated amphibian remains at microvertebrate sites. Unfortunately, braincase elements are rarely identified in such assemblages. However, focused efforts could improve the likelihood of their recovery. Articulated specimens currently considered ‘family *incertae sedis*’ would equally benefit from new low-level diagnostic characters to improve taxonomic resolution (e. g., Gao & Shubin 2001; Gao & Chen 2004; Skutschas & Gubin 2012). In general, the braincase of caecilians was most useful in resolving family-level relationships (Maddin *et al.* 2012b). Increased resolution at this level would greatly improve our understanding of the diversity, biogeography, and evolution of lissamphibians.

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Literature cited

Altig R. (1969). Notes on the ontogeny of the osseous cranium of *Ascaphus truei*. *Herpetol. Monogr.*, 25, 59–62.

Anderson J.S. (2002). Revision of the aïstopod genus *Phlegethontia* (Tetrapoda: Lepospondyli). *J. Paleontol.*, 76, 1029–1046.

Anderson J.S., Reisz R.R., Scott D., Fröbisch N.B. & Sumida S.S. (2008). A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature*, 453, 515–518.

Bellairs A.d'A. (1949). The anterior brain-case and interorbital septum of Sauropsida, with a consideration of the origin of snakes. *Zool. J. Linn. Soc.*, 41, 482–512.

Bolt J.R. (1991). Lissamphibian origins. In: *Origins of the Higher Groups of Tetrapods* (eds. Schultze H-P & Trueb L). Comstock Publishing Associates Ithaca, New York, 194–222.

Bonebrake J.E. & Brandon R.A. (1971). Ontogeny of cranial ossification in the small-mouthed salamander, *Ambystoma texanum* (Matthes). *J. Morphol.*, 133, 189–204.

Borsuk-Bialynicka M., Cook E., Evans S.E. & Maryanska T. (1999). A microvertebrate assemblage from the Early Triassic of Poland. *Acta Palaeontol. Pol.*, 44, 167–188.

Brinkman D.B. (1990). Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 78, 37–54.

Cardini A. & Elton S. (2008). Does the skull carry a phylogenetic signal? Evolution and modularity in the guenons. *Biol. J. Linn. Soc.*, 93, 813–834.

Carroll R.L. (1998a). Order Aïstopoda. In: *Handbuch der Paläoherpetologie* (ed. Wellnhofer P). Verlag Dr. Friedrich Pfeil, München, 163–182.

Carroll R.L. (1998b). Order Microsauria. In: *Handbuch der Paläoherpetologie* (ed. Wellnhofer P). Verlag Dr. Friedrich Pfeil, München, 1–71.

Carroll R.L. (2007). The Paleozoic ancestry of salamanders, frogs and caecilians. *Zool. J. Linn. Soc.*, 150, 1–140.

Carroll R.L. & Holmes R. (1980). The skull and jaw musculature as guides to the ancestry of salamanders. *Zool. J. Linn. Soc.*, 68, 1–40.

Cheverud J.M. (1996). Developmental integration and the evolution of pleiotropy. *Am. Zool.*, 36, 44–50.

Couly G.F., Coltey P.M. & Le Douarin N.M. (1993). The triple origin of the skull in higher vertebrates: a study in quail-chick chimeras. *Development*, 117, 409–429.

Darwin C. (1859). *On the Origin of Species by Means of Natural Selection. Fascimile of the First Edition*. Harvard University Press, Cambridge.

de Beer G. (1937). *The Development of the Vertebrate Skull*. Oxford University Press, Oxford.

de Beer G.A. (1926). Studies on the vertebrate head.–II. The orbitotemporal region of the skull. *Quart. J. Microscop. Sci.*, 70, 263–370.

de Sá R.O. (1988). Chondrocranium and ossification sequence of *Hyla lanciformis*. *J. Morphol.*, 195, 345–355.

de Sá R.O. & Trueb L. (1991). Osteology, skeletal development, and chondrocranial structure of *Hamptophryne boliviana* (Anura: Microhylidae). *J. Morphol.*, 209, 311–330.

de Villiers C.G.S. (1934). Studies of the cranial anatomy of *Ascaphus truei* Stejneger, the American “Liopelmid”. *Bull. Mus. Comp. Zool., Harvard*, 77, 1–38.

Duellman W.E. & Trueb L. (1994). *Biology of Amphibians*. The Johns Hopkins University Press, Baltimore and London.

Dulcey Cala C.J., Tarazona O.A. & Ramirez-Pinilla M.P. (2009). The morphology and post-hatching development of the skull of *Bolitoglossa* *nicefori* (Caudata: Plethodontidae): developmental implications of recapitulation and repatterning. *Zoology*, 112, 227–239.

Evans S.E. & Milner A.R. (1993). Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry 9, Como Bluff) of North America. *J. Vertebr. Paleontol.*, 13, 24–30.

Fong J.J., Brown J.M., Fujita M.K. & Boussau B. (2012). A phylogenomic approach to vertebrate phylogeny supports a turtle-archosaur affinity and a possible paraphyletic Lissamphibia. *PLoS ONE*, 7, e48990.

Fox H. (1959). A study of the development of the head and pharynx of the larval urodele *Hynobius* and its bearing on the evolution of the vertebrate head. *Philos. Trans. Roy. Soc. Lond. Ser. B, Biol. Sci.*, 242, 151–204.

Francis E.T.B. (1934). *The Anatomy of the Salamander*. Oxford University Press, Oxford.

Franzen J.L. (1985). Exceptional preservation of Eocene vertebrates in the lake deposit of Grube Messel (West Germany). *Philos. Trans. Roy. Soc. Lond. Ser. B, Biol. Sci.*, 311, 181–186.

Gao K.-Q. & Chen S. (2004). A new frog (Amphibia: Anura) from the Lower Cretaceous of western Liaoning, China. *Cretac. Res.*, 25, 761–769.

Gao K.-Q. & Shubin N.H. (2001). Late Jurassic salamanders from northern China. *Nature*, 410, 574–577.

Gaupp E. (1896–1904). *A. Ecker's and R. Wiedersheim's Anatomie des Frosches,* Dritte Auflage. Friedrich Vieweg und Sohn, Braunschweig.

Goswami A. (2007). Cranial modularity and sequence heterochrony in mammals. *Evol. Dev.*, 9, 290–298.

Goswami A. & Polly P.D. (2010). The influence of character correlations on phylogenetic analysis: a case study of the carnivoran skull. In: *Carnivoran Evolution: New Views on Phylogeny, Form and Function* (eds. Goswami A & Friscia A). Cambridge University Press Cambridge, 141–164.

Hallgrímsson B., Lieberman D.E., Ford-Hutchinson A.F. & Jirik F.R. (2007). Epigenetic interactions and the structure of phenotypic variation in the cranium. *Evol. Dev.*, 9, 76–91.

Hallgrímsson B., Willmore K., Dorval C. & Cooper D.M.L. (2004). Craniofacial variability and modularity in macaques and mice. *J. Exp. Zool. Part B*, 302B, 207–225.

Hedges S.B. & Maxson L.R. (1993). A molecular perspective on lissamphibian phylogeny. *Herpetol. Monogr.*, 7, 27–42.

Holman J.A. & Harrison D.L. (2002). A new *Thaumastosaurus* (Anura: Familia *incertae sedis*) from the Late Eocene of England, with remarks on the taxonomic and zoogeographic relationships of the genus. *J. Herpetol.*, 36, 621–626.

Jenkins Jr. F.A., Walsh D.M. & Carroll R.L. (2007). Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic. *Bull. Mus. Comp. Zool., Harvard*, 158, 285–366.

Khajuria C.K. & Prasad G.V.R. (1998). Taphonomy of a Late Cretaceous mammal-bearing microvertebrate assemblage from the Deccan intertrappean beds of Naskal, peninsular India. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 137, 153–172.

Kingsbury B.F. & Reed H.D. (1909). The columella auris in Amphibia. *J. Morphol.*, 20, 549–628.

Klingenberg C.P. (2008). Morphological integration and developmental modularity. *Annu. Rev. Ecol., Evol. Syst.*, 39, 115–132.

Laurin M. & Reisz R.R. (1997). A new perspective on tetrapod phylogeny. In: *Amniote Origins* (eds. Sumida SS & Martin KLM). Academic Press San Diego, 9–59.

Lieberman D.E., Ross C.F. & Ravosa M.J. (2000). The primate cranial base: ontogeny, function, and integration. *Yearb. Phys. Anthropol.*, 43, 117–169.

Maddin H.C. (2011). Deciphering morphological variation in the braincase of caecilian amphibians (Gymnophiona). *J. Morphol.*, 272, 850–871.

Maddin H.C. & Anderson J.S. (2012). The evolution of the amphibian ear with implications for lissamphibian phylogeny: insight gained from the caecilian inner ear. *Fieldiana* (*Life Earth Sci.*), 5, 59–76.

Maddin H.C., Jenkins Jr. F.A. & Anderson J.S. (2012a). The braincase of *Eocaecilia micropodia* and the origin of caecilians. *PLoS ONE*, 7, e50743.

Maddin H.C., Reisz R.R. & Anderson J.S. (2010). Evolutionary development of the neurocranium in Dissorophoidea: an integrative approach. *Evol. Dev.*, 12, 393–403.

Maddin H.C., Russell A.P. & Anderson J.S. (2012b). Phylogenetic implications of the morphology of the braincase of caecilian amphibians (Gymnophiona). *Zool. J. Linn. Soc.*, 166, 160–201.

Maglia A.M., Pugener L.A. & Mueller J.M. (2007). Skeletal morphology and postmetamorphic ontogeny of *Acris crepitans* (Anura: Hylidae): a case of miniaturization in frogs. *J. Morphol.*, 268, 194–223.

Marjanovic D. & Laurin M. (2007). Fossils, molecules, divergence times, and the origin of lissamphibians. *Syst. Biol.*, 56, 369–388.

Milner A.R. (1993). The Paleozoic relatives of lissamphibians. *Herpetol. Monogr.*, 7, 8–27.

Monath T. (1965). The opercular apparatus of salamanders. *J. Morphol.*, 116, 149–170.

Müller H. (2006). Ontogeny of the skull, lower jaw, and hyobranchial skeleton of *Hypogeophis rostratus* (Amphibia: Gymnophiona: Caeciliidae) revisited. *J. Morphol.*, 267, 968–986.

Müller H., Oommen O.V. & Bartsch P. (2005). Skeletal development of the direct-developing caecilian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae). *Zoomorphol.* 124, 171–188.

Noble G.K. (1931). *The Biology of the Amphibia*. Dover Publications, Inc., New York.

Parker W.K. (1876). On the structure and development of the skull in the Batrachia. Part II. *Philos. Trans. Roy. Soc. Lond. Ser. B Biol. Sci.*, 166, 601–669.

Parker W.K. (1881). On the structure and development of the skull in the Batrachia. Part III. *Philos. Trans. Roy. Soc. Lond. Ser. B Biol. Sci.*, 172, 1–266.

Prasad G.V.R. & Sahni. A. (1987). Coastal-plain microvertebrate assemblage from the terminal Cretaceous of Asifabad, peninsular India. *J. Palaeontol. Soc. India*, 32, 5–19.

Pusey H.K. (1943). On the head of the leiopelmid frog, *Ascaphus truei*. I. The chondrocranium, jaws, arches and muscles of a partly grown larva. *Quart. J. Microscop. Sci.*, 84, 105–185.

Pyron R.A. (2011). Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Syst. Biol.*, 60, 466–481.

Ramaswami L.S. (1941). Some aspects of the cranial morphology of *Uraeotyphlus narayani. Rec. Indian Mus.*, 43, 143–207.

Reilly S.M. (1986). Ontogeny of cranial ossification in the eastern newt, *Notophthalmus viridescens* (Caudata: Salamandridae), relationship to metamorphosis and neoteny. *J. Morphol.*, 188, 315–326.

Reilly S.M. & Altig R. (1996). Cranial ontogeny in *Siren intermedia* (Caudata: Sirenidae): paedomorphic, metamorphic, and novel patterns of heterochrony. *Copeia*, 1996, 29–41.

Reiss J.O. (1996). Palatal metamorphosis in basal caecilians (Amphibia: Gymnophiona) as evidence for lissamphibian monophyly. *J. Herpetol.*, 30, 27–39.

Reiss J.O. (1997). Early development of chondrocranium in the tailed frog *Ascaphus truei* (Amphibia: Anura): implications for anuran palatoquadrate homologies. *J. Morphol.*, 231, 63–100.

Rieppel O. (1976). The homology of the laterosphenoid bone in snakes. *Herpetologica*, 32, 426–429.

Rocek Z. & Nessov L.A. (1993). Cretaceous anurans from Central Asia. *Palaeontograph.*, 226, 1–54.

Romer A.S. (1962). *The Vertebrate Body*, 3rd Ed. W.B. Saunders Company, Philadelphia, London.

Rose C.S. (1995). Skeletal morphogenesis in the urodele skull: I. postembryonic development in the Hemidactyliini (Amphibia: Plethodontidae). *J. Morphol.*, 223, 125–148.

Rose C.S. (2003). The developmental morphology of salamander skulls. In: *Amphibian Biology*, Vol. 5., *Osteology* (eds. Heatwole H & Davies M). Surrey Beatty, Chipping Norton, Australia, 1686–1783.

Ruta M. & Coates M.I. (2007). Dates, nodes and character conflict: addressing the lissamphibian origins problem. *J. Syst. Palaeontol.*, 5, 69–122.

Schmalhausen I.I. (1968). *The Origin of Terrestrial Vertebrates* translated from Russian by Leon Kelso. Academic Press, New York.

Schoch R.R. & Milner A.R. (2004). Structure and implications of theories on the origin of lissamphibians. In: *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds. Arratia G, Wilson MVH & Cloutier R). Verlag Dr. Friedrich Pfeil, München, 345–377.

Shaner R.F. (1926). The development of the skull of the turtle, with remarks on fossil reptile skulls. *The Anat. Rec.*, 32, 343–367.

Shea B.T. (1985). On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. *Am. J. Phys. Anthropol.*, 68, 329–342.

Skutschas P. & Gubin Y.M. (2012). A new salamander from the Late Paleocene – Early Eocene of Ukraine. *Acta Palaeontol. Pol.*, 57, 135–148.

Trueb L. (1993). Patterns of cranial diversity among the Lissamphibia. In: *The Skull* (eds. Hanken J & Hall BK). The University of Chicago Press Chicago, 255–343.

Trueb L. & Cloutier R. (1991). A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In: *Origins of the Higher Groups of Tetrapods: Controversy and Consensus* (eds. Schultze H-P & Trueb L). Comstock Publishing Associates Ithaca, New York, 223–313.

Tsusaki T. (1922). Zur Morphologie und Entwicklungsgeschichte des Hyobranchialskelettes von *Hynobius*. *Folia Anat. Jap.*, 1, 1–21.

Venczel M. & Csiki Z. (2003). New frogs from the latest Cretaceous of Hateg Basin, Romania. *Acta Palaeontol. Pol.*, 48, 609–616.

Wake M.H. & Hanken J. (1982). Development of the skull of *Dermophis mexicanus* (Amphibia, Gymnophiona), with comments on skull kinesis and amphibian relationships. *J. Morphol.*, 173, 203–223.

Wang Y. & Gao K.-Q. (1999). Earliest Asian discoglossid frog from western Liaoning. *Chin. Sci. Bull.*, 44, 636–642.

Wellstead C.F. (1998). Order Lysorophia. In: *Handbuch der Paläoherpetologie* (ed. Wellnhofer P). Verlag Dr. Friedrich Pfeil, München, 133–148.

Worthington R.D. & Wake D.B. (1971). Larval morphology and ontogeny of the ambystomatid salamander, *Rhyacotriton olympicus*. *Am. Midl. Nat.*, 85, 349–365.

Convergent evolution of body shape in squamate reptiles

Philip J. Bergmann

Department of Biology, Clark University, 950 Main Street, Worcester, Massachusetts 01610, USA; E-mail: pbergmann@clarku.edu

Abstract

Convergent evolution is a common pattern in nature, with many documented examples ranging from molecular and genomic scales to organismal and possibly to ecosystem scales. Although there are many documented examples of convergence, methods for formal testing of convergence are only recently being developed and studies of mechanism are less common still. Here, I construct a phylomorphospace of squamate reptile body shape and use it to test for convergence among clades and taxa that are thought to be under similar selective regimes. I test for convergence by examining the degree of overlap among convergent taxa in the phylomorphospace and by examining the direction of evolution along convergent phylogenetic branches by comparing non-convergent ancestors and convergent descendants. I find strong evidence for convergence in body shape among taxa that have evolved elongation because of fossoriality or because of inhabiting complex environments, gliding, and sand-dwelling. I find some evidence for body shape convergence in taxa that have evolved dry adhesion, but no evidence of convergence among herbivores or bipedal lizards. I also document a near perfect overlap in phylomorphospace between Iguanidae and Agamidae, but find that the analogous clades of Teiidae and Lacertidae inhabit adjacent, non-overlapping portions of the space. I discuss my findings in the context of a theoretical morphospace and make suggestions for future research.

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Introduction

The extent of similarity between organisms is often striking and although the concept of homology to describe this similarity was formalised long ago (Owen 1848), it remains a central theme in studying evolution (Bergstrom & Dugatkin 2011). In an evolutionary context, similarity can arise from either homology—the retention of similarity from common ancestry—or homoplasy—the recurrence of similarity (Darwin 1859; Wake 1991; Hall 2007). Homoplasy is used interchangeably with convergent evolution and it encapsulates the phenomena of true convergence, parallelism, and reversal (Wake 1991). The latter can then be differentiated by their developmental mechanism and pattern of evolution, where convergence tends to occur via different developmental mechanisms among unrelated taxa, parallelism involves the same developmental mechanism and often more closely related taxa, and reversal can have the same or different mechanisms and typically involves the regain of a previously lost phenotype (Hall 2007).

Convergent evolution is widely recognised as an interesting biological phenomenon that is widespread and requires explanation (Stayton 2008; Losos 2011; McGhee 2011). Convergent evolution occurs at all possible levels of organisation, including genomic (Castoe *et al.* 2009), developmental (Eckalbar *et al.* 2012; Sanger *et al.* 2012), physiological (Schulte *et al.* 2000), morphological (Wiens *et al.* 2006), functional (Alfaro *et al.* 2005), and even ecological (Losos 1990b; Rosenblum 2006). Hundreds of examples of convergent evolution are now known (reviewed by McGhee 2011), but the pattern of convergence has only been described in some of these and a mechanistic understanding of why convergence happens exists in only rare cases.

Two alternative general explanations of convergent evolution have emerged. On the one hand, convergent evolution might be the product of adaptive evolution of a similar solution to a common selective regime (Losos 2011). From this perspective, not only must there be a convergent phenotype, but that phenotype must evolve in a similar ecological context with similar selective pressures (Wake 1991; Revell *et al.* 2007). A hypothesis of such adaptive convergence can be tested using functional studies or by measuring selective pressures on the convergent phenotype (Losos 2011). On the other hand, convergent evolution might be the product of constraint, where a finite set of possible phenotypes bias the direction of evolution to a few functional but suboptimal designs (Thomas & Reif 1993). This view argues that although historical contingency affects the course of evolution, the outcome is largely determined by limitations on what can evolve (Thomas & Reif 1993). Indeed, many phenotypic innovations occur repeatedly, suggesting predictability of outcome (Vermeij 2006).

These classical explanations of convergent evolution are not mutually exclusive nor are they the only explanations (Wake 1991; Losos 2011). Recent work has shown that, given a quantitative trait and multiple species evolving through time, convergence is expected simply as a product of random evolution (Stayton 2008), demonstrating that a process like genetic drift can produce a convergent pattern (Losos 2011). Under the simple conditions of random evolution, convergence will increase with the number of taxa considered and decrease as the number of traits involved (i.e., complexity) increases (Stayton 2008). Convergent evolutionary patterns can also arise from traits evolving along genetic lines of least resistance, biogeography, and competitive interactions (Wiens *et al.* 2006; Losos 2011). All these possibilities should be treated as hypotheses to be tested (Losos 2011).

With many examples of convergent evolution having been documented (McGhee 2011), a unified approach to describing convergent patterns has emerged. Whatever its underlying mechanism, convergent evolution can be studied powerfully using a theoretical morphospace on which the convergent taxa and their ancestors are mapped, all in a phylogenetic context (Wake 1991; Thomas & Reif 1993; Stayton 2006; Revell *et al.* 2007; Stayton 2008; Losos 2011; McGhee 2011). Universal constraints in the form of physical laws put bounds on such a morphospace (Thomas & Reif 1993), and the organism's *Bauplan* further constrains the available morphospace (Wake 1991). Factors such as evolution along genetic lines of least resistance (Schluter 1996) and functional constraints can then result in uneven occupation of the morphospace (Losos 2011). Finally, the phylogeny can be mapped onto the space, resulting in a "phylomorphospace" (Sidlauskas 2008) that can readily be used to study convergent evolution.

With a phylomorphospace, patterns of convergent evolution can be identified by comparing ancestors that are not convergent to descendants that are (Stayton 2006; Hall 2007; Revell *et al.* 2007). In this context, convergence can be defined as occurring when two taxa evolve to be more similar to one another than their ancestors were (Stayton 2008). Stayton (2006) uses the phylomorphospace approach to distinguish three patterns of convergence: (1) convergent species evolving to occupy the same area of morphospace; (2) convergent species evolving towards the same area of morphospace, but occupying different areas; and (3) convergent species evolving in the same direction in morphospace, but not converging toward a common phenotype.

My goal in this study is to test the hypothesis that convergent evolution has occurred in the body shape of squamate reptiles in several situations where convergent evolution has been predicted or assumed but often not tested. I then describe the patterns of convergence that I identify. With >8400 species, a cosmopolitan distribution, and species filling every conceivable niche outside of arctic regions (Pough *et al.* 2004; Uetz *et al.* 2007), squamates are an ideal clade for studying macroevolutionary patterns. Squamates contain a rich collection of examples of hypothesised convergent evolution that I test for here (see Appendix). In so doing, I neglect some examples of convergence in squamates, such as the repeated evolution of viviparity (Dunbrack & Ramsay 1989; Shine 1995; Schulte *et al.* 2000), because I would not expect them to influence body-shape evolution. Other examples of purported convergence in squamates might suggest wider patterns because they also occur in other taxa. For example, a snake-like body shape (i.e., elongate body with reduced limbs) has evolved >25 times in squamates (Wiens *et al.* 2006), but is also seen in fishes (Ward & Brainerd 2007), salamanders (Wake 1991), and mammals (Bejder & Hall 2002). Likewise, gliding has evolved at least four times in lizards (see Appendix), but has also evolved in frogs (McCay 2001), snakes (Socha & LaBarbera 2005), and mammals (Paskins *et al.* 2007). Most of the examples of convergence that I examine are in the context of a selective regime: the evolution of adhesion, bipedalism, sand-dwelling, gliding, herbivory, elongation associated with burrowing, and elongation associated with surface-dwelling (see Appendix). If body-shape convergence is indeed happening in these cases, then I would expect unrelated species that are under the same selective regime to either occupy a common area of morphospace or to be more similar to one another than their ancestors are. I also examine two general examples of clade convergence, where it has been noted that Iguanidae are broadly convergent with Agamidae (Melville *et al.* 2006) and that Teiidae are broadly convergent with Lacertidae (Miles *et al.* 2007). In both these cases, the former clade represents the New World analogue of the latter, Old World clade. Finally, I examine the famous example of *Anolis* ecomorphs and their convergence (e. g., Williams 1982).

Methods

Morphospace of squamate body shape

Before testing for convergence, I produced a morphospace to describe important aspects of squamate body shape using the raw morphometric dataset and supertree phylogeny, both of which were published in Bergmann and Irschick (2012). The dataset was collected from 2D radiographs and included the following measurements: head length (HL), body length (BL), body width (BW), hind limb length (HLL), hind limb width at thigh level (HLW), foot length including the longest toe (Foot), and the number of digits on the front (FD) and hind (HD) limbs (Bergmann & Irschick 2012). I used measurements for 636 species distributed from all clades of squamates, but with only rudimentary sampling of snakes belonging to Typhlopidae. I pruned the supertree, which originally included 1375 species (Bergmann & Irschick 2012) to include only those represented in the morphometric dataset using Mesquite v2.75 (Maddison & Maddison 2011).

To prepare the data for analysis, I natural-log transformed the morphometric variables and added two to the digit number variables (FD and HD) before transformation to avoid having zeros in the dataset. I then removed the effects of body size from the morphometric variables (but not digit number variables) in a phylogenetically informed manner (Blomberg *et al.* 2003) as implemented using the "phytools" package (Revell 2009) in R (R Development Core Team 2012). This was necessary because lizards are extremely variable in body size (three orders of magnitude) and this variation overshadowed shape variation in the analyses. I used HL as the proxy for body size because the standard measure of snout-vent or body length has undergone considerable evolution given that many squamates are elongate (Wiens & Singluff 2001; Wiens *et al.* 2006; Brandley *et al.* 2008; Siler & Brown 2011).

I analysed the size-adjusted morphometric data using an evolutionary principal component analysis (ePCA) that takes phylogeny into account again using the "phytools" package in R (Revell 2009; R Development Core Team 20122012). This approach resulted in qualitatively similar results to a regular PCA (Bergmann & Irschick 2012), but accounts for the evolutionary relatedness (non-independence) of species. I visualised the morphospace created by the first two PCs from the ePCA by plotting those PCs on a scatterplot and superimposing the phylogeny using Mesquite (Maddison & Maddison 2011).

This plotting of data and phylogeny into a common space is termed a phylomorphospace (Sidlauskas 2008).

Testing for convergence

I tested for convergence in two different ways: (1) by determining whether convergent taxa overlapped in morphospace and (2) by comparing the position of non-convergent ancestors to convergent descendants in the morphospace. Together, these approaches enabled me to determine whether convergent taxa occupied a common morphospace, evolved to be more similar than their non-convergent ancestors, or were evolving in a similar direction (Stayton 2006). I accomplished the first approach by simply plotting the phylomorphospace for the convergent taxa on a single plot and determining whether or not there was any overlap. By identifying hypothesised convergent taxa *a priori* from the literature (see Appendix), I avoided some of the circularity associated with simply testing whether or not similar-looking species were convergent (i.e., looked the same). I accomplished the second approach by reconstructing the ancestral character states for every node on the phylogeny for the first two PCs and natural-log transformed HL on the phylogeny using squared-change parsimony as implemented in the "Trace Character History" function in Mesquite (Maddison & Maddison 2011). I then extracted the values for the convergent taxa (these could be tip values or ancestral values depending on whether a species or a clade was convergent) and for their immediate ancestors that were not convergent (the parent node of each convergent taxon). To evaluate convergence using this second approach, I compared ancestor-descendant character-value pairs to elucidate direction and magnitude of evolution along the branches on which convergent evolution is hypothesised to have happened.

Results

Evolution of squamate body shape

A scree plot of variance explained by each PC of the ePCA (not shown) indicated that the first two PCs explained the majority of variation. PC-3 explained <8% of variation in the dataset and so is not considered further. The eigenvector for PC-1 (Table 1) shows that this component represents a trade-off between BL on the one hand and BW, digit numbers, and limb measurements on the other, such that high values of PC-1 indicate short, wide bodies with well-developed limbs. As such, I interpret PC-1 as an index of relative elongation and limb reduction: species with high values are lizard-like and species with low values are snake-like. All body dimensions load most strongly on PC-2, whereas limb variables have much smaller loadings (Table 1). Hence, species with high PC-2 values have robust bodies, whereas those with low values have gracile bodies. I interpret PC-2 as an index of body robustness.

Table 1:
Evolutionary PCA loadings for the first two principal components (PCs), with eigenvalues and the proportion of total variance explained by each PC presented. Bold values indicate loadings that are elevated and interpreted.

Variable	**PC-1**	**PC-2**
Head width	0.071	**0.312**
Body length	**–0.125**	**0.379**
Body width	**0.142**	**0.817**
Front digits	**0.241**	–0.128
Hind digits	**0.249**	–0.124
Hind limb width	**0.294**	0.219
Hind limb length	**0.681**	–0.084
Foot length	**0.538**	–0.067
Eigenvalue	0.0045	0.0013
% explained	62.05	17.74

An examination of the phylomorphospace (Fig. 1) defined by the first two PCs indicates that most of the included species are lizard-like. Although only about 10% of extant lizards were sampled (and a negligible number of snakes), species sampling included all major lizard clades without bias based on body shape. Thus, this phylomorphospace should be indicative of lizard body-shape diversity in general. The phylomorphospace shows that most species are either lizard-like or snake-like. Although various intermediate forms do exist, they are simply a lot less frequent. In both the lizard-like and snake-like clusters, there is a range of body shapes from gracile to robust (Fig. 1). Typhlopid snakes and *Amphisbaenia* are the most robust snake-like species (Fig. 1), whereas the cordylid *Chamaesaura* is the most gracile (Fig. 1). The limbless anguids (Fig. 2A) and scincids (not shown) are variable and intermediate in robustness. The scincids have also evolved a snake-like body shape the greatest number of times, accounting for most of the phylogeny branches crossing from left to right of the phylomorphospace (Fig. 1). snakes), species sampling included all major lizard clades without bias based on body shape. Thus, this phylomorphospace should be indicative of lizard body-shape diversity in general. The phylomorphospace shows that most species are either lizard-like or snake-like. Although various intermediate forms do exist, they are simply a lot less frequent. In both the lizard-like and snake-like clusters, there is a range of body shapes from gracile to robust (Fig. 1). Typhlopid snakes and *Amphisbaenia* are the most robust snake-like species (Fig. 1), whereas the cordylid *Chamaesaura* is the most gracile (Fig. 1). The limbless anguids (Fig. 2A) and scincids (not shown) are variable and

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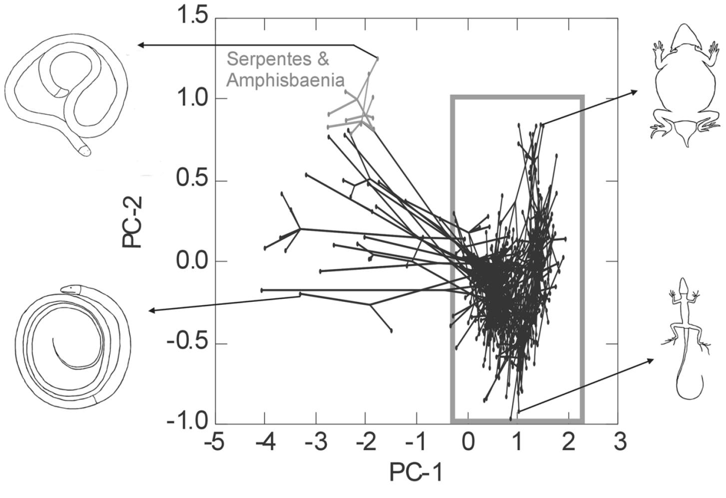

Figure 1:
The phylomorphospace of squamate body shape as defined by PC-1 (an index of elongation) and PC-2 (an index of robustness). The phylomorphospace is shown for all 636 species sampled along with representative body shapes from the edges of the morphospace. The grey rectangle represents the area shown in Figs 3 and 4).

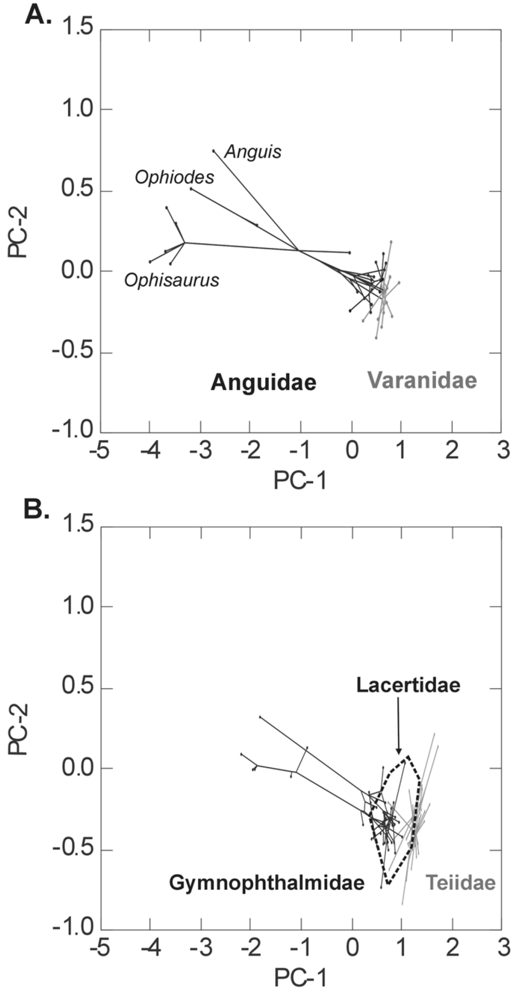

Figure 2:
A phylomorphospace for (A) Anguidae (black) and Varanidae (grey), and (B) for Gymnophthalmidae (black), Teiidae (grey) and Lacertidae (dashed polygon). The boundaries of these plots are the same as for Fig. 1.

Among clades with only lizard-like body shapes, there is also considerable variation in body shape. Iguanidae in general are highly diversified, with the genus *Phrynosoma* having the most robust body shape of all lizards and *Anolis* being among the most gracile (Fig. 3A). The three clades of Phrynosomatinae (sand, horned, and fence lizards) are well differentiated from one another (Fig. 3B). Agamidae are similarly diverse, with *Uromastyx* and *Draco* being the most robust (the latter is not robust *per se*, but has ribs elongated into patagia; McGuire & Dudley 2005) and *Japalura* the most gracile (Fig. 4A). Finally, both major adhesive pad-bearing clades, Gekkota and *Anolis*, occupy relatively restricted areas of the phylomorphospace, coinciding with a relatively gracile body shape. It is important to note that these latter two clades occupy virtually non-overlapping, but adjacent areas of the phylomorphospace (Fig. 4B).

Convergence in squamate body shape

I use the direction of evolution in the phylomorphospace along the phylogenetic branches along which convergence is hypothesised to have occurred as the primary evidence of convergence, with convergent clade overlap being secondary, but also important (Stayton 2006). I address each example in the context of its selective regime in turn.

Dry adhesion has evolved four times independently in the taxa that I sampled: in the gekkotans Diplodactylidae and Gekkonidae, in *Anolis*, and in the skink *Prasinohaema virens* (see Appendix). None of these taxa have converged on a similar body shape as defined by my indices of elongation and robustness, but the two gekkotan clades have evolved in parallel to be more lizard-like than their ancestors (Fig. 5A). The skink and *Anolis* have also evolved in parallel to become more gracile than their ancestors (Fig. 5A). Gekkota and *Anolis* also occupy adjacent, but almost mutually exclusive areas of morphospace (Fig. 4B). The restricted areas of morphospace that these taxa occupy could instead suggest a constraint on body-shape evolution, perhaps resulting from their adhesive abilities (Bergmann & Irschick 2012). It should be noted that other examples of convergence occur within these clades (e. g. Russell 1977) such that it would be interesting to test for convergence within each.

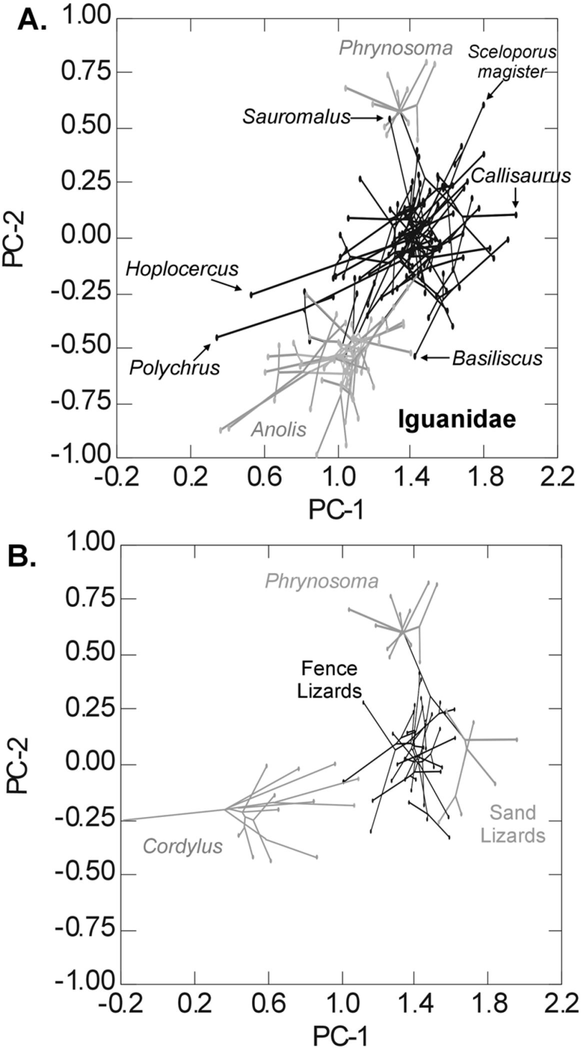

Figure 3:
A phylomorphospace for (A) Iguanidae, and for (B) Phrynosomatidae and Cordylidae, with representative species and major clades labelled. The boundaries of these plots are the same as for Fig. 1.

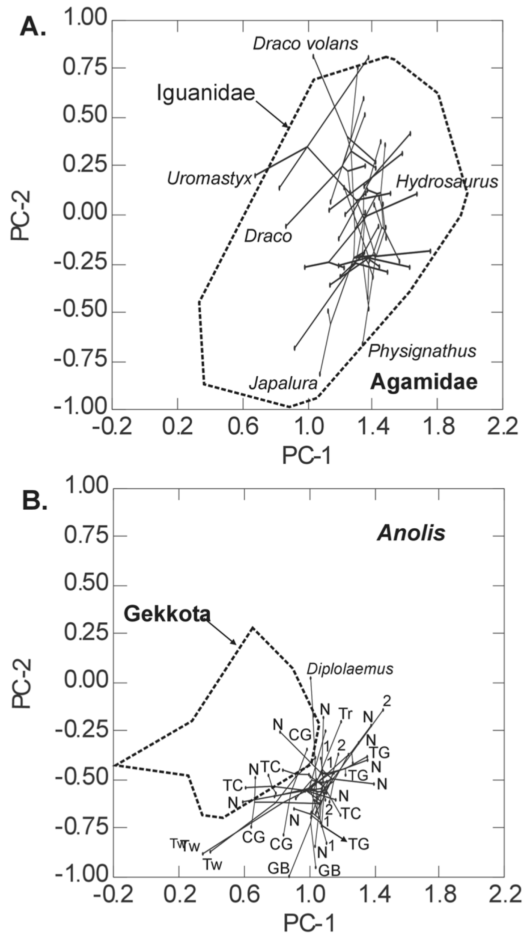

Figure 4:
A phylomorphospace for (A) Agamidae with a polygon showing the morphospace occupied by Iguanidae (Fig. 3A); representative agamid species are labelled. A phylomorphospace for (B) *Anolis* with a polygon representing the morphospace occupied by Gekkota. In (B), *Anolis* ecomorphs are labelled as follows: CG, crown giant; GB, grass-bush; TC, trunk-crown; TG, trunk-ground; Tr, trunk; Tw, twig; N, none (either mainland species or ones for which ecomorph classification has not been determined); 1, from Lesser Antillean islands with a single species; and 2, from Lesser Antillean islands with two species. The boundaries of these plots are shown by the grey rectangle in Fig. 1.

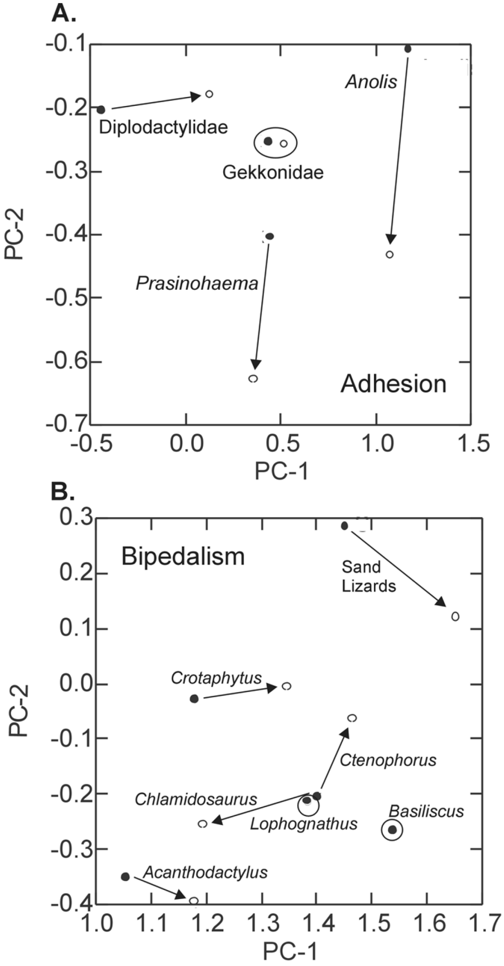

Figure 5:
Plots of of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness). Large ovals indicate no evolution between the ancestor and descendent. Convergence plots are shown for (A) dry adhesion and (B) bipedalism, with putatively convergent taxa labelled.

Bipedalism has evolved six times in the taxa sampled (see Appendix). Although bipedal lizards often have long, gracile hind limbs, short front limbs, narrow pelvic girdles, short trunks, and long tails (Snyder 1962), my data show no evidence of convergence (Fig. 5B). Instead, each convergent taxon evolves in a different direction and not toward any common area in the phylomorphospace.

Sand-dwelling has evolved four times in my dataset (see Appendix) and, although the taxa have not converged morphologically, *Phrynosoma*, *Uma*, and *Lerista* have evolved in a similar direction, whereas the lacertid *Meroles* has not (Fig. 6A). The limited level of convergence in this example is unsurprising because many of these taxa use sand in different ways as exemplified by their different burying behaviours (Arnold 1995).

Gliding has evolved three times independently in the taxa that I sampled (see Appendix). The gekkonid *Ptychozoon* and the agamid *Leiolepis* have evolved in parallel to be more robust and lizard-like than their non-gliding ancestors, whereas *Draco* has evolved along a different trajectory (Fig. 6D). This might be because gliding is highly developed in *Draco*, which has a highly specialised and extreme morphology (McGuire 2003), whereas the other two taxa have relatively rudimentary patagia.

My dataset contains taxa representing eight independent instances of the evolution of herbivory. In addition to examining the first two PCs (Fig. 7A), I also considered body size (Fig. 7B) as represented by ln(HL) because it has long been thought that herbivory coincides with large body size in lizards (see references in Stayton 2006). Exceptions to this “rule” exist, particularly in small, cold-climate *Liolaemus* species (Espinoza *et al.* 2004) and I find little evidence of body shape and size convergence in these taxa (Fig. 7). This result differs from those of Stayton (2006), most likely because he was studying skull shape, which is more directly functionally relevant to herbivory than body shape. In my dataset, only the Giant Prehensile-Tailed Skink, *Corucia zebrata*, has evolved a larger body size relative to its ancestor (Fig. 7B).

Body elongation and limb reduction, or the evolution of a snake-like body shape, has evolved more than 25 times in squamates (see Appendix), but not all snake-like squamates are alike. Elongate body shapes have evolved either as long-tailed surface dwellers that often specialise in moving through dense

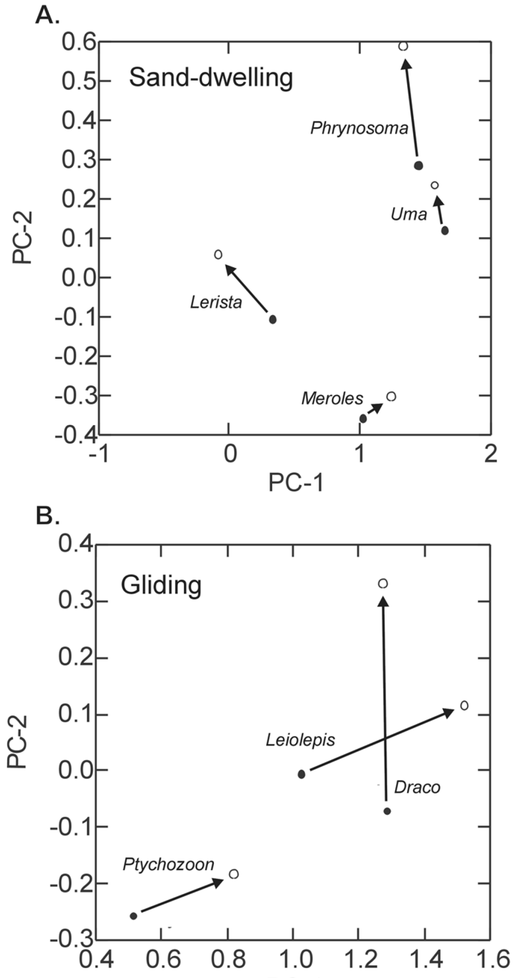

Figure 6:
Plots of pairs of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness). Convergence plots are shown for (A) sand-dwelling and (B) gliding, with taxa putatively convergent labelled.

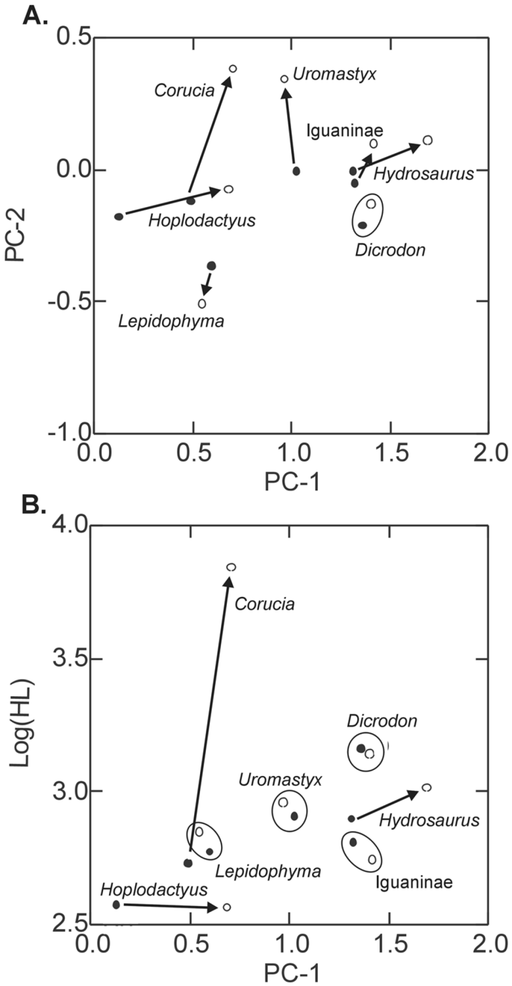

Figure 7:
Plots of pairs of herbivorous non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by (A) PC-1 (an index of elongation) and PC-2 (an index of robustness) and (B) PC-1 and log(head length). Putatively convergent taxa are labelled.

vegetation or as short-tailed burrowers (Wiens *et al.* 2006; Brandley *et al.* 2008). These are likely different selective regimes and so I treat each separately. My dataset includes fifteen (of ~22) instances of the evolution of the elongate burrowing ecotype and the vast majority of these have evolved along parallel trajectories toward a different area of morphospace than that occupied by their ancestors (Fig. 8A). The wide area of morphospace occupied by the descendent burrowers (Fig. 8A) indicates that despite snake-like body shapes appearing simple, there is still considerable variation in the degree of robustness. The results for the surface-dwelling ecomorph are less striking, but three of four examples have also evolved in largely the same direction (Fig 8B). The exceptions are the anguid clades *Ophisaurus* + *Anguis* and *Ophiodes*, which appear to have actually decreased in the degree of elongation over evolutionary time (Fig. 4B), although this result might arise from poor resolution at the base of the anguid clade on the supertree.

Anolis lizards have repeatedly evolved multiple ecomorphs that differ in microhabitat, often defined by the perch diameter that they inhabit (Losos 2009). Despite being one of the best documented examples of convergent evolution, the ecomorphs have only sometimes come to occupy a common morphospace as defined by my body-shape dataset (Fig. 4B). It is likely that the current dataset is not sufficiently detailed to identify the convergence documented by others. For example, limb morphology is a key component of *Anolis* convergence, yet my dataset contains relatively few limb measurements.

Finally, I examined whether Agamidae and Iguanidae as well as Teiidae and Lacertidae represent convergent clades in general (see Appendix). Agamid and iguanid ancestors did not evolve toward a common area of morphospace or in a similar direction (not shown), but their radiations have come to occupy largely the same area of the morphospace (Fig. 4A). By contrast, although the ancestors of teiids and lacertids have evolved in a similar direction to be increasingly lizard-like and gracile (Fig. 9), they occupy close, but adjacent areas of morphospace (Fig. 2B). From a comparison of morphospace occupation, lacertids instead appear to be more convergent with the limbed gymnophthalmids, the sister group to teiids (Fig. 2B).

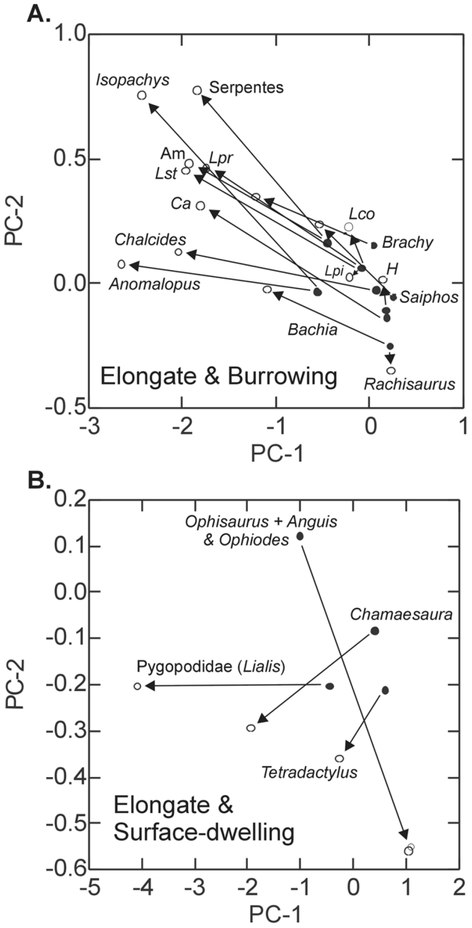

Figure 8:
Plots of pairs of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness) for elongate taxa that are (A)burrowers and those that are (B) surface-dwellers. Abbreviations: Am, *Amphisbaenia*; Brachy, *Brachymeles*; Ca, *Calyptomatus*; H, *Hemiergis peronii*; Lco, *Lerista connivens*; Lpi, *L. picturata*; Lpr, *L. praepedita*; and Lst, *L. stylis*.

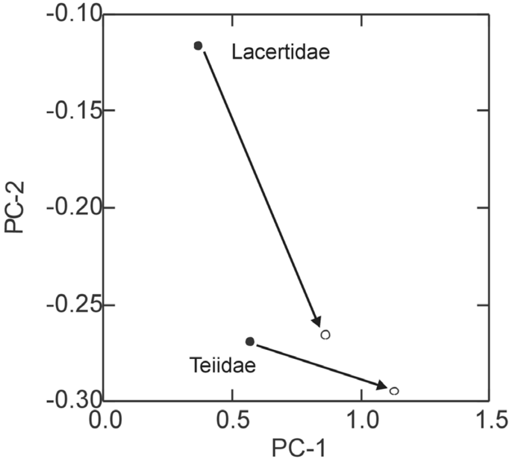

Figure 9:
Plots of pairs of non-convergent ancestors (closed circles) and convergent descendants (open circles) connected by arrows indicating the direction of evolution in a morphospace defined by PC-1 (an index of elongation) and PC-2 (an index of robustness) for Lacertidae and Teiidae.

Discussion

The theoretical morphospace

The construction of morphospaces is a powerful approach to studying phenotypic evolution in general and convergence in particular because it enables one to consider not only the phenotypes that have evolved, but also those that have not (which is why this is sometimes called a theoretical morphospace; Thomas & Reif 1993; McGhee 2011). A morphospace approach implicitly incorporates the concept of constraints, which are thought to play an important role in convergent evolution (Wake 1991; Thomas & Reif 1993). Specifically, physical laws and organismal *Baupläne* set limits on which areas of the morphospace can be inhabited and developmental constraints and genetic correlations can then further curtail the options available to evolution, resulting in the uneven occupation of the morphospace (Thomas & Reif 1993; Losos 2011). When evolved phenotypes are considered in the context of their function and ecological context, the morphospace can also be a tool to help address questions about the role of adaptation in the convergent process (Stayton 2006; Revell *et al.* 2007; Losos 2011).

Similar to other authors (Stayton 2006; Revell *et al.* 2007; Siler & Brown 2011), I generated a continuous morphospace using a PCA approach. My ePCA results and resulting morphospace are largely concordant with those of Bergmann and Irschick (2012), who used the same dataset but did not account for phylogeny with their PCA, and with those of Wiens *et al.* (2006), who used different variables and biased their sampling to include a disproportionate number of elongate species. This suggests that the phylomorphospace is robust to variation in procedure and species sampling.

The phylomorphospace presented here (Fig. 1) is interesting in and of itself because it reveals certain patterns about the variation in snake-like, intermediate, and lizard-like squamates. One might hypothesise that the evolution of a snake-like morphology involves a gross simplification of the body plan on account of the loss of limbs such that one snake-like species looks like all the others. If this were the case, then one would expect snake-like morphologies to occur in a very restricted area of the morphospace, one that is much smaller than the area occupied by lizard-like species. Instead, what is seen is that snake-like species occupy a large area of the morphospace, ranging from robust to gracile across an area that is only slightly smaller than that occupied by lizard-like species. This suggests that not all snake-like morphologies are equivalent. Indeed, the space occupied by elongate burrowers is completely separate from the space occupied by elongate surface-dwellers (Figs. 8A, B; compare the locations of the open circles). This suggests similar, convergent morphologies can arise because of different selective pressures, challenging the view of what convergence is. For example, if convergence is viewed as similar solutions evolving because of similar selective pressures (e. g., Losos 2011), what does it mean when different selective pressures produce the same phenotype? It will be fruitful to examine this question from a functional perspective because it suggests that convergent phenotypes can be multifunctional.

Another important observation from the complete phylomorphospace is that intermediate species are restricted in their morphology. The narrow band of branches crossing from the lizard-like cluster to the snake-like cluster (Fig. 1) is restricted to intermediate robustness; no intermediate species are very robust or very gracile. This is suggestive of a constraint as to how a snake-like shape can evolve, although the constraint is relaxed once it has evolved. Indeed, different selective pressures might be working on species with intermediate body shapes than on snake-like or lizard-like species (Brandley *et al.* 2008), but what these pressures are remains unknown.

Other approaches to creating a morphospace have taken a character-based approach, where multiple characters are coded discretely (Thomas & Reif 1993; McGhee 2011). This is appealing as a thought experiment because the bounds of the morphospace are clearly defined. However, this approach introduces bias arising both from obtaining a complete set of characters and character states, and because many discretely coded-characters actually represent simplifications of continuous variables (Wiens 2001). Although a continuous morphospace, as produced by a PCA, is smooth as opposed to stepped and treats variation in a more organic way, it is still limited by the characters included (although not their states). However, because PCA simplifies patterns of variation to a few axes that explain the majority of this variation, this approach can overinflate apparent convergence because the latter tends to increase as the number of variables (or phenotype complexity) decreases (Stayton 2008). Nevertheless, the greater the number of variables or morphospace axes, the harder they are to visualise and interpret.

Detecting convergence

With the growing availability of robust phylogenies and the mainstream use of ancestral reconstruction techniques, researchers have focused on identifying convergence by studying the evolution of the phenotype along the branches of the phylogeny on which convergence is thought to have occurred (Stayton 2006; Revell *et al.* 2007). This is the primary approach taken here (Figs. 5–9). However, comparing ancestor-descendant pairs failed to detect convergence in Agamidae and Iguanidae (not shown), whereas examining the morphospace occupied by each clade gave compelling evidence for convergence (Fig. 4A). In this example, the premise for convergence was not predicated on both clades being subjected to similar selective pressures because both clades contain extremely diverse species both morphologically and ecologically (Melville *et al.* 2006). The common occupation of morphospace by these two clades might be more suggestive of shared constraints arising from their evolutionary history and body plan. For example, neither clade has ever evolved elongate, limb-reduced forms and every species has five digits on each limb (Greer 1991). Instead, Agamidae and Iguanidae appear to be parallel radiations, likely with many examples of adaptive convergence

(Losos 2011) within them. Because these two clades occur in mutually exclusive geographic areas, this suggests that ecological opportunity and biogeography have played a large role in their evolution, similar to what has been hypothesised for snake-like morphologies (Wiens *et al.* 2006). The findings presented here argue that a diversity of approaches to detecting and studying convergent evolution is important because it represents a complex evolutionary pattern that can arise from a diversity of processes.

Although hundreds of examples of convergence have been documented (McGhee 2011) and specific patterns of evolution have been described for some of these (e. g., Wiens & Singluff 2001; Herrel *et al.* 2004; Stayton 2006; Wiens *et al.* 2006; Revell *et al.* 2007; this study), research into why convergence happens is lagging (but see Irschick *et al.* 1996; Herrel *et al.* 2008; Eckalbar *et al.* 2012). The mechanisms behind convergence can be studied in a variety of ways, including functional studies and measurement of selective pressures (Losos 2011). Studies of genetic covariance structure underlying traits that have converged in multiple taxa would also be compelling because constraints on genetic covariance and integration might then constrain the evolutionary options available to respond to a particular selective pressure (Kolbe *et al.* 2011). Macroevolutionary modelling is another appealing approach that might be able to differentiate random evolution from common selective regimes resulting in convergent evolution (Hansen 1997; Butler & King 2004). There are now a variety of powerful tools available that can be brought to bear on the underlying reasons for convergent evolution and, in applying them, it is important to keep in mind that these underlying reasons might not be mutually exclusive.

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Literature cited

Aerts P., Van Damme R., D'Août K. & Van Hooydonck B. (2003). Bipedalism in lizards: whole-body modelling reveals a possible spandrel. *Philos. Trans. Roy. Soc., Ser. B*, 358, 1525–1533.

Alfaro M.E., Bolnick D.I. & Wainwright P.C. (2005). Evolutionary consequences of a redundant map of morphology to mechanics: an example using the jaws of labrid fishes. *Am. Nat.*, 165, E140–E154.

Arnold E.N. (1995). Identifying the effects of history on adaptation: origins of different sand-diving techniques in lizards. *J. Zool.*, 235, 351–388.

Bejder L. & Hall B.K. (2002). Limbs in whales and limblessness in other vertebrates: mechanisms of evolutionary and developmental transformation and loss. *Evol. Dev.*, 4, 445–458.

Bergmann P.J. & Irschick D.J. (2012). Vertebral evolution and the diversification of squamate reptiles. *Evolution*, 66, 1044–1058.

Bergstrom C.T. & Dugatkin L.A. (2011). *Evolution*. W.W. Norton & Co., New York, USA.

Blomberg S.P., Garland Jr. T. & Ives A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.

Brandley M.C., Huelsenbeck J.P. & Wiens J.J. (2008). Rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. *Evolution*, 62, 2042–2064.

Butler M.A. & King A.A. (2004). Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.*, 164, 683–695.

Castoe T.A., de Koning A.P.J., Kim H.-M., Gu W., Noonan B.P., Naylor G., Jiang Z.J., Parkinson C.L. & Pollock D.D. (2009). Evidence for an ancient adaptive episode of convergent molecular evolution. *Proc. Natl. Acad. Sci. USA*, 106, 8986–8991.

Clemente C.J., Withers P.C., Thompson G. & Lloyd D. (2008). Why go bipedal? Locomotion and morphology in Australian agamid lizards. *J. Exp. Biol.*, 211, 2058–2065.

Daniels S.R., Heideman N.J.L., Hendricks M.G.J., Mokone M.E. & Crandall K.A. (2005). Unraveling evolutionary lineages in the limbless fossorial skink genus *Acontias* (Sauria: Scincidae): are subspecies equivalent systematic units? *Mol. Phylogenet. Evol.*, 34, 645–654.

Darwin C. (1859). *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London, England.

Dunbrack R.L. & Ramsay M.A. (1989). The evolution of viviparity in amniote vertebrates: egg retention versus egg size reduction. *Am. Nat.*, 133, 138–148.

Eckalbar W.L., Lasku E., Infante C.R., Elsey R.M., Markov G.J., Allen A.N., Corneveaux J.J., Losos J.B., DeNardo D.F., Huentelman M.J., Wilson-Rawls J., Rawls A. & Kusumi K. (2012). Somitogenesis in the anole lizard and alligator reveals evolutionary convergence and divergence in the amniote segmentation clock. *Dev. Biol.*, 363, 308–319.

Espinoza R.E., Wiens J.J. & Tracy C.R. (2004). Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proc. Natl. Acad. Sci. USA*, 101, 16819–16824.

Goodman B.A. & Isaac J.L. (2008). Convergent body flattening in a clade of tropical rock-using lizards (Scincidae: Lygosominae). *Biol. J. Linn. Soc.*, 94, 399–411.

Greer A.E. (1991). Limb reduction in squamates: identification of the lineages and discussion of the trends. *J. Herpetol.*, 25, 166–173.

Greer A.E., Caputo V., Lanza B. & Palmieri R. (1998). Observations on limb reduction in the scincid lizard genus *Chalcides*. *J. Herpetol.*, 32, 244–252.

Greer A.E. & Cogger H.G. (1985). Systematics of the reduced-limbed and limbless skinks currently assigned to the genus *Anomalopus* (Lacertilia: Scincidae). *Rec. Aust. Mus.*, 37, 11–54.

Hall B.K. (2007). Homoplasy and homology: dichotomy or continuum? *J. Human Evol.*, 52, 473–479.

Hansen T.F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, 51, 1341–1351.

Heideman N.J.L., Mulcahy D.G., Sites J.W., Hendricks M.G.J. & Daniels S.R. (2011). Cryptic diversity and morphological convergence in threatened species of fossorial skinks in the genus *Scelotes* (Squamata: Scincidae) from the Western Cape Coast of South Africa: implications for species boundaries, digit reduction and conservation. *Mol. Phylogenet. Evol.*, 61, 823–833.

Herrel A., Vanhooydonck B. & Van Damme R. (2004). Omnivory in lacertid lizards: adaptive evolution or constraint? *J. Evol. Biol.*, 17, 974–984.

Herrel A., Vincent S.E., Alfaro M.E., Van Wassenbergh S., Vanhooydonck B. & Irschick D.J. (2008). Morphological convergence as a consequence of extreme functional demands: examples from the feeding system of natricine snakes. *J. Evol. Biol.*, 21, 1438–1448.

Irschick D.J., Austin C.C., Petren K., Fisher R.N., Losos J.B. & Ellers O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.*, 59, 21–35.

Irschick D.J. & Jayne B.C. (1999). A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. *Physiol. Biochem. Zool.*, 72, 44–56.

Jackman T.R., Losos J.B., Larson A. & de Queiroz K. (1997). Phylogenetic studies of convergent faunal evolution in Caribbean *Anolis* lizards. In: *Molecular evolution and adaptive radiation* (eds. Givnish T & Sytsma K). Cambridge University Press Cambridge, 535–557.

Kearney M. & Stuart B.L. (2004). Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones. *Proc. Roy. Soc., Biol. Sci.*, 271, 1677–1683.

Kendrick P.G. (1991). The Phylogenetics and Comparative Ecology of *Lerista* Bell, 1983; Patterns of Evolution in a Genus of Sand-Swimming Skinks. In: Department of Zoology. University of Western Australia, p. 300.

Kohlsdorf T. & Wagner G.P. (2006). Evidence for the reversibility of digit loss: a phylogenetic study of limb evolution in *Bachia* (Gymnophthalmidae: Squamata). *Evolution*, 60, 1896–1912.

Kolbe J.J., Revell L.J., Szekely B., Brodie III E.D. & Losos J.B. (2011). Convergent evolution of phenotypic integration and its alignment with morphological diversification in Caribbean *Anolis* ecomorphs. *Evolution*, 65, 3608–3624.

Lamb T., Meeker A.M., Bauer A.M. & Branch W.R. (2003). On the systematic status of the desert plated lizard (*Angolosaurus skoogi*): phylogenetic inference from DNA sequence analysis of the African Gerrhosauridae. *Biol. J. Linn. Soc.*, 78, 253–261.

Lee M.S.Y. (1998). Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol. J. Linn. Soc.*, 65, 369–453.

Losos J.B. (1990a). Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. *Anim. Behav.*, 39, 879–890.

Losos J.B. (1990b). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution*, 44, 1189–1203.

Losos J.B. (2009). *Lizards in an Evolutionary Tree*. California University Press, Berkeley, CA.

Losos J.B. (2011). Convergence, adaptation, and constraint. *Evolution*, 65, 1827–1840.

Losos J.B., Papenfuss T. & Macey J.R. (1989). Correlates of running, jumping, and parachuting performance in the butterfly lizard, *Leiolepis belliana*. *J. Zool.*, 217, 559–568.

Maddison W.P. & Maddison D.R. (2011). *Mesquite: A Modular System for Evolutionary Analysis v.2.75*. http://mesquiteproject.org

McCay M.G. (2001). Aerodynamic stability and maneuverability of the gliding frog *Polypedates dennysi*. *J. Exp. Biol.*, 204, 2817–2826.

McGhee G.R. (2011). *Convergent Evolution: Limited Forms Most Beautiful*. MIT Press, Cambridge, USA.

McGuire J.A. (2003). Allometric prediction of locomotor performance: an example from Southeast Asian flying lizards. *Am. Nat.*, 161, 337–349.

McGuire J.A. & Dudley R. (2005). The cost of living large: comparative gliding performance in flying lizards (Agamidae: *Draco*). *Am. Nat.*, 166, 93–106.

Melville J., Harmon L.J. & Losos J.B. (2006). Intercontinental community convergence of ecology and morphology in desert lizards. *Proc. Roy. Soc., Biol. Sci.*, 273, 557–563.

Miles D.B., Losos J.B. & Irschick D.J. (2007). Morphology, performance, and foraging mode. In: *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. (eds. Reilly SM, McBrayer LD & Miles DB). Cambridge University Press Cambridge, England, 49–93.

Owen R. (1848). *On the Archetype and Homologies of the Vertebrate Skeleton*. John Van Voorst, Peternoster Row, London, England.

Paskins K.E., Bowyer A., Megill W.M. & Scheibe J.S. (2007). Take-off and landing forces and the evolution of controlled gliding in northern flying squirrels *Glaucomys sabrinus*. *J. Exp. Biol.*, 210, 1413–1423.

Pellegrino K.C.M., Rodrigues M.T., Yonenaga-Yassuda Y. & Sites J.W. (2001). A molecular perspective on the evolution of microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. *Biol. J. Linn. Soc.*, 74, 315–338.

Pough F.H., Andrews R.M., Cadle J.E., Crump M.L., Savitzky A.H. & Wells K.D. (2004). *Herpetology*. 3rd edn. Pearson Education Inc., Upper Saddle River, USA.

Revell L.J. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution*, 63, 3258–3268.

Revell L.J., Johnson M.A., Schulte II J.A., Kolbe J.J. & Losos J.B. (2007). A phylogenetic test for adaptive convergence in rock-dwelling lizards. *Evolution*, 61, 2898–2912.

Rosenblum E.B. (2006). Convergent evolution and divergent selection: lizards at the White Sands ecotone. *Am. Nat.*, 167, 1–15.

Russell A.P. (1977). The genera *Rhoptropus* and *Phelsuma* (Reptilia: Gekkonidae) in southern Africa: a case of convergence and a reconsideration of the biogeography of *Phelsuma*. *Zool. Afr.*, 12, 393–408.

Russell A.P. (1979). Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia*, 1979, 1–21.

Sanger T.J., Revell L.J., Gibson-Brown J.J. & Losos J.B. (2012). Repeated modification of early limb morphogenesis programmes underlies the convergence of relative limb length in *Anolis* lizards. *Proc. Roy. Soc., Biol. Sci.*, 279, 739–748.

Schluter D. (1996). Adaptive radiation along genetic lines of least resistance. *Evolution*, 50, 1768–1774.

Schmitz A., Brandley M.C., Mausfeld P., Vences M., Glaw F., Nussbaum R.A. & Reeder T.W. (2005). Opening the black box: phylogenetics and morphological evolution of the Malagasy fossorial lizards of the subfamily "Scincinae". *Mol. Phylogenet. Evol.*, 34, 118–133.

Schulte J.A., Macey J.R., Espinoza R.E. & Larson A. (2000). Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biol. J. Linn. Soc.*, 69, 75–102.

Shine R. (1995). A new hypothesis for the evolution of viviparity in reptiles. *Am. Nat.*, 145, 809–823.

Sidlauskas B. (2008). Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach. *Evolution*, 62, 3135–3156.

Siler C.D. & Brown R.M. (2011). Evidence for repeated acquisition and loss of complex body-form characters in an insular clade of Southeast Asian semi-fossorial skinks. *Evolution*, 65, 2641–2663.

Skinner A., Lee M.S.Y. & Hutchinson M.N. (2008). Rapid and repeated limb loss in a clade of scincid lizards. *BMC Evol. Biol.*, 8, 310.

Snyder R.C. (1949). Bipedal locomotion of the lizard *Basiliscus basiliscus*. *Copeia*, 1949, 129–137.

Snyder R.C. (1962). Adaptations for bipedal locomotion of lizards. *Am. Zool.*, 2, 191–203.

Socha J.J. & LaBarbera M. (2005). Effects of size and behavior on aerial performance of two species of flying snakes (Chrysopelea). *J. Exp. Biol.*, 208, 1835–1847.

Stayton C.T. (2006). Testing hypothesis of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. *Evolution*, 60, 824–841.

Stayton C.T. (2008). Is convergence surprising? An examination of the frequency of convergence in simulated datasets. *J. Theor. Biol.*, 252, 1–14.

R Development Core Team. (2012). *R: A Language and Environment for Statistical Computing*. Vienna, Austria.

Thomas R.D.K. & Reif W.-E. (1993). The skeleton space: a finite set of organic designs. *Evolution*, 47, 341–360.

Townsend T.M., Larson A., Louis E. & Macey J.R. (2004). Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Syst. Biol.*, 53, 735–757.

Uetz P., Goll J. & Hallermann J. (2007). Die TIGR-Reptiliendatenbank. *Elaphe*, 15, 22–25.

Urban E.K. (1965). Quantitative study of locomotion in teiid lizards. *Anim. Behav.*, 13, 513–529.

Vanhooydonck B., Meulepas G., Herrel A., Boistel R., Tafforeau P., Fernandez V. & Aerts P. (2009). Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis guentheri*. *J. Exp. Biol.*, 212, 2475–2482.

Vermeij G.J. (2006). Historical contingency and the purported uniqueness of evolutionary innovations. *Proc. Natl. Acad. Sci. USA*, 103, 1804–1809.

Wake D.B. (1991). Homoplasy: the result of natural selection, or evidence of design limitations? *Am. Nat.*, 138, 543–567.

Ward A.B. & Brainerd E.L. (2007). Evolution of axial patterning in elongate fishes. *Biol. J. Linn. Soc.*, 90, 97–116.

Whiting A.S., Bauer A.M. & Sites J.W. (2003). Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). *Mol. Phylogenet. Evol.*, 29, 582–598.

Wiens J.J. (2001). Character analysis in morphological phylogenetics: problems and solutions. *Syst. Biol.*, 50, 689–699.

Wiens J.J., Brandley M.C. & Reeder T.W. (2006). Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution*, 60, 123–141.

Wiens J.J. & Singluff J.L. (2001). How lizards turn into snakes: a phylogenetic analysis of body form evolution in anguid lizards. *Evolution*, 55, 2303–2318.

Williams E.E. (1982). Ecomorphs, faunas, island size, and diverse endpoints in island radiations of *Anolis*. In: *Lizard Ecology: Studies of a Model Organism*. (eds. Huey RB, Pianka ER & Schoener TW). Harvard University Press Cambridge, USA, 326–370.

Appendix

Examples of convergent evolution possibly related to body shape in Squamates. Times refers to the number of times a feature has evolved independently in each clade.

Agamidae and Iguanidae in general

Clade (Taxa)	Times	References
Agamidae (all), Iguanidae (all)	1	Melville *et al.* (2006)

Teiidae and Lacertidae in general

Clade (Taxa)	Times	References
Teiidae (all), Lacertidae (all)	1	Miles *et al.* (2007)

Anolis ecomorphs

Clade (Taxa)	Times	References
Polychrotinae (*Anolis* spp.)	many	Williams (1982); Losos (1990a, b); Jackman *et al.* (1997)

Bipedalism

Clade (Taxa)	Times	References
Agamidae (*Chlamidosaurus kingii*, *Ctenophorus* spp., *Lophognathus* spp.)	3	Clemente *et al.* (2008)
Iguanidae (*Basiliscus* spp., *Crotaphytus* spp.)	2	Snyder (1949); Urban (1965)
Lacertidae (*Acanthodactylus erythrurus*)	1	Aerts *et al.* (2003)
Phrynosomatinae (sand lizards)	1	Irschick & Jayne (1999)

Body flattening in rock dwellers

Clade (Taxa)	Times	References
Cordylidae (*Platysaurus capensis*, *Pseudocordylus capensis*)	2	Revell *et al.* (2007)
Phrynosomatinae (*Petrosaurus* spp.)	1	Revell *et al.* (2007)
Polychrotinae (*Anolis bartschi*)	1	Revell *et al.* (2007)
Scincidae (*Carlia mundivensis*, *Carlia rococo*, *Carlia scirtetis*, *Cryptoblepharis litoralis*, *Eulamprus brachysoma*, *Lampropholis mirabilis*, *Techmarscincus jigurru*)	6	Goodman & Isaac (2008)
Tropidurinae (*Tropidurus semitaeniatus*)	1	Revell *et al.* (2007)

Dry adhesion

Clade (Taxa)	Times	References
Gekkota (Diplodactylidae, Gekkonidae)	2	Russell (1979); Irschick *et al.* (1996)
Polychrotinae (*Anolis* spp.)	1	Russell (1979); Irschick *et al.* (1996)
Scincidae (*Prasinohaema virens*)	1	Russell (1979); Irschick *et al.* (1996)

Herbivory

Clade (Taxa)	Times	References
Agamidae (*Hydrosaurus* spp., *Uromastyx* spp.)	2	Stayton (2006)
Diplodactylidae (*Hoplodactylus* spp.)	1	Stayton (2006)
Iguaninae (Iguaninae)	1	Stayton (2006)
Lacertidae (*Lacerta lepida*)	1	Stayton (2006)
Scincidae (*Corucia zebrata*)	1	Stayton (2006)
Teiidae (*Dicrodon guttulatum*)	1	Stayton (2006)
Tropidurinae (*Liolaemus buergeri*, *Liolaemus fitzingeri*, *Liolaemus lineomaculatus*, *Phymaturus* spp.)	2^+	Espinoza *et al.* (2004)
Varanidae (*Varanus olivaceus*)	1	Stayton (2006)
Xantusiidae (*Lepidophyma smithi*)	1	Stayton (2006)

Gliding

Clade (Taxa)	Times	References
Agamidae (*Draco* spp., *Leiolepis* spp.)	2	Losos *et al.* (1989); McGuire & Dudley (2005)
Gekkota (*Ptychozoon* spp.)	1	Vanhooydonck *et al.* (2009)
Lacertidae (*Holaspis gunteri*)	1	Vanhooydonck *et al.* (2009)

Sand-diving/burying

Clade (Taxa)	Times	References
Agamidae (*Agama etoshae*, *Phrynocephalus* spp.)	2	Arnold (1995); Lamb *et al.* (2003)
Gerrhosauridae (*Angolosaurus skoogi*)	1	Arnold (1995); Lamb *et al.* (2003)
Lacertidae (*Meroles* spp.)	1	Arnold (1995); Lamb *et al.* (2003)
Phrynosomatinae (*Phrynosoma* spp., *Uma* spp.)	2	Arnold (1995); Lamb *et al.* (2003)
Scincidae (*Lerista* spp., *Scincus* spp., *Mabuya acutilabris*)	3	Kendrick (1991); Arnold (1995); Lamb *et al.* (2003)

Elongate burrowers

Clade (Taxa)	Times	References
Amphisbaenia (all)	1	Kearney & Stuart (2004); Wiens *et al.* (2006)
Anguidae (*Anniella* spp., *Sauresia* spp.)	2	Wiens & Singluff (2001)
Dibamidae (all)	1	Lee (1998)
Gymnophthalmidae (*Bachia* spp., *Calyptommatus* spp., *Nothobachia ablephara*, *Rachisaurus* spp.)	3^+	Pellegrino *et al.* (2001); Kohlsdorf & Wagner (2006)
Scincidae (*Acontias* spp., *Acontophiops* spp., *Anomalopus* spp., *Brachymeles* spp., *Chalcides* spp., *Feylinia polylepis*, *Hemiergis polylepis*, *Isopachys* spp., *Opiomorus* spp., *Lerista* spp., *Paracontias* spp., *Plestiodon reynoldsi*, *Sygomeles* spp., *Saiphos* spp., *Sepsina* spp., *Sphenops* spp., *Typhlacontias* spp., *Voeltzkowia* spp., *Typhlosaurus* spp.)	14^+	Greer & Cogger (1985); Greer (1991); Kendrick (1991); Greer *et al.* (1998); Whiting *et al.* (2003); Daniels *et al.* (2005); Schmitz *et al.* (2005); Wiens *et al.* (2006); Skinner *et al.* (2008); Heideman *et al.* (2011); Siler & Brown (2011)
Serpentes (all)	1	Townsend *et al.* (2004)

Elongate surface-dwellers

Clade (Taxa)	Times	References
Anguidae (*Ophiodes* spp., *Ophisaurus* spp.)	2	Wiens & Singluff (2001)
Cordylidae (*Chamaesaura* spp.)	1	Wiens *et al.* (2006)
Gekkota (most Pygopodidae)	1	Wiens *et al.* (2006)
Gerrhosauridae (*Tetradactylus* spp.)	1	Wiens *et al.* (2006)

Bolting, bouldering, and burrowing: functional morphology and biomechanics of pedal specialisations in desert-dwelling lizards

Timothy E. Higham

Department of Biology, University of California, 900 University Avenue, Riverside, California 92521, USA; E-mail: thigham@ucr.edu

Abstract

Animals often move in a variety of complex habitats and they often exhibit morphological variation that can be explained, at least in part, by the habitat in which they live. The habitats of animals are often generally categorised based on dominant structures. Although this scheme can be fruitful, it ignores the intricacies of the microhabitat and the actual habitat utilisation of an animal. This is especially the case for desert habitats, which are often regarded as uniform and simple. Desert-dwelling lizards, however, occupy a range of structures in a desert including trees, rocks, and sand, and they have been noted as being a dominant form in almost all the warm deserts of the world. Along with this disparity in microhabitat, lizards often exhibit pedal specialisations, or modifications, that enhance a given behaviour (e. g., digging or running). Much work has examined the thermal influences on lizard biology, but pedal specialisations have not been discussed in an integrative and comprehensive way. Here, I review the pedal specialisations in desert-dwelling lizards and discuss their functional ramifications. I will also propose links between these specialisations/modifications and characteristics of habitat structure. Some of the pedal specialisations of desert-dwelling lizards include adhesive toe pads for climbing (geckos), toe fringes and webbed feet for maximising the surface area in contact with the substrate (sand-dwelling lizards), a multifunctional foot (sand-dwelling lizards), zygodactylus feet (chameleons), and claws (rock-dwelling lizards). Finally, I propose a frame-

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work for future studies of biomechanics and functional morphology in desert-dwelling lizards.

Introduction

Differences in locomotor morphology are often related to the habitat in which an animal lives (Losos 1990; Bauer *et al.* 1996; Melville & Swain 2000; Herrel *et al.* 2001; Wainwright *et al.* 2002; Johnson *et al.* 2005; Goodman *et al.* 2008; Higham & Russell 2010). For example, skinks that live in habitats that are rock-dominated exhibit longer limbs than those species occupying forest habitats (Goodman *et al.* 2008). However, there are cases where the relationships between morphology and habitat use/occupation are non-existent, weak, or unpredictable (Vanhooydonck & Van Damme 1999; Schulte *et al.* 2004; Birn-Jeffery *et al.* 2012; Logan *et al.* 2012). One possible confounding factor is that many studies categorise animals based on macro- rather than their microhabitat, which might miss key aspects of habitat utilisation that exert selective pressures on morphology. Desert-dwelling lizards offer a diverse system in which the species occupy a range of habitat types. Moreover, microhabitat utilisation of desert-dwelling lizards can be quantified, making it an ideal system for determining the relationship between morphology and habitat. In addition, lizards are often very abundant and dominant in these habitats.

Desert ecosystems often convey the idea of a paucity of life, continuous heat, lack of moisture, and the presence of endless sand (Jaeger 1955). In fact, deserts can be hot or cold, and are chiefly characterised by a dearth of precipitation relative to water loss by evaporation (Bradshaw 1986). Deserts exist everywhere in the world, including polar and sub-tropical areas. Deserts exist on coastal areas (e. g., Namibia, Peru, or Chile), but also inland (e. g., Mojave, Great Basin, or Central Asian) and are often subjected to persistent wind (Bradshaw 1986). Although the climate is often a key topic of desert research, the habitat structure of deserts is extremely complex, diverse, and, in sandy areas, often in flux. In addition, many animals that live in deserts are not only specialised for dealing with temperature and humidity extremes, but also specialised for locomotion in these extreme habitats (e. g., sand dunes). How these animals move and how their pedal specialisations enhance locomotion in these complex habitats will help us understand the evolution of morphological disparity. It will also reveal how ecological demand influences the form-function relationship.

Lizards are often the dominant vertebrate group in desert habitats. The fact that they are ectotherms likely enables them to cope with the extreme climate (Pianka 1986). Desert habitats are extremely complex and often contain three-dimensional structures such as boulders, bushes, trees, sand dunes, or sheet-rock outcrops (Fig. 1). Despite this complexity, lizards occupying desert habitats are often characterised as either arboreal (trees), saxicolous (rocks), or psammophilous (sand). Unfortunately, this categorisation does little to capture the natural movements of lizards and the biomechanical and morphological underpinnings of locomotion. The microhabitat use of desert-dwelling lizards is something we know little about and will be a vital area of future research when considering the ramifications of pedal specialisations. For example, saxicolous lizards might occupy flat rock sheets, irregularly shaped boulders, or vertical (or inverted) rock faces. In addition to this variation in macro-topography, rocks can vary substantially with respect to their rugosity or roughness at the micro level and this could have a significant impact on the ability of lizards to gain purchase on the substrate (Russell & Johnson 2007).

The goals of this paper are (1) to examine the key features of common pedal specialisations of desert-dwelling lizards, (2) to examine what is known about how desert-dwelling lizards use their natural habitat, and (3) to propose and define a framework for future work that might address the consequences of ecological and morphological diversity among desert-dwelling lizards.

Pedal specialisations for desert locomotion: an overview

Lizards exhibit an array of pedal specialisations/modifications for running, climbing, or digging in desert habitats (Solano 1964; Dixon & Huey 1970; Haacke 1976; Carothers 1986; Luke 1986; Russell & Bauer 1988, 1990; Bauer & Russell 1991; Pianka & Vitt 2003; Lamb & Bauer 2006; Korff & McHenry 2011; Li *et al.* 2012). These include, but are not limited to, toe fringes, interdigital webs, modified claws, elongation of foot tendons or toes, adhesive toe pads, paraphalangeal elements, and prehensile feet (Fig. 2). The relative importance of these modifications will depend on whether the lizard

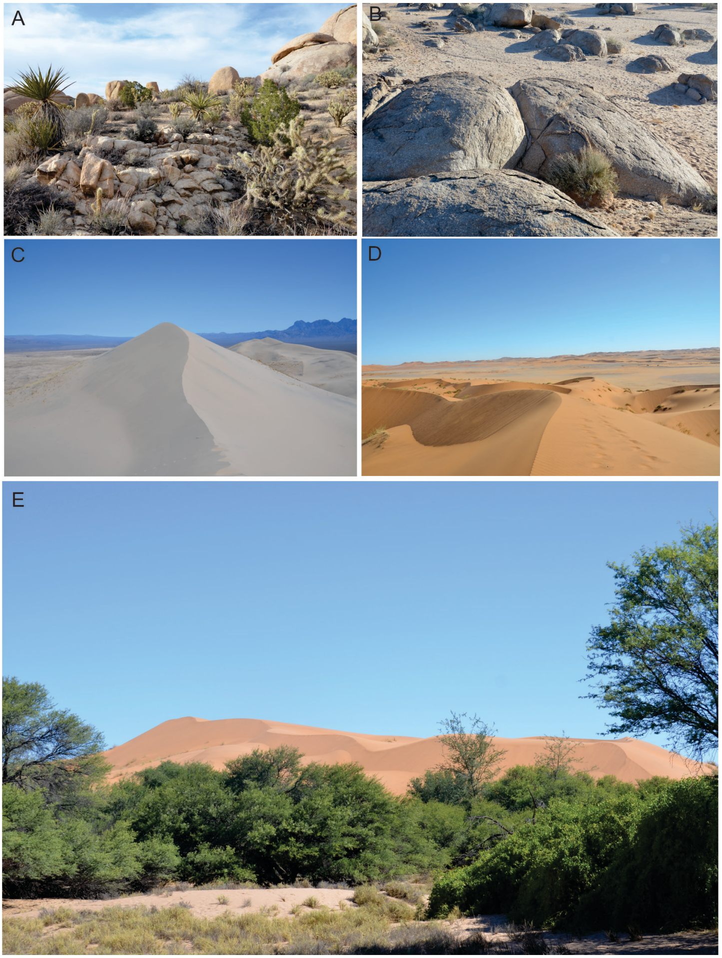

Figure 1:
Examples of desert habitats, highlighting structural diversity. A: Granite Mountains, Mojave Desert, California, USA. This habitat is commonly occupied by a variety of lizards such as *Uta stansburiana*, *Colenyx variegatus*, and *Sceloporus magister*. B: rocky area in gravel plains, Gobabeb, Namib Desert, Namibia. This area is commonly occupied by lizards such as *Ptenopus garrulus*, *Pachydactylus rangei*, and *Rhoptropus afer*. C: Kelso Dunes, Mojave Desert, California, USA. A common lizard in this habitat is *Uma scoparia*. D: sand dunes, Gobabeb, Namib Desert, Namibia. A common lizard in this habitat is *Moroles anchietae*. E: Kuiseb River, Gobabeb, Namib Desert, Namibia. Arboreal geckos from the genus *Lygodactylus* can be found here. All photos taken by the author.

is arboreal, saxicolous, or psammophilous, and will depend on how the lizards use these types of habitat (e. g., Collins *et al.* in press). For example, claws and adhesive toe pads will be important for climbing (up and down both rocks and trees), but toe fringes and interdigital webs will be important for moving on soft, sandy surfaces. Whatever the function, these aspects of morphology are key for all forms of locomotor movements involving limbs given that these structures are what contact the substrate and exert forces on the ground (Biewener 2003). Forces are distributed across the pedal surface in contact with the ground and pedal specialisations likely maximise and/or enhance running or clinging performance (Higham & Irschick 2013). The specific pedal specialisations will each be discussed in detail below.

Toe fringes

Toe fringes are laterally projecting, elongated scales that originate from epidermal and dermal tissue (Fig. 2; Luke 1986). In addition to being important for locomotion on moving sand, they can be important for "swimming" through sand, running across water, digging, and potentially gliding (Carothers 1986; Luke 1986; Bauer & Russell 1991; Hsieh 2003). Although toe fringes are well suited for studies of convergence, it is difficult to link toe fringes to a particular habitat. As far as locomotion goes, they likely increase context-dependent performance and they might increase efficiency. It is clear that toe fringes are useful on, or in, substrates that are relatively fluid such as water or dune sand.

There are four types of fringes in lizards, including triangular fringes (e. g., *Uma* and *Bunopus*), projectional fringes (e. g., *Scincus*), conical fringes (e. g., *Teratoscincus* and *Ptenopus*), and rectangular fringes (e. g., *Basiliscus*). Although it is possible that the different fringe types address different functional challenges, the differences might not be adaptive. Some functional differences have been suggested after preliminary functional studies (Luke 1986). Triangular, projectional, and conical fringes are found on species that occupy sandy habitats and are collectively referred to as denticulate fringes, projecting independently from the toe. The rectangular fringes found on water-running lizards contact one other, preventing water from flowing between adjacent scales. By contrast, the denticulate fringes prevent sand from flowing between adjacent scales. Thus, denticulate fringes provide a greater effective surface area for those lizards that run over sand in desert habitats (Luke 1986). Despite this preliminary functional examination, we still lack a clear understanding of the biomechanical mechanisms underlying fringe function during locomotion. How does the presence of toe fringes influence the mechanics of locomotion? How do the forces exerted by the feet differ when toe fringes are present?

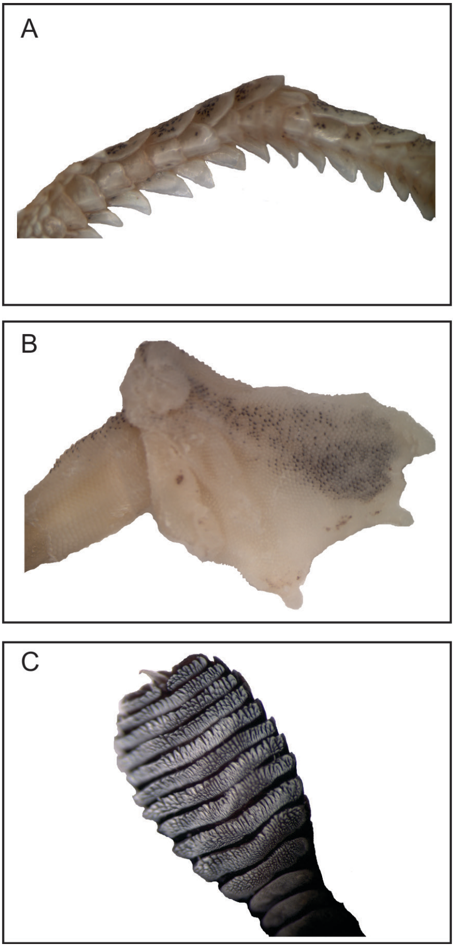

Figure 2:
Examples of pedal specializations, including A: toe fringes (*Meroles anchietae*), B: webbed feet (*Pachydactylus rangei*), and C: adhesive toe pads (*Rhoptropus bradfieldi*). All photos taken by the author.

Current data regarding the impact of toe fringes on running speed across different species are limited. However, recent work suggests that factors other than toe fringes might predict differences in speed across species. For example, *Callisaurus draconoides* (without fringes) sprints faster than *Uma scoparia* (with fringes) (Irschick & Jayne 1999b). Another recent study examined the sprinting ability of *U. scoparia* and *C. draconoides* on two different substrates (fine dune-sand and coarse wash-sand), and found that *C. draconoides* ran slightly faster on dune sand, but not on the wash sand (Korff & McHenry 2011). The authors concluded that sprinting ability is thus not dominated by environmental differences in the substrate nor the presence of toe fringes. Interestingly, there are populations of *C. draconoides* in Baja California that exhibit toe fringes (Luke 1986; pers. obs.). This variation between populations provides an ideal natural experiment for examining the functional importance of toe fringes.

Interdigital webs

A webbed foot can be used either as a “shovel” or a “snowshoe” (Russell & Bauer 1990; Bauer & Russell 1991). In the former case, lizards can dig, typically in sand, with the increased surface area and surface preventing sand particles from passing between the digits. The functional benefit associated with increased surface area can also be implicated in running on top of soft sandy substrates, thus implicating the analogy of snowshoes, which adopt a similar function. One gecko, *Pachydactylus rangei*, utilises webbed feet in the Namib Desert for both excavating a burrow and running over soft sand (see Fig. 2). However, the functional benefits in terms of mechanics or efficiency have yet to be determined. There might also be trade-offs associated with interdigital webbing that have yet to be identified. For example, the range of motion of each digit might be constrained with the existence of webbing. In addition, it is not clear how the mechanics of propulsion during locomotion are influenced by the presence of webbing. Assessing the mechanics of locomotion in *P. rangei* in comparison with closely related taxa lacking interdigital webbing would provide a functional understanding of this interesting and rare pedal specialisation.

Modified claws

Claws are important for clinging to substrata, especially those surfaces that are rough (Fig. 2; Zani 2000). The functional implications are relatively unexplored, but anecdotal information suggests that geckos with their claws removed are no longer able to cling to the underside of horizontal surfaces (Bellairs 1969). Additionally, geckos without claws appear to struggle when climbing up rough vertical surfaces (Mahendra 1941). This struggle, however, does not appear to occur when these same geckos climb smooth surfaces. Thus, the adhesive system appears to be important for smooth surfaces, whereas the claws become important on rough surfaces, such as rocks. Why some geckos lack claws but exhibit extensive adhesive systems is not fully understood.

In an overview of claw morphology (Mahendra 1941), noted the importance of joint structure at the proximal origin of the claw. In Gekkonidae, the articulation of the penultimate phalanx with the last phalanx is substantially dorsal to the insertion of the contractor tendon, which bends the claw in the ventral direction. This distance between the tendon and the joint effectively increases the mechanical advantage and enhances the ability for the claw to be forcefully pushed into the substrate. Although not examined in detail, it might be hypothesised that climbing lizards have an increased ability to contract their claws.

Claw morphology can be related to habitat within certain groups of lizards. A study of neotropical iguanian lizards examined the relationship between habitat use (arenicolous, arboreal, and saxicolous) and claw morphology, and found that those species that often climb (arboreal and saxicolous) exhibit higher and more sharply curved claws (Tulli *et al.* 2009). Non-climbers tended to have longer and less-curved claws. This was also observed in a study that focused on lizards from the genus *Liolaemus* (Etheridge 2000). Coupling these conclusions with a previous study of clinging performance (Zani 2000) suggests that increased claw height and sharp curvature enable lizards to climb by “hooking” into the substrate while still maintaining stability. The longer and flatter claws of terrestrial lizards might increase the effective limb length and increase the surface area of the digit, much like toe fringes. Biomechanical analyses of claw morphology and locomotion on different substrates will help answer some of these questions.

Although claw morphology is an attractive area for connecting behaviour with morphology, a recent study highlights that this relationship can be somewhat complex (Birn-Jeffery *et al.* 2012). One important consideration is what an animal actually does in its natural habitat. Although claw morphology might be expected to differ between arboreal and terrestrial species (Tulli *et al.* 2009), animals often occupy a range of habitats and thus exhibit a generalised morphology. Quantification of claw function, including manipulation of claw morphology, will be beneficial in future research. In addition, phylogenetic constraint might limit the variation in claw function in relation to habitat. Thus, any quantification of claw morphology in relation to habitat should include phylogenetic information.

Elongation of foot tendons and/or toes

A long foot increases the effective limb length of a lizard and enables it to increase locomotor speed by increasing the lever in contact with the substrate (Higham & Russell 2010). In the genus *Rhoptropus*, the elongate metatarsus and phalanx 1 of digit III (Bauer *et al.* 1996) results in a longer digit and thus increased locomotor speeds (Higham & Russell 2010). This is one way of increasing the length of the foot and it is somewhat constrained by the presence of the adhesive system on the distal phalanges. How other desert-dwelling lizards increase the length of their feet and how this impacts locomotor mechanics would be important to consider in the context of pedal specialisations.

The zebra-tailed lizard, *C. draconoides*, has one of the longest feet of phrynosomatid lizards and can run incredibly fast, reaching speeds close to 6 m s^{-1} (Irschick & Jayne 1999a, b). This species has a multifunctional foot that exhibits substrate-specific mechanisms for locomotion (Li *et al.* 2012). On a solid substrate, springs (tendons), skeletal elements, and muscles work to enable *C. draconoides* to store and release elastic energy. On a soft, sandy substrate, the foot acts like a force-generating paddle as it penetrates the surface of the sand. It is clear that the importance of this pedal specialisation is related to the openness and hardness of the habitat and the speeds at which the lizard must run.

Adhesive toe pads of geckos

Adhesive toe pads are sub-digital structures that consist of a series of lamellae that are shrouded in arrays of hair-like setae (Fig. 2; Russell 1975, 1979, 1986, 2002; Russell & Bauer 1989; Autumn & Peattie 2002; Johnson *et al.* 2005; Johnson & Russell 2009). They are formed from β-keratin and, in geckos, they often branch at the tips into spatulae. Gecko adhesion has been the subject of many studies and the disparity in morphology between genera is striking (Loveridge 1947; Russell 1976; Gamble *et al.* 2012). In addition to the diversity of sub-digital pad structure, there appears to be a number of "solutions" with respect to other aspects of the manus and pes when it comes to obtaining an adhesive system (Russell 1976). One aspect of the adhesive system that appears to have many solutions relates to digit I (Russell 1976) because it typically has only two phalanges, thereby limiting the ability to hyperextend the digit. In fact, the hyperextension in digit I typically occurs between the first phalanx and the first metacarpal/metatarsal (Russell 1976). This constraint has, in some cases, resulted in the reduction and disuse of digit I altogether. One important exception is within the *Pachydactylus* radiation, in which hyperphalangy of digit I (resulting in three phalanges instead of two) has permitted the expansion of the sub-digital adhesive toepad. In addition, hyperextension in this radiation can include the distal two phalanges. This radiation is commonly found in African deserts and the ability to utilise digit I during locomotion might have contributed to their success.

Although typically thought of as an adaptation for climbing in arboreal habitats, perhaps driven by the focus on the arboreal tokay gecko (*Gekko gecko*), adhesion is also important for any climbing gecko (e. g., saxicolous) because it provides a "stickiness" via van-der-Waals interactions, which are weak intermolecular forces (Autumn *et al.* 2000). Vertical orientations seem to be common in rocky outcrops that are typically found in deserts; thus, the adhesive system of geckos might play a role in the ability to move up, down, and around rocks. This is supported by the fact that secondarily padless species (or those with reduced toe pads) in these same general habitats are terrestrial, have longer toes, and are faster (Johnson *et al.* 2005; Johnson & Russell 2009; Higham & Russell 2010; Collins *et al.* in press). Many of the species from the *Pachydactylus* radiation in Southern Africa often climb on rocks and those that do have well-developed adhesive systems.

In addition to adhesion, what selective advantage might exist for having a sub-digital adhesive system arranged how it is? As highlighted almost 40 years ago, little attention has been paid to the spreading of the digits over 180º or more, which is often associated with well-developed toe pads (Russell 1976). It has been proposed that this arrangement of the toes facilitates moving in lateral as well as upward and downward directions on vertical surfaces (Russell 1975). This type of habitat is typified by vertical rock faces, which are often found in desert habitats. Future work should test this hypothesised advantage of the spreading of the digits in conjunction with adhesion, and the *Pachydactylus* radiation could be an ideal group in this context.

The adhesive system does a very effective job when it comes to clinging to smooth surfaces, but the ability to cling to rough surfaces depends on the microtopography of the habitat (Russell & Johnson 2007). As the habitat gets increasingly rugose, the importance of claws might also increase. Actively modulating both the adhesive system and the claws is one way to ensure full contact with a given surface. It is important to note that the adhesive system is only useful when an animal is on an inclined surface given that geckos do not deploy the adhesive system on a level surface (Russell & Higham 2009). Future work should examine the functional interactions between claws and the adhesive system in habitats that vary in rugosity.

Many species of gecko that occupy sandy desert habitats have secondarily lost the adhesive system or did not have it in the first place (Johnson *et al.* 2005). The *Pachydactylus* radiation found in Southern Africa offers an ideal group for studying the impacts of habitat structure on the morphology and function of the adhesive system (Russell 1976). In several of the genera, including *Chondrodactylus*, *Pachydactylus*, and *Rhoptropus*, there are examples of species that are terrestrial and exhibit reduced or lost adhesive systems (Johnson *et al.* 2005). The loss or reduction of adhesion in these cases might be due, in part, to the functional constraints that are imparted by the adhesive system. For example, the deployment and hyperextension of the system with each stride cycle slows locomotion (Russell & Higham 2009). Therefore, it is likely that selection favours a reduction in the system in species that no longer need to climb extensively (Collins *et al.* in press). Little is known regarding the adhesive system of other groups of desert-dwelling geckos in relation to locomotion and/or habitat despite the fact that they are very common in these habitats, including Peru (Dixon & Huey 1970; Huey 1979; Espinoza *et al.* 1990), Mexico (Grismer 2002), Egypt (El Din 2006), Israel (Espinoza *et al.* 1990), Namibia (Werner 1977), Australia (Kluge 1967; King & Rofe 1976; Pianka 1986; Bauer 1990), and the United States (Jones &

Lovich 2009), among others. A comprehensive analysis of the function of adhesive toe pads during locomotion in multiple desert lineages is needed to fully understand the importance in this type of habitat.

Interestingly, recent work suggests that adhesive toe pads have evolved independently 11 times and have been lost nine times (Gamble *et al.* 2012). Although the loss of adhesive toe pads is commonly associated with increased aridity, this is not necessarily the case for desert-dwelling geckos that occupy rocky habitats. Regardless, the impressive number of gains and reversions provides a rich framework for future investigations into the morphology and function of the adhesive system.

Paraphalangeal elements of geckos

Paraphalangeal elements are cartilaginous structures that are associated with interphalangeal joints. They appear to be quite diverse among geckos, occurring in a variety of locations along the phalanges. A main function of the paraphalangeal elements is likely to help control the adhesive toe pads when the penultimate phalanx cannot impart appropriate pressure on the scansors. In sand-dwelling species such as *P. rangei*, the distal phalanges are reduced and the paraphalanges occur only in the proximal areas of the foot (Russell & Bauer 1988). The paraphalangeal elements, in this case, appear to be associated with digging. The elements project laterally and are associated with the interparaphalangeal muscles. These muscles are also associated with the short flexor muscles of the digit, which might enable the webbing to be controlled during digging (Russell and Bauer 1988). This unique function of paraphalangeal elements in desert-dwelling geckos needs to be experimentally tested.

Zygodactyly

Chameleons are unique among lizards in that they exhibit the ability to grasp small branches with their feet (Peterson 1973, 1984; Higham & Jayne 2004; Higham & Anderson 2013). Effective and stable progression in arboreal habitats, where small branches can be far from the ground, is critical for maintaining stability (Peterson 1973; Cartmill 1985; Foster & Higham 2012). Chameleons accomplish this by having hands and feet in which the metacarpals and metatarsals are grouped into opposing bundles (Gasc 1963; Gans 1967; Peterson 1984; Losos *et al.* 1993; Russell & Bauer 2008). Although

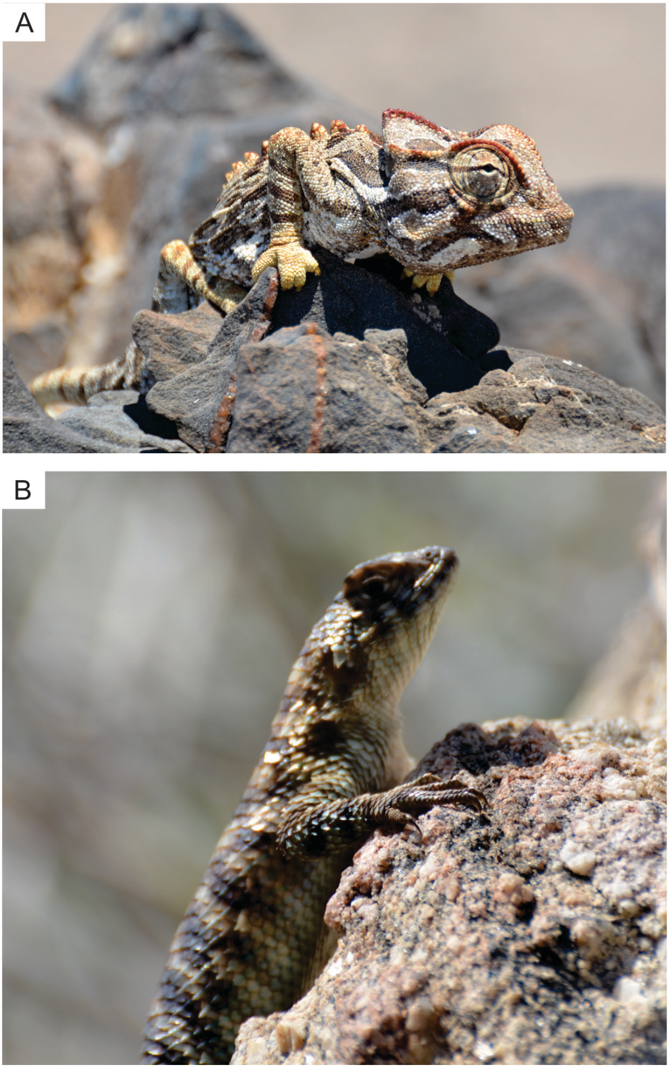

Figure 3:
Images of lizards in their natural habitat to highlight the pedal specializations. A: *Chamaeleo namaquensis* perching on a rocky outcrop near Gobabeb, Namibia. Note the prehensile feet grasping to the rocky projections. B: *Sceloporus orcutti* on a rocky surface in California, USA. Note the claws gripping the surface of the rock. All photos taken by the author.

this pedal specialisation has been implicated in arboreal locomotion in non-desert habitats, desert-dwelling chameleons (*Chamaeleo namaquensis*) also exhibit prehensile feet. This might simply be a consequence of evolutionary history and might not enhance the ability to move in a sandy, desert habitat. In this case, one might expect other aspects of locomotor morphology (or function) to compensate for the prehensile limbs that have been retained. Interestingly, *C. namaquensis* can be found in the middle of a rocky outcrop where they might benefit from having prehensile feet and hands (Fig. 3; Herrel *et al.* 2013). Although not examined in this context, *C. namaquensis* likely exerts adduction forces on the rock projections, generating friction. Future work detailing how these prehensile appendages apply forces to rock surfaces (as compared to arboreal branches) is needed to determine if this species of chameleon utilises its locomotor system in a comparable way as other species of chameleon. In addition, determining whether other features of the locomotor system have been modified in desert-dwelling chameleons is also important.

How desert-dwelling lizards use their habitat

Although detailing the morphological specialisations among lizards is incredibly important, determining how these pedal specialisations are actually used in natural habitats is critical for understanding the functional ramifications of this phenotypic variation. Few studies have examined how desert-dwelling lizards use their habitat, although this type of habitat is ideal for such studies for three reasons. First, desert-dwelling lizards often use sand and desert habitats are often windy. Thus, tracks left from running lizards can be examined over a relatively short time period. The wind will then erase the footprints and another trackway can be analysed. Second, desert habitats are arid and often sunny, providing ideal conditions for viewing lizards as they move throughout their habitat. Third, few obstructions (other than rocks and small bushes) preclude the observations of moving lizards. This is unlike the cluttered habitat of a forest, which can make this process quite challenging.

A key question that has not been addressed in detail is whether species that occupy a general category of habitat (e. g., saxicolous) use their habitats in a similar way, even if the available habitat structure is disparate. For example, one saxicolous species might seek out vertical surfaces, whereas other species might prefer relatively horizontal surfaces. Alternatively, two species that live in disparate rocky habitats might converge on their microhabitat use by seeking out comparable inclines and/or curvatures. Another source of variation is the type of rock that a saxicolous species prefers. Rocks vary considerably in their composition and topography depending on their source and the climate (Dolgoff 1996). This could have significant implications for the relationships between morphology, ecology, and function.

A recent study examined the microtopography of rock surfaces used by *Rhoptropus* cf. *biporosus*, a species of gecko found on sandstone outcrops in the Gai-As region of Namibia, and compared this to the form, configuration, compliance, and functional morphology of the setal fields (Russell & Johnson 2007). The rock samples analysed in this study were taken directly from the field and were those that were actually traversed during a run. Thus, the actual use of the habitat could be linked to habitat structure and morphology of the pes. The sandstone surfaces examined in this study exhibit comparable degrees of unpredictability with respect to the peaks and valleys (Russell & Johnson 2007). The main conclusion is that the actual surfaces available to the lizard result in only a small fraction of setae actually being able to adhere to the surface. This realistic assessment of locomotion and morphology diverges drastically from the smooth surfaces used in studies that typically examine adhesion in geckos (Irschick *et al.* 1996; Autumn *et al.* 2000). Although this study by Russell & Johnson (2007) examined ecologically relevant morphology, more information is needed regarding how lizards run in their habitat and what they might prefer/avoid.

Another recent study examined how a Namibian cursorial gecko, *Rhoptropus afer,* uses its habitat and how habitat availability and use differ between populations (Collins *et al.* in press). When escaping, *R. afer* generally avoided steep inclines and declines as well as heterogeneous substrates, thereby selecting escape routes that were not direct. Variation in the use of available habitat also varied among populations. For example, a population close to the coast in Namibia used substrates that were less inclined than what was generally available (Collins *et al.* in press). Whether this variation at the population level is replicated at an interspecific level is not understood at this point.

Two studies have quantified the locomotor activity of a dune-dwelling lizard (*Uma scoparia*) in its natural habitat (Jayne & Ellis 1998; Jayne & Irschick 2000). A goal of the study by Jayne & Irschick (2000) was to determine how frequently lizards run near their maximal speed. Surprisingly, the lizards often moved very fast during undisturbed locomotion. In addition, bipedal locomotion was extremely rare (< 0.5% of all strides). The study by Jayne & Ellis (1998) examined the impacts and use of inclines on the escape behaviour of *U. scoparia*. Surprisingly, *U. scoparia* rarely used level surfaces, despite being considered a terrestrial lizard. In fact, normal escape behaviour included substantial movements up and down inclines (Jayne & Ellis 1998). Additionally, escaping lizards turned minimally, thus commonly moving in relatively straight paths. These types of studies are extremely rare, but yield incredibly important information. Desert-dwelling lizards are ideal for this type of research given that footprints are visible (and speed can often be determined from these footprints) and lizards can be viewed with relative ease. This is in contrast to forest-dwelling lizards, in which the habitat might obstruct the view of the lizard.

Future directions

The biomechanics of desert-dwelling lizards in the field need to be determined. This could include high-speed video of natural movements, but also comparisons of field movements and lab movements. Although locomotor speeds can be obtained under certain conditions without cameras (e. g., footprints left in the sand), the development of field-portable high-speed cameras can enable researchers to examine how natural habitat structure impacts three-dimensional limb movements. Indeed, several studies have utilised field-portable cameras to examine lizard locomotion (Bergmann & Irschick 2010; Higham & Russell 2010). However, we are lacking information about high-speed movements of lizards in their natural habitat.

In addition to high-speed video cameras, wireless accelerometers and gyros are permitting a high-resolution examination of natural animal movements (Hedrick *et al.* 2004). One issue is that desert-dwelling lizards are often small (a few grams), making these measurements difficult. However, technological advancements are likely to reach a stage where very small wireless chips (< 1 g) will be suitable for these small lizards. If these can record three-dimensional accelerations as a desert-dwelling lizard runs through its natural habitat, we can assess whether general habitat categories are linked to actual movements.

Although the variation within a pedal specialisation might not be telling in terms of predicting habitat structure or use, the broad-scale differences in pedal specialisations might predict a general habitat type. For example, toe fringes are likely suitable for moving under, through, or on soft surfaces such as water or soft sand. By contrast, highly curved claws might be important for moving up rough surfaces such as rocks. Finally, a combination of adhesive toe pads and claws are likely important for desert-dwelling lizards that occupy a range of habitats, including both smooth and rough surfaces. Future work examining the evolution of pedal specialisations across all lizards will permit the identification of convergence in relation to ecology (Losos 2011). Evidence of the operation of natural selection is likely if certain specialisations are arising independently in comparable ecological conditions. At the same time, one must be cautious given that convergence in morphology does not always convey adaptation (for discussion, see Losos 2011).

Finally, a biomechanical understanding of pedal specialisations is lacking. What does it mean to have long claws and toe pads? What are the consequences of having paraphalangeal elements? How do neuromuscular control, neuromuscular anatomy, and muscle mechanics (force, strain, and velocity) change with respect to different pedal specialisations? How do propulsive mechanics and overall patterns of ground reaction forces change with respect to pedal specialisations? This is an exciting time in which we can build upon the excellent morphological work that has been done over the last 50 years and determine the mechanical and ecological ramifications of these pedal specialisations.

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Literature cited

Autumn K., Liang Y.A., Hsieh S.T., Zesch W., Chan W.P., Kenny T.W., Fearing R. & Full R.J. (2000). Adhesive force of a single gecko foot-hair. *Nature*, 405, 681–684.

Autumn K. & Peattie A.M. (2002). Mechanisms of adhesion in geckos. *Integr. Comp. Biol.*, 42, 1081–1090.

Bauer A.M. (1990). Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn. Zool. Monogr.*, 30, 1–220.

Bauer A.M. & Russell A.P. (1991). Pedal specializations in dune-dwelling geckos. *J. Arid Environ.*, 20, 43–62.

Bauer A.M., Russell A.P. & Powell G.L. (1996). The evolution of locomotor morphology in *Rhoptropus* (Squamata: Gekkonidae): functional and phylogenetic considerations. *Afr. J. Zool.*, 45, 8–30.

Bellairs A. (1969). *The Life of Reptiles*. Weidenfeld and Nicolson, London.

Bergmann P.J. & Irschick D.J. (2010). Alternate pathways of body shape evolution translate into common patterns of locomotor evolution in two clades of lizards. *Evolution*, 64, 1569–1582.

Biewener A.A. (2003). *Animal Locomotion*. Oxford University Press, Oxford.

Birn-Jeffery A.V., Miller C.E., Naish D., Rayfield E.J. & Hone D.W.E. (2012). Pedal claw curvature in birds, lizards and mesozoic dinosaurs – complicated categories and compensating for mass-specific and phylogenetic control. *PLoS ONE*, 7, e50555.

Bradshaw S.D. (1986). E*cophysiology of Desert Reptiles*. Academic Press, Orlando.

Carothers J.H. (1986). An experimental confirmation of morphological adaptation: toe fringes in the sand-dwelling lizard *Uma scoparia*. *Evolution*, 40, 871–874.

Cartmill M. (1985). Climbing. In: *Functional Vertebrate Morphology* (eds. Hildebrand M, Bramble DM, Liem KF & Wake DB). Belknap Press Cambridge, 73–88.

Collins C.E., Russell A.P. & Higham, T.E. (in press). Subdigital adhesive pad morphology varies in relation to structural habitat use in the Namib Day Gecko, *Rhoptropus afer*. *Funct. Ecol.*

Dixon J.R. & Huey R.B. (1970). Systematics of the lizards of the gekkonid genus *Phyllodactylus* of mainland South America. *Los Ang. County Mus. Contrib. Sci.*, 1–78.

Dolgoff A. (1996). *Physical Geology*. D.C. Heath and Company, Lexington.

El Din S.B. (2006). *A Guide to the Reptiles and Amphibians of Egypt*. The American University in Cairo Press, Cairo.

Espinoza N.C., Rothenstein D., Salas A. & Werner Y.L. (1990). Radiation and convergence among desert geckos: *Phyllodactylus* species resembling both *Ptyodactylus* and *Stenodactylus*. *Amphib.-Reptilia*, 11, 1–13.

Etheridge R. (2000). A review of lizards of the *Liolaemus wiegmannii* group (Squamata, Iguania, Tropiduridae), and a history of morphological change in the sand-dwelling species. *Herpetol. Monogr.*, 14, 293–352.

Foster K.L. & Higham T.E. (2012). How fore- and hindlimb function changes with incline and perch diameter in the green anole (*Anolis carolinensis*). *J. Exp. Biol.*, 215, 2288–2300.

Gamble T., Greenbaum E., Jackman T.R., Russell A.P. & Bauer A.M. (2012). Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, 7, e39429.

Gans C. (1967). The chameleon. *Nat. Hist.*, 76, 52–59.

Gasc J.-P. (1963). Adaptation a la marche arboricole chez le cameleon. *Arch. Anat. Hist. Embryol. Normal. Exp.*, 46, 81–115.

Goodman B.A., Miles D.B. & Schwarzkopf L. (2008). Life on the rocks: habitat use drives morphological and performance evolution in lizards. *Ecology*, 89, 3462–3471.

Grismer L.L. (2002). *Amphibians and Reptiles of Baja California*. University of California Press, Los Angeles.

Haacke W.D. (1976). The burrowing geckos of Southern Africa, 5 (Reptilia: Gekkonidae). *Ann. Transvaal Mus.*, 30, 71–89.

Hedrick T.L., Usherwood J.R. & Biewener A.A. (2004). Wing inertia and whole-body acceleration: an analysis of instantaneous aerodynamic force production in cockatiels (*Nymphicus hollandicus*) flying across a range of speeds. *J. Exp. Biol.*, 207, 1689–1702.

Herrel A., Meyers J.J. & Vanhooydonck B. (2001). Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biol. J. Linn. Soc.*, 74, 305–314.

Herrel A., Tolley K.A., Measey G.J., da Silva J.M., Potgieter D.F., Boller E., Boistel R. & Vanhooydonck B. (2013). Slow but tenacious: an analysis of running and gripping performance in chameleons. *J. Exp. Biol.*, 216, 1025–1030.

Higham T.E. & Anderson C.V. (2013). Function and adaptation. In: *The Biology of Chameleons* (eds. Tolley KA & Herrel A). University of California Press Berkeley.

Higham T.E. & Irschick D.J. (2013). Springs, steroids, and slingshots: the roles of enhancers and constraints in animal movement. *J. Comp. Physiol. B*, 183, 583–595.

Higham T.E. & Jayne B.C. (2004). Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist. *J. Exp. Biol.*, 207, 233–248.

Higham T.E. & Russell A.P. (2010). Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko. *Biol. J. Linn. Soc.*, 101, 860–869.

Hsieh S.T. (2003). Three-dimensional hindlimb kinematics of water running in the plumed basilisk lizard (*Basiliscus plumifrons*). *J. Exp. Biol.*, 206, 4363–4377.

Huey R.B. (1979). Parapatry and niche complimentarity of Peruvian desert geckos (*Phyllodactylus*): the ambiguous role of competition. *Oecologia*, 38, 249–259.

Irschick D.J., Austin C.C., Petren K., Fisher R.N., Losos J.B. & Ellers O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.*, 59, 21–35.

Irschick D.J. & Jayne B.C. (1999a). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. Exp. Biol.*, 202, 1047–1065.

Irschick D.J. & Jayne B.C. (1999b). A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. *Physiol. Biochem. Zool.*, 72, 44–56.

Jaeger E.C. (1955). *The California Deserts*, 3rd edn. Stanford University Press, Stanford.

Jayne B.C. & Ellis R.V. (1998). How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia*. *Anim. Behav.*, 55, 1115–1130.

Jayne B.C. & Irschick D.J. (2000). A field study of incline use and preferred speeds for the locomotion of lizards. *Ecology*, 81, 2969–2983.

Johnson M.K. & Russell A.P. (2009). Configuration of the setal fields of *Rhoptropus* (Gekkota: Gekkonidae): functional, evolutionary, ecological and phylogenetic implications of observed pattern. *J. Anat.*, 214, 937–955.

Johnson M.K., Russell A.P. & Bauer A.M. (2005). Locomotor morphometry of the *Pachydactylus* radiation of lizards (Geckkota: Geckkonidae): a phylogenetically and ecologically informed analysis. *Can. J. Zool.*, 83, 1511–1524.

Jones L.L.C. & Lovich R.E. (2009). *Lizards of the American Southwest: a Photographic Field Guide*. Rio Nuevo Publishers, Tuscon.

King M. & Rofe R. (1976). Karyotypic variation in the Australian gecko *Phyllodactylus marmoratus* (Gray) (Gekkonidae: Reptilia). *Chromosoma (Berl.)*, 54, 75–87.

Kluge A.G. (1967). Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Aust. J. Zool.*, 15, 1007–1080.

Korff W.L. & McHenry M.J. (2011). Environmental differences in substrate mechanics do not affect sprinting performance in sand lizards (*Uma scoparia* and *Callisaurus draconoides*). *J. Exp. Biol.*, 214, 122–130.

Lamb T. & Bauer A.M. (2006). Footprints in the sand: independent reduction of subdigital lamellae in the Namib-Kalahari burrowing geckos. *Proc. R. Soc. B*, 273, 855–864.

Li C., Hsieh S.T. & Goldman D.I. (2012). Multi-functional foot use during running in the zebra-tailed lizard (*Callisaurus draconoides*). *J. Exp. Biol.*, 215, 3293–3308.

Logan M.L., Montgomery C.E., Boback S.M., Reed R.N. & Campbell J.A. (2012). Divergence in morphology, but not habitat use, despite low genetic differentiation among insular populations of the lizard *Anolis lemurinus* in Honduras. *J. Trop. Ecol.*, 28, 215–222.

Losos J.B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution*, 44, 1189–1203.

Losos J.B. (2011). Convergence, adaptation, and constraint. *Evolution*, 65, 1827–1840.

Losos J.B., Walton B.M. & Bennett A.F. (1993). Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Func. Ecol.*, 7, 281–286.

Loveridge A. (1947). Revision of the African lizards of the family Gekkonidae. *Bull. Mus. Comp. Zool.*, 98, 1–469.

Luke C. (1986). Convergent evolution of lizard toe fringes. *Biol. J. Linn. Soc.*, 27, 1–16.

Mahendra B.C. (1941). Contributions to the bionomics, anatomy, reproduction and development of the Indian house-gecko, *Hemidactylus flaviviridis* Ruppel. Part II. The problem of locomotion. *Proc. Indian Acad. Sci. B*, 13, 288–306.

Melville J. & Swain R. (2000). Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae: Lygosominae). *Biol. J. Linn. Soc.*, 70, 667–683.

Peterson J.A. (1973). *Adaptation for arboreal locomotion in the shoulder region of lizards*. PhD dissertation, University of Chicago, Chicago, Illinois, USA, 1–370.

Peterson J.A. (1984). The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J. Zool.*, 202, 1–42.

Pianka E.R. (1986). *Ecology and Natural History of Desert Lizards*. Princeton University Press, Princeton.

Pianka E.R. & Vitt L.J. (2003). *Lizards: Windows to the Evolution of Diversity*. University of California Press, Berkeley.

Russell A.P. (1975). A contribution to the functional analysis of the foot of the Tokay, *Gekko gecko* (Reptilia: Gekkonidae). *J. Zool.*, 176, 437–476.

Russell A.P. (1976). Some comments concerning interrelationships amongst gekkonine geckos. In: *Morphology and Biology of Reptiles* (eds. Bellairs A & Cox CB). Academic Press Inc. London, 217–244.

Russell A.P. (1979). Parallelism and integrated design in the foot structure of Gekkonine and Diplodactyline geckos. *Copeia*, 1979, 1–21.

Russell A.P. (1986). The morphological basis of weight-bearing in the scansors of the tokay (Reptilia: Sauria). *Can. J. Zool.*, 64, 948–955.

Russell A.P. (2002). Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integr. Comp. Biol.*, 42, 1154–1163.

Russell A.P. & Bauer A.M. (1988). Paraphalangeal elements of gekkonid lizards: a comparative survey. *J. Morphol.*, 197, 221–240.

Russell A.P. & Bauer A.M. (1989). The morphology of the digits of the golden gecko, *Calodactylodes aureus* and its implications for the occupation of rupiculous habitats. *Amphib.-Reptilia*, 10, 125–140.

Russell A.P. & Bauer A.M. (1990). Substrate excavation in the Namibian web-footed gecko, *Palmatogecko rangei* Andersson 1908, and its ecological significance. *Trop. Zool.*, 3, 197–207.

Russell A.P. & Bauer A.M. (2008). The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. In: *Biology of the Reptilia* (eds. Gans C, Gaunt AS & Adler K). Society for the Study of Amphibians and Reptiles, 1–466.

Russell A.P. & Higham T.E. (2009). A new angle on clinging in geckos: incline, not substrate, triggers the deployment of the adhesive system. *Proc. R. Soc. B*, 276, 3705–3709.

Russell A.P. & Johnson M.K. (2007). Real-world challenges to, and capabilities of, the gekkotan adhesive system: contrasting the rough and the smooth. *Can. J. Zool.*, 85, 1228–1238.

Schulte J.A.I., Losos J.B., Cruz F.B. & Nunez H. (2004). The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae*: Liolaemini). *J. Evol. Biol.*, 17, 408–420.

Solano G.H. (1964). Adaptive radiation in the family Gekkonidae. *Pub. Oc. Mus. Cienc. Nat., Caracas Zool.*, 8, 12 pp (unpaginated).

Tulli M.J., Cruz F.B., Herrel A., Vanhooydonck B. & Abdala V. (2009). The interplay between claw morphology and microhabitat use in neotropical iguanian lizards. *Zoology*, 112, 379–392.

Vanhooydonck B. & Van Damme R. (1999). Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evol. Ecol. Res.*, 1, 785–805.

Wainwright P.C., Bellwood D.R. & Westneat M.W. (2002). Ecomorphology of locomotion in labrid fishes. *Environ. Biol. Fish*, 65, 47–62.

Werner Y.L. (1977). Ecological comments on some gekkonid lizards of the Namib Desert, South West Africa. *Madoqua*, 10, 157–169.

Zani P.A. (2000). The comparative evolution of lizard claw and toe morphology and clinging performance. *J. Evol. Biol.*, 13, 316–325.

Cranial anatomy of the pygopodid lizard *Aprasia repens*, a gekkotan masquerading as a scolecophidian

Juan D. Daza[1,2] *and Aaron M. Bauer*[1]

[1] Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA; E-mail: aaron.bauer@villanova.edu

[2] Current address: Department of Biological Sciences, Sam Houston State University, 1900 Avenue I, Huntsville, Texas 77341, USA; E-mail: juand.daza@gmail.com

Abstract

Aprasia repens is a miniaturised, burrowing, limbless gekkotan belonging to the family Pygopodidae. We used high-resolution X-ray computed tomography to investigate the osteology of this species and describe all ossified elements of the skull using terminology standardised for gekkotan lizards. *Aprasia repens* is characterised by a short mandible comprising only three discrete elements and bearing only two teeth on each ramus; the upper jaw is edentulous (in females). The basicranium is completely fused. The bones of the snout are strongly imbricating. The middle ear is much reduced; no stapes is evident and the fenestra ovalis is confluent with the lateral aperture of the recessus scalae tympani. However, inner-ear morphology suggests normal auditory function. The quadrate is columnar, abuts the paroccipital process, and might play a role in the transmission of ground-borne vibrations to the inner ear. The eyes are smaller than in other gekkotans, but larger than in most fossorial squamates and the number of scleral ossicles is reduced. Overall, the skull of *A. repens* is highly reminiscent of that of scolecophidians, reflecting similarities with respect to the reduced size, fossoriality and myrmecophagy of these animals.

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Introduction

The flap-footed lizards of the family Pygopodidae unquestionably exhibit the most extraordinary morphological modifications of any gekkotans. Limb reduction with element loss occurs in no other gekkotan group, but in addition to this most obvious characteristic, specific taxa of pygopodids exhibit other suites of highly derived morphological features (Greer 1989). The genus *Lialis*, for example, is known for its highly specialised trophic morphology that is associated with its saurophagous habits (Patchell & Shine 1986a, 1986b). *Lialis* species, like those of several other pygopodid genera, are surface-active and their attenuate, nearly limbless body form has been associated with "grass-swimming" or climbing in low vegetation (Greer 1989; Pianka & Vitt 2003; Pianka 2011). However, two pygopodid genera—*Ophidiocephalus* and *Aprasia*—are characterised by a more subterranean existence (Parker 1956; Kluge 1974) and, even if sometimes surface-active (Ehmann 1976), they do not climb in vegetation (Greer 1989). Although the elongate body form of pygopodids is compatible with either burrowing or climbing (Camp 1923), cranial structure can be expected to exhibit marked differences between lizards exhibiting these two lifestyles because fossorial squamates typically display a suite of specialisations attributable to both mechanical and sensory adaptation (Brandley *et al.* 2008). *Ophidiocephalus* and *Aprasia* are further modified in association with their miniaturisation that, with respect to the skull, is rivalled among gekkotans by only the smallest species of sphaerodactylid geckos (Rieppel 1984b; Daza *et al.* 2008; Gamble *et al.* 2011). This combination of miniaturisation and fossorial specialisation results in a distinctive morphology that departs extensively from the standard gekkotan *Bauplan*.

The modified burrowing genus *Aprasia* is represented by 13 described species of worm-like lizards (Kluge 1974, 2001; Jennings *et al.* 2003; Uetz *et al.* 2013). *Aprasia* was once interpreted as a link between lizards and snakes (Bocage 1873; Boulenger 1887) and understandably so in light of its superficial similarity to snakes, especially scolecophidians (Camp 1923). Some of the structural similarities shared with scolecophidians—many of which are correlated with head-first burrowing (Lee 1998) and others perhaps with myrmecophagy (Kluge 1976; Hutchinson 1997)—are small size, body elongation (although the proportional lengths of the trunk and tail differ from those typical of both snakes and most other reduced-limbed lizards; Wiens *et al.* 2006; Brandley *et al.* 2008), limb reduction, cranial consolidation, modified head shape (undershot lower jaws—alternatively interpreted as a projecting snout and described as "shark-shaped" by McCoy [1888]), cheeks covered by large scales, rigid jaws, near-edentulousness, and the lack of a tympanum (in most species; *Aprasia aurita* has an external auditory meatus; Kluge 1974). Pygopodids also resemble snakes and amphisbaenians with respect to complex structures associated with the eye, such as the drainage system (i.e., lacrimal canal; Bellairs & Underwood 1950), although, despite some notable reduction in ocular size compared with other members of the Pygopodidae (Parker 1956; Underwood 1957), *Aprasia* still possess large eyes (Gray 1838), one of the distinguishing characters of geckos (Fig. 1).

The cranial anatomy of *Aprasia* has been studied by several authors in different contexts. The earliest description of an *Aprasia* skull was based on a juvenile specimen studied by Jensen (1901; Smith 2007), who considered it to represent *Ophiopsiseps nasutus* (Bocage 1873), now regarded as a synonym of the Western Australian *Aprasia pulchella* Gray 1839 (Parker 1956; Kluge 1974, 2001; see also Camp 1923). However, the specimen from Hochkirch (today the village Tarrington), Victoria has since been reinterpreted as referable to *Aprasia striolata* (Parker 1956). Jensen (1901) recognised that his specimen was unambiguously a lizard, but considered it distinctive enough that he erected the monotypic family Ophiopsisepidae for it. (In assigning the species to *Ophiopsiseps*, Jensen followed Boulenger [1887], who recognised *Ophiseps* Bocage 1873 as a junior homonym of *Ophiseps* Blyth 1853 = *Dopasia* Gray 1853 [Anguidae] and provided the replacement name *Ophiopsiseps*.) Jensen speculated that this family had affinities with skinks, but later workers interpreted Ophiopsisepidae as a synonym of Pygopodidae (e. g., Werner 1912; Fry 1914; Zietz 1921; Kinghorn 1923, 1926). McDowell and Bogert (1954) likewise recognised the gekkotan affinities of Jensen's family, but resurrected it (as Ophiosepidae [sic]) to include *Ophioseps* and *Aprasia*. Parker (1956) and Underwood (1957), however, considered all pygopodids as referable to Pygopodidae and stabilised the current concept of the family, although recently Wells (2007) has proposed the recognition of Aprasiaidae to include species usually allocated to *Aprasia* and *Ophidiocephalus* (Gray [1845] had earlier recognised a monotypic Aprasiadae that included only *A. pulchella*).

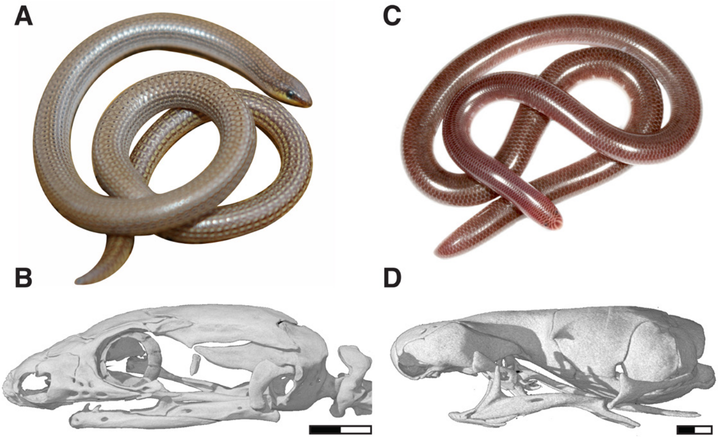

Figure 1:
Convergent body plans and skulls of the worm lizard *Aprasia repens* (A, B; Pygopodidae) and the blind snake *Typhlops jamaicensis* (C, D; Typhlopidae). Images courtesy of Ian Brennan (A), S. Blair Hedges (C), and the Deep Scaly Project via Maureen Kearney (D). Scale bar equals 1 mm. Maximum total lengths of these species are 210 mm for *A. repens* and 445 mm for *T. jamaicensis*.

The confusion about the distinctiveness (or not) of *Ophioseps* / *Ophiopsiseps* from *Aprasia* stems from differences between Jensen's (1901) skull and those of other *Aprasia* due to to the immaturity of the former (Jensen 1901; Parker 1956), mechanical damage during skeletonisation (Evans 2008), and errors of illustration. Some of the characters inconsistent with the anatomy of *Aprasia* are paired frontals, fused parietals, the lack of a postorbitofrontal and jugal, and an unfused parabasisphenoid-basioccipital joint.

Subsequently, the cranial osteology of *Aprasia* has been considered by McDowell and Bogert (1954), who both reprinted Jensen's (1901) skull illustration and provided an accurate representation of the articulated skull of *Aprasia repens*, and by Stephenson (1962), who figured the skull of *A. pulchella*. Rieppel (1984b) reinvestigated and newly figured the skull of *A. repens* in his review of miniaturisation, Hutchinson (1997) figured and described mandibular morphology of *A. striolata*, and, most recently, this same species was included as part of a complete bone-by-bone monographic revision of the lizard skull (Evans 2008). In addition, detailed illustrations of histological sections of the head of *A. repens* were provided by Underwood

(1957), osteological characters for several species have been incorporated in phylogenetic analyses (Kluge 1976; Conrad 2008), and postcranial osteology has been discussed and illustrated by several authors (Stokely 1947; Parker 1956; Stephenson 1962; Greer 1989).

These previous investigations of *Aprasia* species characterise their overall morphology, but the degree of miniaturisation seen in these lizards limits detailed description of the anatomy using traditional methods. Of the illustrations available, that of *A. repens* published by McDowell and Bogert (1954), and based upon drawings by Alma Frodestrom, is one of the most accurate, but still displays some striking inconsistencies when compared with others. For example, whereas McDowell and Bogert (1954) suggest the presence of a small fenestra ovalis and toothless maxillae, Rieppel's (1984b) illustration suggests that the fenestra ovalis is not visible and that the maxilla is tooth-bearing (but see Greer 1989). Previously, this genus had been characterised as having an edentulous maxilla, with teeth present only on the dentary (all species) or also on the premaxilla of adult males (and persistent in juveniles of at least *A. striolata*) (Kinghorn 1926; Parker 1956; Stephenson 1962; Evans 2008).

To overcome limitations on the study of this miniaturised lizard and to reconcile inconsistencies in previous descriptions, we used the non-invasive technique of high-resolution X-ray computed tomography (HXRCT) to study the cranial anatomy of *A. repens*. This method is superior to alternative approaches in which bones are disarticulated chemically or mechanically (e. g., Oelrich 1956; Montero & Gans 1999; Conrad 2004; Daza *et al.* 2008; Jones *et al.* 2009; Olori & Bell 2012). Digital segmentation of the bony components of the skull enables us to revisit this species and to perform a thorough description of its cranial anatomy, with emphasis on modifications in the context of fossoriality and myrmecophagy.

Materials and methods

The head of an adult female specimen (SVL = 112.0 mm) of *A. repens* (California Academy of Sciences [CAS] 104382 from Mundaring Weir, Western Australia) was scanned with an Xradia MicroCT scanner (Pleasanton, CA, USA) at the High Resolution X-Ray CT facility at the Department of Geological Sciences of the University of Texas at Austin using a 4x detector objective and an X-ray source set at 80 kV and 10 W. The specimen was scanned in two halves anteroposteriorly (total 1633 slices) and digitally matched. The voxel (volumetric pixel) value is 3.67 microns.

Three-dimensional rendering and all measurements (lengths and angles) were done with Avizo® 6.3.1 (VSG, Visualization Sciences Group; Burlington, Massachusetts, USA). All unpaired bones of the skull and right elements in the case of paired bones were digitally segmented and an endocast of the inner ear was prepared using the above program. To facilitate visualisation, individual elements were colour coded using a 21 banded-rainbow scheme (21-Color Salute; Tol 2012) developed with the RColorBrewer computer package for R (R Core Team 2013). Digital movies with three-dimensional cutaways of the specimen were also produced using VGSTUDIO MAX 1.2 (Volume Graphics; Heidelberg, Germany) along the specimen's true orthogonal axes (animations available at http://www.digimorph.org).

Identifications of anatomical structures were based on the miniaturised gecko *Sphaerodactylus roosevelti* as a general reference gekkotan because the cranial osteology of this species has been described in great detail (Daza *et al.* 2008). Interpretations of identity were informed by broad-scale comparisons with a diversity of gekkotan skeletal specimens (both dry and cleared and stained preparations; see Daza & Bauer 2010, 2012) and HXRCT scans of gekkotans (see Appendix) and other squamates (see www.digimorph.org). Anatomically homologous designations follow the terminology in Daza *et al.* (2008, 2012) and Gamble *et al.* (2011). Additional terms follow Evans (2008), Olori & Bell (2012), and Gauthier *et al.* (2012).

Results

Joints

We followed the proposal of Jones *et al.* (2011) in distinguishing facets (articulating surfaces of bones), seams (boundaries between the bones in articulation), and interfaces (the articulations as they appear in cross section). The construction of the skull is very solid, especially in the basicranium, where there is complete fusion. The dermal bones of the snout are angular in shape and their facets are wide, with a high degree of overlap. The snout is a self-supporting vaulted structure analogous to a Roman arch in which all loads are transferred to the basal abutments—for this lizard, the palatal components of he skull (Fig. 2). The interface of the snout bones also exhibits some facets that have developed additional anchor surfaces for receiving adjacent bones, resulting in a variety of planar joints. For example, there is a lap joint between the nasal and prefrontal, a recessed scarf joint between the maxilla and the nasal, and an asymmetrical horizontal slot joint with a tab and pocket between the maxilla and the premaxilla (Fig. 2). The seams are well-spaced (Fig. 3), as in pygopodids in general, which might establish structural shock absorbers or allow micro-movements to dissipate forces acting between bones on the skull (Pritchard *et al.* 1956), especially during burrowing.

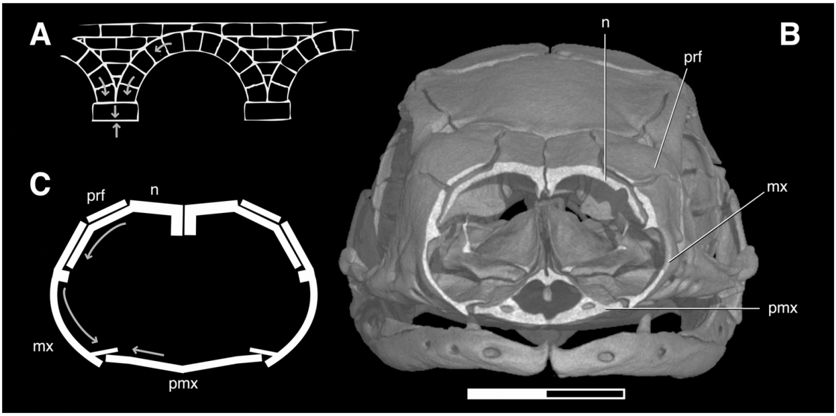

Figure 2:
A) Sketch of a Roman arch showing the distribution of the compressive forces towards the abutments. B) Transverse section of the skull of *Aprasia repens* (CAS 104382) showing the relationship between the nasal (n), prefrontal (prf), maxilla (mx), and premaxilla (pmx). C) Diagram of the joints among the same snout elements at the same transverse section. Scale bar equals 1 mm.

Overall morphology of the skull

The shape of the skull approximates an ellipsoid, with the two poles along the longest axis being the tip of the snout and the posterior-most point of the creating an almost continuous opening (not interrupted by a bony wall) from side to side. The orbit is proportionally large and incomplete posteriorly as in all gekkotans (Estes *et al.* 1988; Daza & Bauer 2010; Daza *et al.* 2013) and its posterior margin, as defined by the sclerotic ring, is approximately at the midpoint of the total skull length. The frontal bone is excluded entirely from

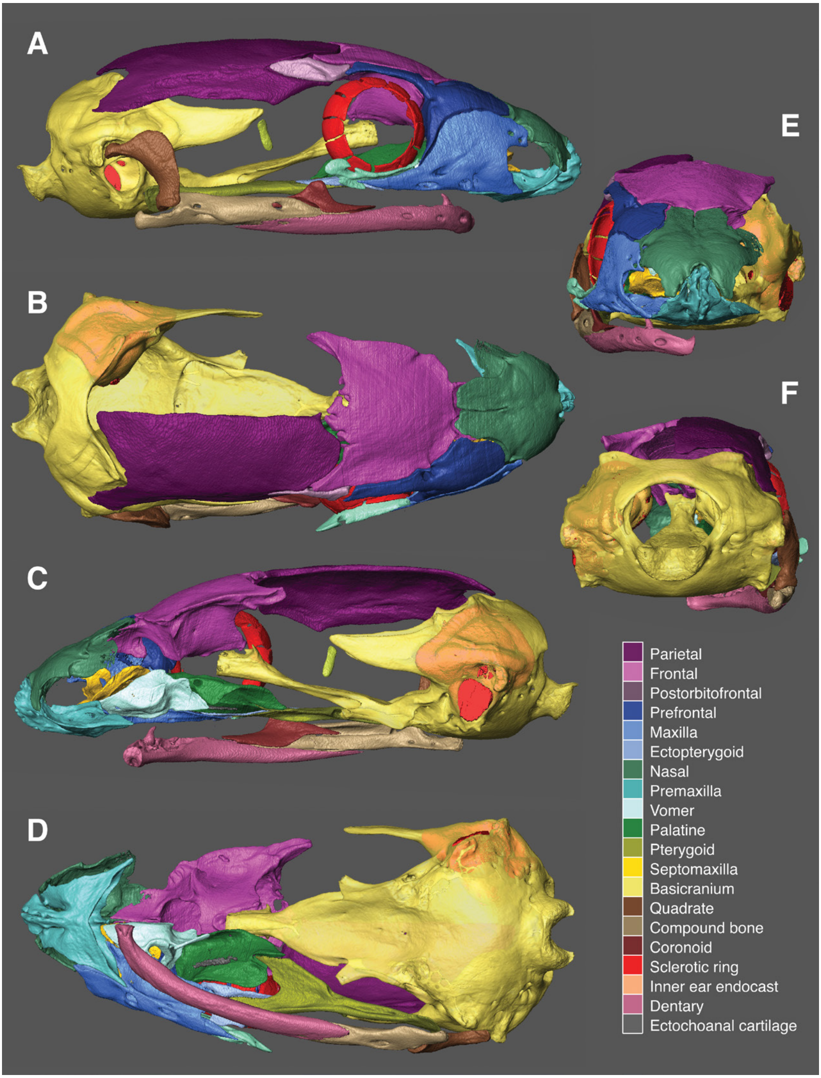

Figure 3:
HRXCT of *Aprasia repens* (CAS 104382). Paired bones from the left side have been removed from the skull. A) lateral, B) dorsal, C) medial, D) ventral, E) anterior, and F) posterior views. Colour scale also works as a scale bar and equals 4 mm. The braincase was rendered partly transparent to expose the osseous labyrinth.

the orbital rim as in all pygopodids (Boulenger 1884; Boulenger 1885; Kinghorn 1926; Daza & Bauer 2010), a rare gekkotan character state that is also variably present in the gekkonid genus *Phelsuma* (Evans 2008; pers. obs.).

The premaxilla-vomer fenestra is V-shaped and is covered ventrally by a slender incisive process of the premaxilla. The fenestra is extended laterally by two short, narrow slits that are partially filled by the maxillary lappets. The palate of *Aprasia* exhibits a modification of the incomplete neo-choanate condition of the palate, in which the vomer develops an extensive lap joint with the medial shelf of the maxilla anterior to the fenestra vomeronasalis. Posterior to this fenestra, the vomer develops a short septum that overlaps but does not contact the maxilla and maintains the separation of the latter from the fenestra exochoanalis. The fenestra vomeronasalis is roofed dorsally by the septomaxilla.

The maximum width of the skull is at the level of the posterior edge of the jugal bones; the maximum width of the basicranium is slightly smaller. The temporal fenestrae are confluent as in nearly all gekkotans (*Chondrodactylus bibronii* develops a secondary supratemporal bar adjacent to the lateral margin of the parietal with no supratemporal fenestra; Rieppel 1984c) and this space is continuous with the posterior part of the orbit (Kluge 1962; Rieppel 1984c; Herrel *et al.* 2000). The bones that surround the brain are hypertrophied, with the parietal and the basicranium forming a nearly continuous dorsolateral wall; the epipterygoid is notably reduced and does not contact the pterygoid or the basicranium. This indicates either that its epiphyses are cartilaginous or that it is supported by another cartilaginous element. The epipterygoid might also be associated with the internal pseudotemporalis superficialis muscles as in the pygopod *Lialis burtonis* (Daza *et al.* 2011). The braincase extends anteriorly along the palate, where the rostrum of the parabasisphenoid fills most of the interpterygoid vacuity.

The skull of the specimen studied is highly asymmetrical in having the right maxilla and prefrontal fused as well as unequal numbers of foramina in the maxillary, dentary, and prefrontal pairs. Asymmetry is also reflected in the irregular margin of the posteromedial process of the frontal bone.

The bones of the braincase form a completely fused structure and there is no indication of seams among the major bones. There is a large rounded fenestra on the lateral aspect of the braincase, which we interpret as the combined space of the lateral aperture of the recessus scalae tympani (LARST) and the fenestra ovalis (see below for the description of this structure and additional interpretations of the stapes). Similarly, there is extensive fusion in the postdentary bones of the jaw, where only the coronoid remains discrete.

The lower jaw is much shorter than the skull, a reduction in size that can be attributed to the diminution of the dentary. Several foramina of the jaw are lost (e. g., the anterior inferior alveolar and the anterior mylohyoid foramina). Alternative courses for these foramina are described below.

Morphology of the cranial elements

Premaxilla

The premaxilla (Fig. 4A–E) is unpaired but shows some evidence of incomplete fusion (Stephenson 1962); one specimen of *A. striolata* has been reported with paired premaxillae (Evans 2008). This bone is irregular and thick, appearing somewhat inflated. It is completely edentulous in this specimen as is typical of adult female *Aprasia*. The ascending nasal process is paired and has a serrated anteroventral margin. The unfused portion of the ascending nasal process tapers dorsally and only the left part of the element forms a peg (premaxilla) and socket (nasal) joint with the nasal bones. Lateral to the ascending nasal process, the premaxilla has two additional facets for receiving the nasal bones. The premaxilla contributes extensively to the palate, having two triangular posterolateral palatal processes and forming a deep cavity that opens posteriorly. These two processes meet posteroventrally, forming a single, slender incisive process. This process is analogous to that in anguimorphs, but differs in its orientation (horizontal rather than anterodorsal; Rieppel 1980a). The same lamina develops two facets that abut the medial shelf of the maxilla. Inside the palatal cavity, there is a central foramen, presumably the incisive foramen, and two additional foramina that are the posterior openings of a complex system of osseous canals that also have openings anteriorly and dorsolaterally. The anterior foramina of this system are within two oval recesses that are lateral to the ascending nasal process. The left foramen has an additional lateral foramen, thereby presenting another case of asymmetry. The channels from these foramina follow a short course and branch out into two main subdivisions, one of which opens posteriorly towards the cavity of the palate and the other laterally towards the naris. Intermixed with the canals are a number of imperforate indentations of indeterminate function.

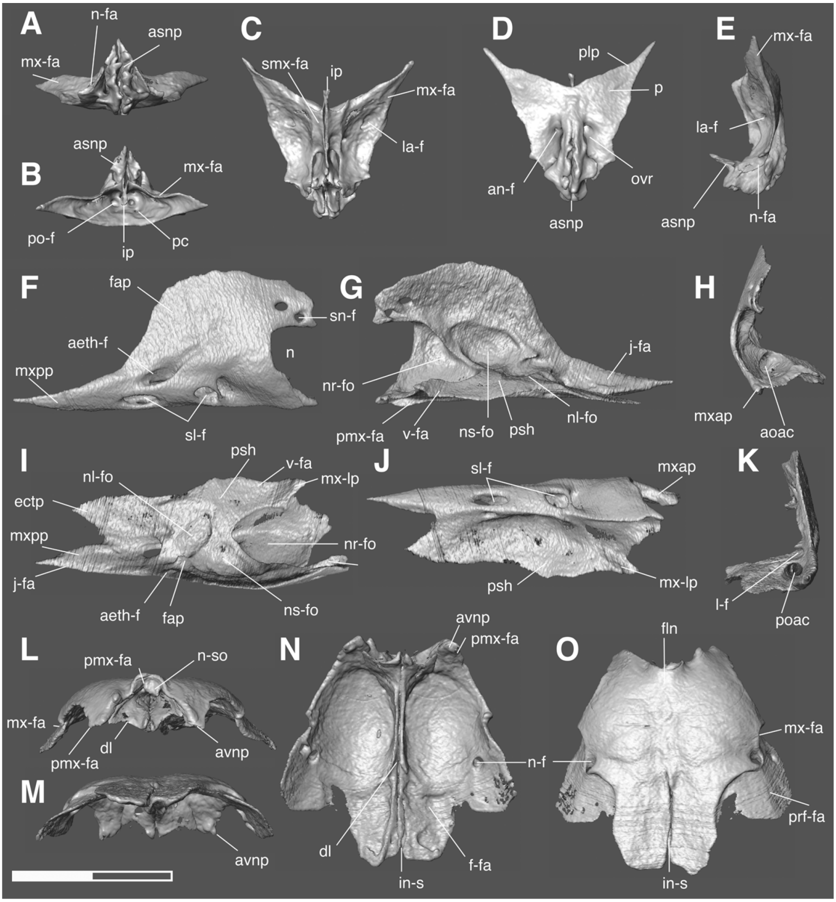

Figure 4:
Premaxilla (A–E), maxilla (F–K), and nasal (L–O) bones of *Aprasia repens* (CAS 104382). Views: anterior—A, H, and L; posterior—B, K, and M; dorsal—C, I, and O; ventral—D, J, and N; lateral—E and F; and medial—G. Abbreviations: aeth-f, anterior ethmoidal nerve foramen; an-f, anterior foramen; aoac, anterior opening of alveolar canal; asnp, ascending nasal process; avnp, anteroventral narial process; dl, descending lamina; ectp, ectopterygoid process; fap, facial process; fln, fused lamina of nasal; in-s, internasal seam; ip, incisive process; j-fa, jugal facet; la-f, lateral foramen; l-f, lacrimal foramen; mx-fa, maxilla facet; mx-lp, maxillary lappet; mxap, maxilla anterior process; mxpp, maxilla posterior process; n, naris; n-f, nasal foramen; n-fa, nasal facet; n-so, nasal socket; na-fo, nasal fossa; nl-fo, naso-lacrimal fossa; nr-fo, narial fossa; ovr, oval recess; p, palate; pc, palatal cavity; plp, posterolateral process; pmx-fa, premaxilla facet; po-f, posterior foramen; poac, posterior opening of alveolar canal; prf-fa, prefrontal facet; psh, palatal shelf; sl-f, supralabial foramen; smx-fa, septomaxilla-facet; sn-f, supranarial foramen; and v-fa, vomer facet. Scale bar equals 1 mm.

Maxilla

The maxilla (Fig. 4F–K) is a curved bone, almost L-shaped in anterior view; it has a narrow anterolateral process with a facet for the nasal bone. It is completely edentulous. The facial process has an anterior emargination that forms the posterior edge of the naris. The dorsal margin of the facial process is slightly sinuous and nearly horizontal; the posterior edge slopes down steeply and meets the acute posterior process of the maxilla. The posterior process of the maxilla develops a mainly medial lap joint with the jugal. The medial side of the facial process exhibits three major fossae: a triangular narial fossa at the base of the naris, a central nasal fossa that is part of the nasal cavity, and a nasolacrimal fossa that is less shallow than the other two and is located adjacent to the medial maxillary shelf. These depressed areas are separated by narrow ridges. The maxilla has a broad palatal shelf; the anterior and posterior edges end in narrow projections, a maxillary lappet anteriorly and an ectopterygoid process posteriorly. The maxilla is pierced by a variable number of proportionally large foramina that are asymmetrically distributed. For example, there are two large foramina piercing the facial process above the naris on the right side, whereas there are none on the left. The bone above the edentulous area of the palatal shelf is hollow, traversed by a large, longitudinal alveolar canal that opens anteriorly at the narial fossa. This canal is connected to several supralabial foramina that open on the lateral side of the maxilla and correspond to the alveolar foramina. Above the posterior-most supralabial foramen there is a large oval foramen, possibly for the anterior ethmoid nerve, that also opens into the nasal cavity. There is also a foramen opening on the lateral edge of the palatal shelf. The alveolar canal opens posteriorly into a single large foramen ventral to the lacrimal foramen.

Nasal

The fused nasals (Fig. 4L–O) are vaulted anteriorly; the anterior width of the combined element is subequal to the width of the nasofrontal seam. The vaulted form of this bone produces an anteroventral narial process that extends considerably anteriorly, exceeding the anterior reach of the maxilla and contacting the premaxilla. This bone roofs the naris anterodorsally; thus, this opening is only visible ventrolaterally. The nasal is incompletely fused (Stephenson 1962), forming a continuous bony lamina only anterodorsally (Underwood 1957). It remains unpaired ventrally along the whole internasal suture. The medial part of each nasal develops a descending lamina of bone that is formed by a paired ventral projection along the internasal joint. At the anterior portion of this projection, the two sides diverge and expand laterally, forming, together with the anterodorsally fused lamina, a socket for reception of the ascending nasal process. This dorsal contact of the nasals over the ascending nasal process of the premaxilla is even more extensive than that described for other fossorial lizards such as *Dibamus novaeguineae* (Rieppel 1984a; Conrad 2008; Gauthier *et al.* 2012). The nasal flattens posteriorly where the two sides remain separated, but, from this point, both medial sides continue the descending lamina into two low keels, forming the medial nasal flange and the facet for the nasofrontal joint; the nasofrontal seam is nearly transverse. The nasal overlaps the frontal and is itself overlapped narrowly by the maxilla and extensively by the prefrontal, presenting a depressed facet for these bones, which results in a well-defined sinuous seam. The nasal is pierced asymmetrically by two foramina on the right side and one on the left. These foramina are continuous with the corresponding foramina in the maxilla and are located either at the seam or at the facet for the prefrontal.

Prefrontal

The prefrontal (Fig. 5A–F) is a goblet-shaped bone in which the cup-shaped portion corresponds to the nasal cavity and the stalk is a narrow and slightly curved posterior process that forms almost the entire anterodorsal edge of the orbital rim. The posterior process almost contacts the postorbitofrontal and a small gap remains between the prefrontal and postorbitofrontal, forming an almost continuous bridge that excludes the frontal from the orbital rim. The prefrontal bone has a lateral facet for the facial process of the maxilla. It also develops lap joints with the frontal bone in two areas; a great part of its dorsal edge is recessed into the ventrolateral surface of this latter bone. The orbitonasal flange curves anteromedially, forming the medial wall of the nasal cavity and contacting the anterior flange of the crista cranii, almost flanking the lateral edge of the tract for the olfactory nerve (cranial nerve I). The prefrontal is pierced by one (left) or two (right) foramina at the point of origin of the posterior process. The orbitonasal flange is very broad and does not contact its counterpart medially; its medial margin slopes ventromedially. The ventral edge is concave and develops two small lateral projections, which form the dorsolateral edge of the lacrimal foramen. These projections do not contact the jugal.

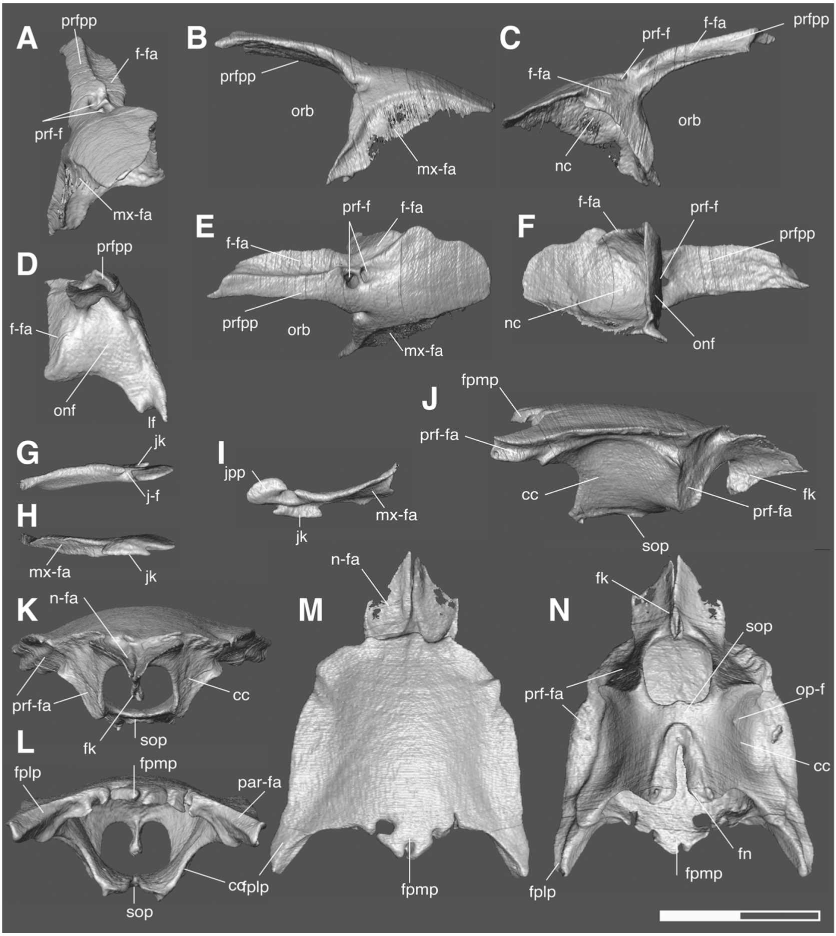

Figure 5:
Prefrontal (A–F), jugal (G–I), and frontal (K–N) bones of *Aprasia repens* (CAS 104382). Views: anterior—A and K; posterior—D and L; dorsal—E, G, and M; ventral—F, H, and N; lateral—B, I, and J; and medial—C. Abbreviations: c, crista cranii; f-fa, frontal facet; fk, frontal keel; fn, frontal notch; fplp, frontal posterolateral process; fpmp, frontal posteromedial process; j-f, jugal foramen (notch); jk, jugal ventral keel; jpp, jugal posterior process; lf, lacrimal foramen; mx-fa, maxilla facet; n-fa, nasal facet; nc, nasal cavity; onf, orbitonasal flange; op-f, optic foramen; or, orbit; par-fa, parietal facet; prf-f, prefrontal foramen; prf-fa, prefrontal facet; prfpp, prefrontal posterior process; and sop, subolfactory processes. Scale bar equals 1 mm.

Jugal

The jugal (Fig. 5G–I), which is typically just a slender splint of bone in most gekkotans, is unusually complex in shape. In both *Aprasia* and *Pletholax*, this bone is relatively large and its anterior margin approaches the prefrontal and the lacrimal foramen (Rieppel 1984c). In *A. repens*, this bone forms the entire ventral edge of the orbital rim. It is thin at the suborbital part and expands posteriorly into a club-like structure. It also bears a ventrally directed keel. It is pierced by a large foramen (right) or notch (left) that opens ventrolaterally. In pygopodids, the jugal extends further posteriorly than in limbed gekkotans, sometimes being almost entirely posterior to the maxilla (e. g., *Delma borea*) and just parallel to the ectopterygoid. Considering the relationship of this bone to the maxilla, the jugal of *A. repens* occupies a position more consistent with that of limbed gekkotans.

Frontal

The frontal (Fig. 5J–N) is a fused bone (Boulenger 1885; contra Jensen 1901; Kinghorn 1926) both dorsally and ventrally. In dorsal view, the frontal is shield-like and its surface is bowed outward. It has an anterior facet to receive the nasals and bears a ventral keel just anterior to the olfactory tract; this is the only part the bone showing some indication of the ontogenetic fusion of the two precursor bones. The frontal is excluded from the orbit in pygopodids, is almost dorsal to the eye, and does not have a medial constriction. Although extremely modified in *Aprasia*, this bone still exhibits the overall tubular shape of all the members of the crown clade Gekkota (except some *Pristurus*), having crista cranii that meet ventrally to form the subolfactory process. Contrary to reports that the subolfactory processes do not contact ventrally in *Aprasia* (Underwood 1957; Stephenson 1962; Bellairs & Kamal 1981; Rieppel 1984c), we found contact almost halfway along the subolfactory process in *A. repens*. On the left side, the optic foramen pierces the crista cranii, but no foramen is evident on the right side. Posteriorly, the bone develops an elongated notch that participates in a joint with the braincase. Underwood (1957) described *A. repens* and *A. pulchella* as lacking ventral fusion of the frontals and stated that the olfactory-tract floor was formed by dense connective tissue. Such dense connective tissue might floor the notch, but might also be part of a fibrous joint of the frontal with the rostrum of the parabasisphenoid portion of the basicranium (see below). The connection between the frontal and the basicranium in other lizards, including most gekkotans, is established indirectly via the septal cartilage and a series of membranous tissues between a slender cartilaginous trabecular structure and the crista cranii (Oelrich 1956). However, a similar solid articulation between the frontal and the braincase is developed in amphisbaenians and snakes (Montero & Gans 1999; Cundall & Irish 2008; Montero & Gans 2008). The posterior end of this bone develops three processes, two lateral and one medial, giving the frontoparietal suture a W-shape when viewed dorsally along the long axis of the skull. The lateral processes are wedge-shaped tabs that fit into a deep shelf formed by the parietal and the postorbitofrontal. The medial process is triangular with its border interrupted by a series of notches.

Postorbitofrontal

The postorbitofrontal (Fig. 6A–D) is a small and slender bone. It can be divided in two parts: an expanded anterior portion that is mainly in contact with the frontal and a mediolaterally flattened posterior portion that contacts the parietal. Hence, it is located at the frontoparietal suture. The lateral margins of the two parts intersect one other, forming a 130° angle. On the medial surface, it has a depressed facet to receive the frontal bone. On the lateral side, just posterior to the vertex, it has a depression that contains a small foramen.

Sclerotic ring

There are 11 scleral ossicles in the specimen (Fig. 6E–F). The periphery of the eye is covered by mostly discrete ossicles, all of approximately the same size and rectangular in shape. There is some slight overlap of ossicles towards the aperture. Following the method of Gugg (1939; with the modifications of Underwood 1970) for counting and numbering, ossicles 2, 4, and 10 are negative (overlapped at both sides), 3 is positive (overlapping the two adjacent ossicles), and the remaining ossicles are overlapped on one side but not the other. Ossicle pairs 5 and 6 as well as 8 and 9 are fused. The aperture diameter is approximately 70% the external sclerotic-ring diameter.

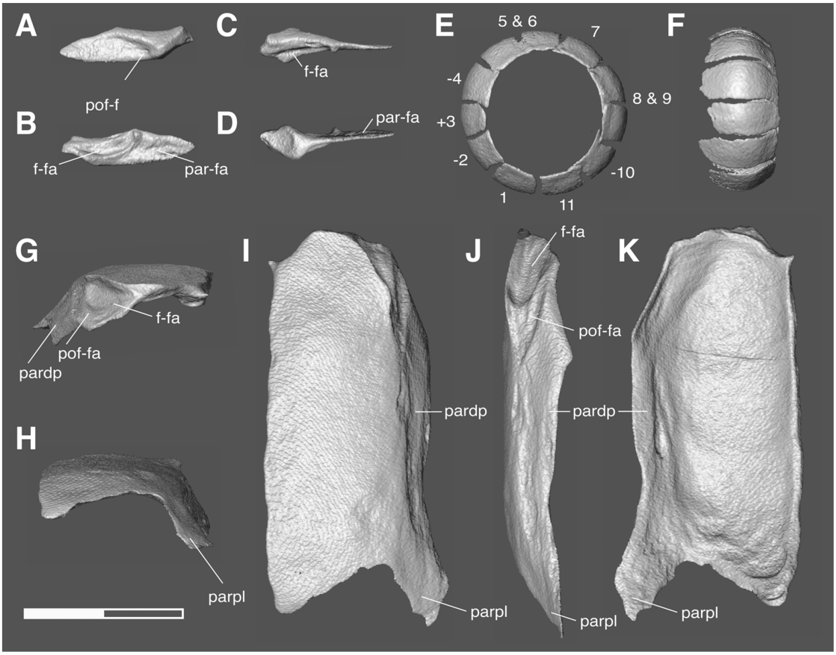

Figure 6:
Postorbitofrontal (A–D), sclerotic ring (E–F), and parietal (G–K) bones of *Aprasia repens* (CAS 104382). Views: anterior—F and G; posterior—H; dorsal—C and I; ventral—D and K; and lateral—A, E, and J. Abbreviations: f-fa, frontal facet; par-fa, parietal facet; pardp, descending process of parietal; parplp, parietal posterolateral process; pof-f, postorbitofrontal foramen; and pof-fa, postorbitofrontal facet. Scale bar equals 1 mm.

Parietal

The parietal (Fig. 6G–K) is a nearly rectangular paired bone that remains separate or distinct from its counterpart (Boulenger 1885) in contrast to the fused parietals of "*Ophiopsiseps nasutus*" as illustrated by Jensen (1901). This difference in character state was used as support for the distinctiveness of this latter genus from *Aprasia* (Kinghorn 1923, 1926). The dorsal surface of the parietal is almost flat. It is wedge-shaped anteriorly and deeply emarginated posteriorly. On the anterolateral surface, it has a depressed triangular facet for the frontoparietal joint (medially) and the postorbitofrontal joint (laterally). Posterior to this facet, the parietal has a lateral wall, probably derived from the much reduced descending process of the parietal in other gekkotans, which is continuous with the lateral edge of the skull in this genus and in *Pletholax* (Stephenson 1962), thereby limiting the jaw musculature from extending onto the dorsal surface of the parietal from the side of the skull (Rieppel 1984b). This wall closes the braincase laterally and provides surface area for the insertion of the jaw muscles (A2-SUPj, A2-SUP-M, and A2-M; *sensu* Daza *et al.* 2011). The posterolateral process is triangular, flattened, and wide, forming a joint with the posterodorsal surface of the basicranium, mainly in the exooccipital portion. The posteromedial part of the parietal does not contact the basicranium although both are at the same level, thereby leaving a narrow slit between the two.

Vomer

The vomers (Fig. 7A–E) are paired concave bones. In the HRXCT images, each vomer appears to contact only its counterpart, the maxilla, and the palatine, but some interface via connective tissue with the premaxilla and the septomaxilla must also exist. The vomer is expanded laterally and completely encapsulates the vomeronasal organ posteriorly. Together with the septomaxillae and the maxillae, the vomers entirely enclose the vomeronasal organ and the mushroom body (which is separated completely from the nasal cavity). In contrast to the condition found in other squamates, the vomer develops extensive contact with the palatal shelf of the maxilla anterior to the fenestra vomeronasalis. The fenestra vomeronasalis is partially separated from the fenestra exochoanalis by a slightly curved septum. On the anterolateral side, it develops a ventrolaterally oriented facet for the maxilla. At its posterodorsal corner posterior to the vomeronasal area, the vomer has an angled facet that is overlapped by the palatine and that slopes down posteroventrally. The septum of the vomer is high and separates the olfactory chambers. The palatal surface of each vomer is pierced anteriorly by a foramen.

Septomaxilla

The septomaxilla (Fig. 7F–J) forms the dorsolateral roof of the vomeronasal organ and the mushroom-body region. The septomaxilla has a well-developed lateral flange and no medial flange; the lateral flange is parallel to the main part of the septomaxilla. The anterior end of the septomaxilla develops a slender medial process that contacts the premaxilla. The two sides of Jacobson's organ are separated by the concavity of the vomer and not by ventral projections of the septomaxilla as in other squamates (Gauthier *et al.* 2012). The posterolateral edge of the septomaxilla (posterior to the lateral flange) approaches, but does not contact, the ridge that separates the narial depression from the nasal depression of the maxilla.

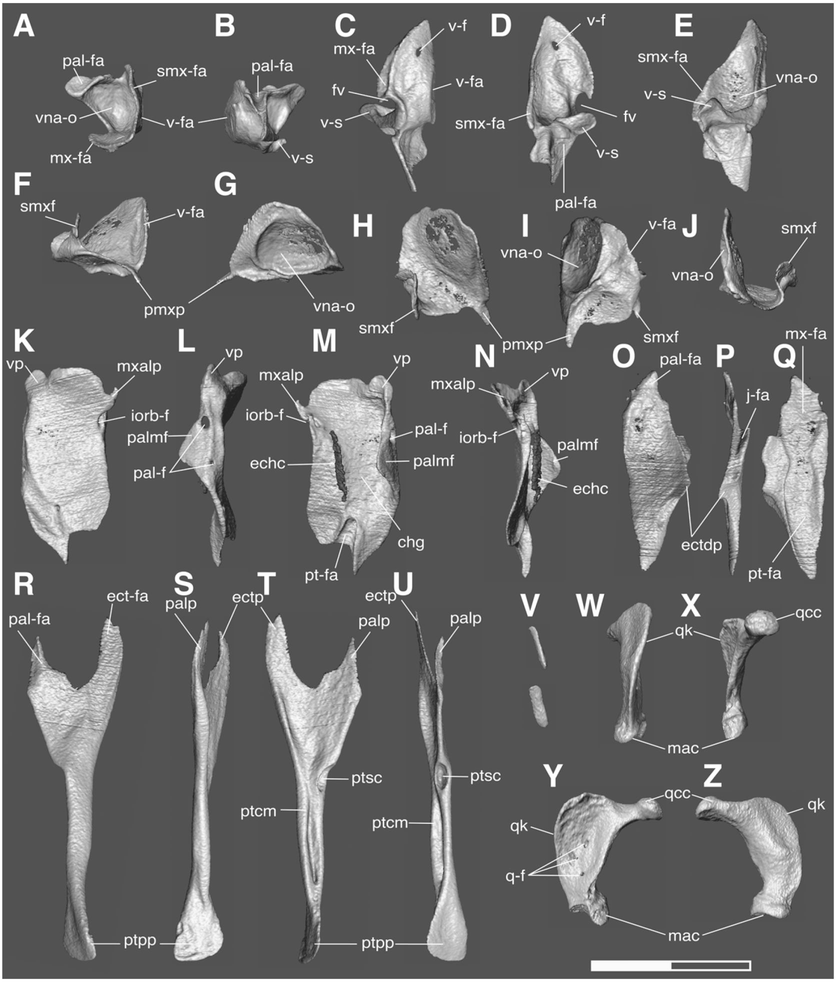

Figure 7:
Vomer (A–E), septomaxilla (F–J), palatine and ectochoanal cartilage (K–N), ectopterygoid (O–Q), pterygoid (R–U), epipterygoid (V), and quadrate (W–Z) bones of *Aprasia repens* (CAS 104382). Views: anterior—A, F, and V (above), and W; anterolateral—J; posterior—B and X; dorsal—D, H, K, O, and R; ventral—C, I, M, Q and T; lateral—E, G, P, S, V *(continued overleaf)*

(continued from overleaf) (below), and Z; and medial—N, U, and Y. Abbreviations: chg, choanal groove; echc, ectochoanal cartilage; ectdp, ectopterygoid dorsal process; ectp, ectopterygoid process; fv, fenestra vomeronasalis; iorb-f, infraorbital foramen; j-fa, jugal facet; mac, mandibular *(continued overleaf)* condyles; mx-fa, maxilla facet; mxalp, maxilla anterolateral processes; pal-f, palatine foramina; pal-fa, palatine facet; palmf, palatine medial flange; palp, palatine process; pmxp, premaxilla process; pt-fa, pterygoid facet; ptcm, pterygoid creased margin; ptpp, pterygoid posterior process; ptsc, pterygoid synovial cavity; q-f, quadrate foramina; qcc, quadrate cephalic condyle; qk, quadrate keel; smxf, septomaxilla lateral flange; v-f, vomer foramen; v-fa, vomer facet; v-s, vomer septum; vna-o, space for the vomeronasal organ; and vp, vomerine process. Scale bar equals 1 mm.

Palatine

The palatine (Fig. 7K–N) is a bowed bone and remains separated from its counterpart. Anterolaterally, it has two short, narrow processes. These might represent the maxillary processes, but, although they overlap the palatal shelf of the maxilla, they do not establish sutural contact because the ectopterygoid intervenes. At the base of these two processes there is a large, distinct infraorbital foramen that opens medially into the choanal groove. The ectopterygoid lies adjacent to the palatine, narrowly separated from it anteriorly by the suborbital fenestra. This fenestra is expanded at the point where the pterygoid and the ectopterygoid meet, giving it a ladle-shaped outline. The vomerine process is very broad. Ventrally, it is keel-like and is received by a Y-shaped facet in the vomer. The broad anteromedial terminus overlaps a great portion of the posterior edge of the vomer, possibly reducing the mobility of this joint. This broad joint with the vomer is also present in *Pletholax* and has been suggested to strengthen the snout complex in association with burrowing (Rieppel 1984c). The ventral surface of the palatine has a deep choanal groove (duplicipalatinate condition). On the lateral edge of the choanal groove, a rod-like ectochoanal element is present and, together with the posterior process of the vomer, delimits a nearly tubular choana, but without the development of a bony secondary palate. The choanal groove is flanked medially by a ventral triangular projection. Sphaerodactyl geckos also exhibit a strongly duplicipalatinate condition (Gamble *et al.* 2011), but develop a ventral process (curved medially) on the medial side of the choanal groove, whereas the ventral projection is more prominent on the lateral margin in *Aprasia.* Lateral to the choanal groove, the palatine has a ventral facet for the articulation of the palatine ramus of the pterygoid. On the anterior wall of this facet, there is a foramen that opens dorsolaterally. Two additional foramina are on the medial flank of the choanal groove.

Ectopterygoid

The ectopterygoid (Fig. 7O–Q) is nearly flat and its overall shape approximates a parallelogram, although its lateral side slopes medially. It has a tall dorsal process and its ventral surface has a depressed longitudinal facet for the palatal shelf of the maxilla and the ectopterygoid ramus of the pterygoid. Laterally, its dorsal surface has a facet for the jugal bone and its lateral edge contacts the posterior process of the maxilla ventrally. It has narrow contact with the palatine anteromedially.

Pterygoid

The pterygoid (Fig. 7R–U) is a Y-shaped bone and its horizontal surface is inclined mediolaterally. This bone contacts the cranium at three points: the ventral surface of the palatine (palatine process), the ventral surface of the ectopterygoid (ectopterygoid process), and the braincase by means of a synovial articulation with the basipterygoid process of the parabasisphenoid. The ectopterygoid process is longer than the palatine process and, although it tapers abruptly into a small point, more or less uniform in width. The joint with the ectopterygoid is also more extensive than that with the palatine, which is typical in gekkotans (Daza *et al.* 2008). The palatine process tapers more gradually and ends in a small point. The dorsal surface is mostly flat, but this bone develops a well-defined laterally creased margin ventrally that marks the attachment of m. protractor pterygoidei. On the medial side, at the mid-length of the bone, the pterygoid has a very deep, oval cavity that might be part of the synovial cavity of the joint with the basipterygoid process. There is no fossa columellae in the dorsal surface of the bone, indicating a lack of contact with the epipterygoid. The posterior process is flattened mediolaterally and has no osseous connection with the quadrate.

Epipterygoid

The epipterygoid (Fig 7V) is a very simple, mediolaterally flattened splint of bone and has no bony joints with either the prootic portion of the basicranium or the pterygoid. It is closer to the crista alaris, to which it might be joined by cartilage.

Quadrate

The quadrate (Fig. 7W–Z) is highly modified, being compressed mediolaterally (Stephenson 1962). It develops a strong keel anteriorly for the attachment of the m. adductor mandibulae externus complex. Because there is no tympanum in this taxon, both the tympanic crest and quadrate conch are lost. The mandibular condyles are well-developed and subequal, the medial condyle being only slightly larger than the lateral one. One of the most distinct characters of the quadrate is the elongated dorsomedial part, where a short stem separates the main body from the knob-like cephalic condyle. The suspension of the quadrate is also modified, being mainly streptostylic and developing a complete paroccipital abutment that is applied against the anterior margin of the paroccipital process. The cephalic condyle fills a well-defined socket in the lateral side of the braincase that is anterior to the paroccipital process and just ventral to the bulge of the horizontal semicircular canal. The quadrate is traversed internally by a channel extending from the cephalic condyle into each mandibular condyle. This descending channel opens anteromedially through three quadrate foramina.

Braincase (spheno-otooccipital complex):

The basicranium (Fig. 8A–F) is consolidated into a single bony structure with no traces of joints among the constituent bones (McDowell & Bogert 1954; Underwood 1957; Stephenson 1962). We use the osseous labyrinth to indicate the margins of some of the bones that contain this structure (Olori & Bell 2012). For orientation purposes, we refer to the assumed bone that contains the structure mentioned (e. g., the prootic portion), but without establishing any decisive boundaries for adjacent elements unless this is indicated by a foramen or fused seam.

The parabasisphenoid part is long; the cristae trabecularis define two lateral buttresses that converge, forming the rostrum (previously referred to as the septosphenoid rostrum), which anteriorly is tubular with a large marrow cavity (Underwood 1957). The anterior part of the rostrum extends anteriorly to the level of the frontal bone. This part of the rostrum has the form of a square with rounded corners in cross section. The anterior terminus of this long process forms an interface with the posterior part of the crista cranii and there is no evidence on the HRXCT scans of any cultriform process. The crista cranii remain separated posteriorly, forming an elongated notch that

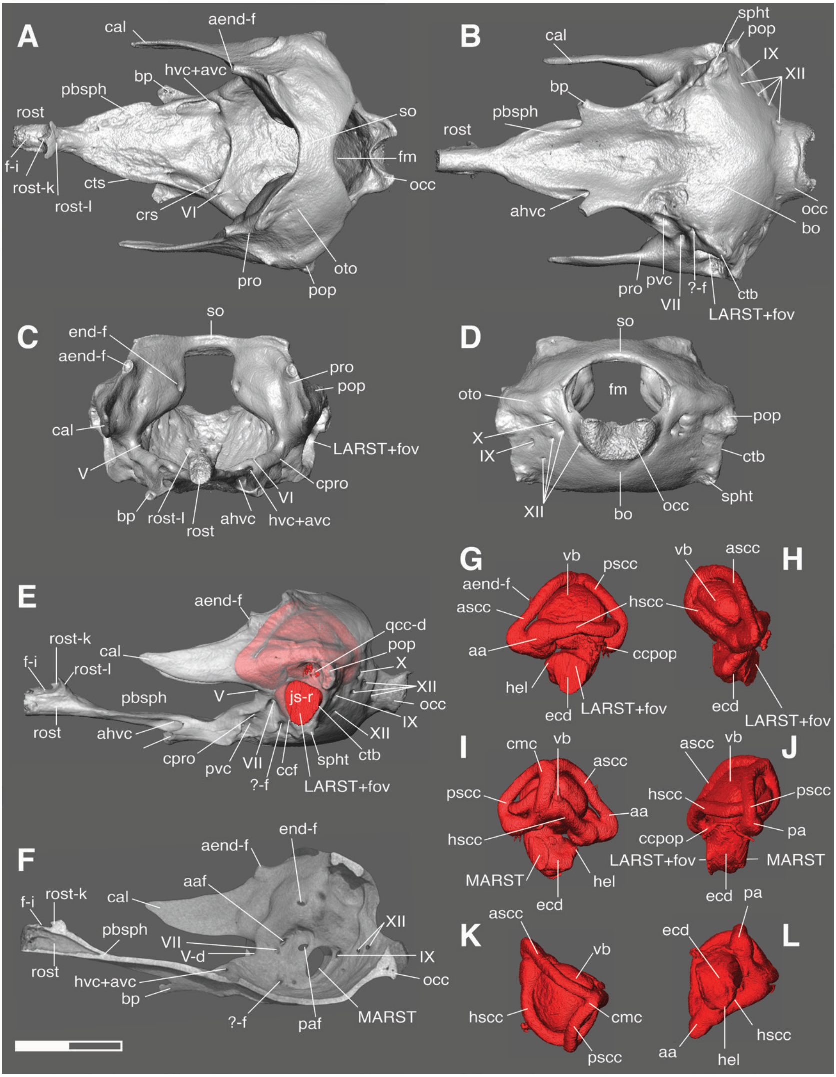

Figure 8:
Basicranium (A–F) and endocast of the osseous labyrinth (G–L) of *Aprasia repens* (CAS 104382). Views: anterior—C and H; posterior—D and J; dorsal—A and K; ventral—B and L; lateral—E and G; and medial—F and I. Abbreviations: V, incisura prootica; VI, course for the abducens nerve; VII, foramen for the facial nerve; VIII, foramina for the vestibular nerve; *(continued overleaf)*

(continued from overleaf) IX, foramen for the glossopharyngeal nerve; X, foramen for the vagus nerve; XII, foramina for the branches of the hypoglossal nerve; aa, anterior ampulla; aaf, anterior auditory foramen; aend-f, accessory endolymphatic foramen; ahvc, anterior opening of the lateral head head vein; ascc, anterior semicircular canal; avc, anterior opening of vidian canal; bo, basioccipital; bp, basipterygoid process; cal, crista alaris; ccf, crista circumfenestralis; cmc, common crus; cpro, crista prootica; crs, crista sella; ctb, crista tuberalis; cts, crista trabecularis; ecd, endosseous cochlear duct; end-f, endolymphatic foramen; f-i, frontal interface; fov, fenestra ovalis; ha, horizontal ampulla; hel, helicotrema; hscc, horizontal semicircular canal; js-r, juxtastapedial recess; LARST, lateral aperture of the recessus scalae tympani; occ, occipital condyle; oto, otooccipital; pa, posterior ampulla; paf, posterior auditory foramen; pbsph, parabasisphenoid; pop, paroccipital process; popcc, cochlear channels of the paroccipital process; pscc, posterior semicircular canal; pvc, posterior opening of the vidian canal; qcc-d, cephalic condyle depression; rost, rostrum; rost-k, rostrum keel; rost-l, rostrum lamina; rvj, recesus vena jugularis; so, supraoccipital; spht, sphenooccipital tubercle; V-d, trigeminal depression; and ?-f, unidentified foramen. Scale bar equals 1 mm.

interfaces with the dorsal surface of the rostrum. The latter has a low transverse keel near its anterior end. The space between the frontal and the rostrum is filled by dense connective tissue (see also Fig. 2, which is based on a histological section through the head of *A. repens*, in Underwood 1957). There is a transverse lamina posterior to the rostral keel and, posterior to this structure, the rostrum becomes flattened dorsally (with a concave ventral surface) and flares out towards the basipterygoid processes. The latter are very short (Stephenson 1962) with rounded, concave tips. Dorsomedial to these processes, the large, oval foramen for the lateral-head vein opens anterolaterally. The passages for the vidian nerve and the lateral-head vein are confluent through the braincase and exit as the posterior opening of the vidian canal as described for *A. pulchella* (Underwood 1957). In *Lialis* and *Delma*, there are two separate passages for these structures, but *Pletholax* has a condition similar to that in *Aprasia*. The posterior openings of the vidian canal are bilaterally symmetrical in size. The crista sella is very low and there is a shallow depression in front of this crest in which the hypophysis is seated. Just dorsal to the anterior opening of the vidian canal, there is a notch (left) or foramen (right) for the abducens nerve (cranial nerve VI).

The transition from the parabasisphenoid into the basioccipital is marked by a change in the ventral surface; posterior to the opening of the vidian canal, the ventral concavity of the former element becomes convex. There is a single discrete depression on each side and the ventral surface is roughened just lateral to the point where the surface changes from concave to convex and just ventral to the posterior opening of the vidian canal. The posterior surface of the bicipital occipital condyle is convex.

The most conspicuous structure of the prootic portion of the basicranium is the crista alaris, which is elongated and knife-like, with a more or less straight dorsal margin and a convex ventral margin. Dorsal to the base of the crista alaris, an accessory endolymphatic duct joining the anterior semicircular canal pierces a short process with a spongy interior. In *L. burtonis*, this structure continues into endolymphatic sacs that fill the postocular area of the skull medial to the temporal fenestrae (pers. obs.). Ventral to the crista alaris, there is a deep notch or incisura prootica, but there is no trigeminal foramen; therefore the trigeminal nerve (cranial nerve V) does not pass through the braincase but flanks it medially as indicated by a shallow trigeminal depression. There is a very reduced crista prootica; in other pygopodids, this structure can be similarly reduced or absent. The recessus vena jugularis extends ventrolaterally from the posterior opening of the vidian canal and ends in a foramen for the facial nerve (cranial nerve VII). Ventral to this foramen, there is an unidentified foramen. In some other gekkotans (e. g., the phyllodactylid *Garthia gaudichaudi*, pers. obs.), there is a similarly located foramen at the joint between the prootic and otooccipital bones.

The crista prootica extends posteriorly into the otooccipital area and, together with the crista tuberalis, forms the crista circumfenestralis, which delimits the boundaries of the juxtastapedial recess. The crista tuberalis is obliquely oriented between the stub-like paroccipital process and the sphenoccipital tubercle. The paroccipital process is perforated by a series of channels that extend from the cochlear recess or endosseous cochlear duct (ECD; Witmer *et al.* 2008) of the inner ear to the horizontal semicircular canal. The juxtastapedial recess contains a large opening, representing the LARST + fenestra ovalis. Inside the LARST, a small portion of the medial wall of the braincase is visible that includes the posterior auditory foramen and a medial aperture of the recessus scalae tympani (MARST). There is a deep auditory recess in the medial wall of the braincase, which, in addition to the posterior auditory foramen (connecting the brain to the ECD), bears a single anterior auditory foramen (dorsal to the facial foramen and connecting the brain to the anterior ampulla) and two dorsal foramina that serve for the passage of the vestibular nerve (cranial nerve VIII). Dorsal to the auditory recess, there is a large endolymphatic foramen. The MARST is subdivided, but not as in *Eublepharis macularius*, in which the glossopharyngeal foramen (cranial nerve IX) opens posteriorly inside the juxtastapedial recess and posterior to the crista interfenestralis (Gauthier *et al.* 2012), but rather outside the juxtastapedial recess and posterior to the crista tuberalis. In most lizards, the vagus foramen of cranial nerve X is posterior to the crista tuberalis (Rieppel 1985; Rieppel & Kearney 2002), but it appears that these foramina have shifted even further back in *Aprasia*; the foramen for cranial nerve IX is located posterior to the crista tuberalis adjacent to the bulge of the cochlear recess and ventral to the posterior ampulla bulge, whereas that of cranial nerve X takes a more dorsal position behind the paroccipital process adjacent to the posterior ampullary bulge. This is consistent with the typical crescent shape of this foramen (Jollie 1960; Bever *et al.* 2005). Ventral to cranial nerves IX and X, four hypoglossal foramina (transmitting branches of cranial nerve XII) arranged in an arc pierce the braincase. The last of these is on the base of the neck of the occipital condyle and is confluent with the penultimate, whereas the first and the second are separate. The foramen magnum is large and oval.

One characteristic feature of the juxtastapedial recess in *A. repens* is the presence of a single opening. Underwood (1957) stated that the opening in the juxtastapedial recess in *A. pulchella* corresponds to the fenestra ovalis and that this opening is covered by a membrane that has a tiny nodule of bone embedded in it—presumably a vestige of the footplate of the stapes. Alternatively, Rieppel (1984c) described the single opening of the juxtastapedial recess in *A. repens* as containing both the LARST and fenestra ovalis. This opening has been described as occluded by a calcareous nodule or heterotopic ossification in *A. striolata* or closed by a membrane in *A. repens* (Rieppel 1984c). Greer (1989) also reported a nodule in this position in *A. repens*, which he interpreted as a remnant of the footplate with a ligamentous attachment to the posterior side of the quadrate. Although we could not find any indication in the HRXCT data of a stapes, we agree with the interpretation of the combined space of the fenestra ovalis and the LARST in *A. repens*, with the loss of the crista interfenestralis. This interpretation is also consistent with the morphology of the inner ear (see below). Dorsal to this large opening, there is a socket that is mainly occupied by the cephalic condyle of the quadrate. From the scans, it can be seen that the quadrate does not contact the lateral wall of the braincase (see above).

The endocast (Fig. 8G–L) of the osseous labyrinth is similar to that of other miniaturised fossorial burrowing squamates in which the semicircular canals are situated very close to the vestibule, thereby giving the inner ear a compact appearance (Weber & Gans 1973; Comeaux *et al.* 2010; Olori 2010) and contrasting with larger, arboreal, terrestrial, and semiaquatic lizards (e. g., *Ctenosaura*, *Iguana*, *Gambelia*, or *Shinisaurus*; Oelrich 1956; Bever *et al.* 2005;

Spaw *et al.* 2013; Walsh *et al.* 2013) in which the semicircular canals are more widely spaced. (The latter is especially the case in sampled iguanians, which are characterised by a curved and highly arched anterior semicircular canal.) The inner ear is generally divided into two main parts: the vestibule, which corresponds to the superior part where the semicircular canals converge, and an inferior part, which corresponds to the cochlear recess or ECD (Hamilton 1960, 1964; Miller 1966; Baird 1970; Wever 1978) and which contains the hearing organ or basilar papilla (Miller 1966). In many squamates, including gekkotans, the vestibule includes a condensation of calcareous material (statolithic mass) that indicates the position of the membranous sacculus (Baird 1970), but there is no statolith in *A. repens*. The vestibule is connected to the brain by means of the endolymphatic foramen and the two foramina for the vestibular nerve (cranial nerve VIII). A constriction marks the separation between the vestibule and ECD. The ECD has an anterior swelling, the helicotrema (= perilymphatic sac of Wever 1978), that establishes a direct communication between the scala vestibuli and the recessus scalae tympani (Freeman 1990). In *A. repens,* a large portion of the ECD is occupied by the large LARST and MARST; however, some of the structures contained within it (e. g., the lagenar and limbic portions) are very similar to gekkotans with no reduced hearing capabilities (Wever 1973, 1978).

The supraoccipital portion of the basicranium is exposed dorsally. It lies almost at the same level as the parietal, but there is a small gap between them. In *A. repens,* the squamosal bone is absent (Kluge 1976; Rieppel 1984c), but, in other *Aprasia* species where this bone is present (e. g., *Aprasia parapulchella*, *Aprasia pseudopulchella*, *A. pulchella*, *A. striolata*; Stephenson 1962; Kluge 1976; Evans 2008), it has the club-like terminus typical of pygopodids and carphodactylids (Kluge 1976; Bauer 1990; Daza & Bauer 2012); in some species (e. g., *A. aurita*), it has been reported to be partially fused to the otooccipital portion of the braincase (i.e., fused to the exooccipital; Kluge 1976). The loss of the squamosal in *A. repens* produces a very simple postemporal bar formed by the posterolateral process of the parietal and the paroccipital process, and leaves a very reduced postemporal fenestra.

Mandible

The jaw (Fig. 3) of *A. repens* is very short and simple and is formed by only three discrete elements: the dentary, coronoid, and a compound bone. The splenial is absent; it is, therefore, possible that the inferior alveolar nerve innervates the jaw through a gap between the dentary and the coronoid instead of through an anterior inferior alveolar foramen. The typical symphyseal joint in geckos, as seen in cross section, tapers laterally away from the midline, giving the joint an inverted V-shape (Holliday *et al.* 2010) with no clear symphyseal facets (Evans 2008; Jones *et al.* 2012). In *A. repens*, the symphysis has the same shape, but the facets are well-defined and in strong contact, interrupted only ventrally by the anteroventral opening of the Meckelian canal.

Dentary

The dentary (Fig. 9A–D) is gently curved and is tubular for about one-third of its total length from the symphyseal facet to the posterior edge of the toothed portion of the bone. In lateral view, it is slighted bowed. The notched part of the bone forms a gutter, which, in contrast to the condition in the majority of gekkotans, is open mainly dorsally, overlapping the postdentary bones ventrally. The anterior part of the notch is roofed only by the coronoid. The coronoid does not insert into the dentary, but these two bones form a closed tube (for the Meckelian cartilage) that also accommodates the insertion of the anterior process of the compound bone. The dentary ends posteriorly in a single blunt process and the entire bone extends along two-thirds of the total jaw length. The dentary is pierced by two or three mental foramina on the labial surface. The tooth row is very short; this species retains only two teeth in each ramus (Camp 1923) and has the lowest tooth count among gekkotans. The teeth are well-spaced (one crown diameter apart) and strongly recurved, with sharp, inward-twisted crowns. The teeth are pleurodont and the lateral walling is notably reduced, resulting in a considerable protrusion of the tooth above the bone margin. The replacement tooth buds develop lingually in a distinct, depressed shelf adjacent to the tooth row. These replacement teeth erupt horizontally and then rotate toward the base of the functional tooth. Mental foramina connect the tooth bases with the external wall of the dentary.

Coronoid

The coronoid (Fig. 9E–H) is a very simple bone. In lateral view, the outline of the coronoid eminence follows an almost symmetrical bell-shaped curve; it is high, duplicating the anterior jaw height at its maximum. The eminence is compressed and it has a lateral insertion point for the jaw muscle A2-M

(Daza *et al.* 2011). The anterolateral process of the coronoid extends only slightly onto the labial side of the jaw, contacting the dentary and overlaying the anterior process of the compound bone. The ventromedial outline is sigmoid, with the anterior process stouter than the posterior. The posterior process covers the dorsal rim of the mandibular fossa.

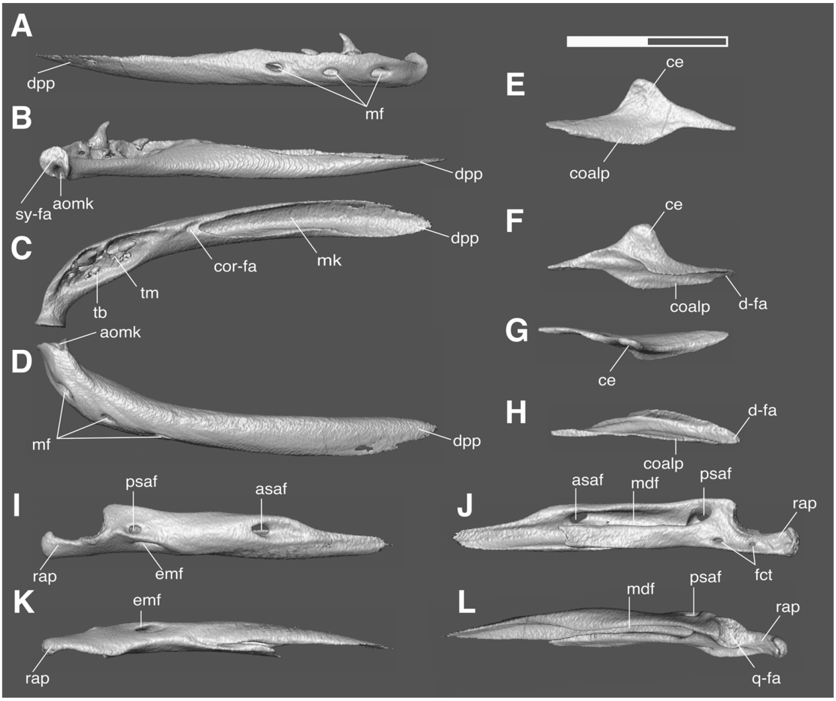

Figure 9:
Dentary (A–D), coronoid (E–H), and compound bone (I–L) of *Aprasia repens* (CAS 104382). Views: lateral—A, F, and I; medial—B, E, and J; dorsal—C, G, and L; and ventral—D, H, and K. Abbreviations: aomk, anteroventral opening of the Meckelian canal; asaf, anterior surangular foramen; ce, coronoid eminence; coalp, coronoid anterolateral process; cor-fa, coronoid facet; d-fa, dentary facet; dpp, dentary posterior process; emf, external mandibular fenestra; fct, foramina for chorda tympany; mdf, mandibular fossa; mf, mental foramina; mk, Meckelian canal; psaf, posterior surangular foramina; q-fa, quadrate facet; rap, retroarticular process; sa, surangular portion of compound bone; sy-fa, symphysis mandibular; tb, tooth bud; and tm, toothed margin. Scale bar equals 1 mm.

Compound bone

In pygopodids, this bone (Fig. 9I–L) is presumably formed by the fusion of the surangular, articular, and prearticular (Hutchinson, 1997). The angular is assumed to be lost in the majority of geckos (gekkotans), but it is known to be present in Eublepharidae (except in *Coleonyx*; McDowell and Bogert 1954; Kluge 1962; Grismer 1988) and in the sphaerodactylid genus *Teratoscincus* (Kluge 1987; see also Evans 2008). Rieppel (1984c) illustrated a small angular in the jaw of *Lialis jicaris* and *Pygopus lepidopodus*, although this bone is not mentioned by other authors (e. g., McDowell & Bogert 1954; Parker 1956; Stephenson 1962; Hutchinson 1997). The apparent variation in this bone among Gekkota, as well as discrepancies among different authors, necessitate its critical review, ideally incorporating developmental data. We cannot confirm the presence or absence of the angular in *A. repens* because the compound bone does not show any seams among its putative component bones. For this reason, we treat this compound bone in a manner similar to that used to describe the braincase above. The surangular portion is pierced by three foramina. The anteriormost is the anterior surangular foramen. The remaining two are located anterior to the articular portion of the compound bone, one below the other. The ventral one is almost three times the diameter of the dorsal one and, although both have been identified as posterior surangular foramina in *Delma fraseri* (Hutchinson 1997), we note that only the dorsal foramen is present in *Delma molleri* (AMNH R-24850) with only a seam marking the fusion of the compound surangular with the articular and prearticular in the position homologous to the ventral foramen. There are also two foramina in the posterior part of the surangular portion of the compound bone of *A. repens.* It is thus possible that the ventral foramen is in fact a small fenestra analogous to the one formed between the surangular and the compound bone of other gekkotans (i.e., the external mandibular fenestra; Daza *et al.* 2008). This identification is consistent with the presence of a buttress between the two foramina, which might be some indication of bone fusion. The external mandibular fenestra connects the mandibular fossa with the lateral side of the compound bone. The prearticular portion forms the medial wall of the mandibular fossa and does not contact the surangular portion anteriorly. The retroarticular process is cylindrical with no prearticular crest; it is oriented along the main axis of the jaw (i.e., not twisted posteriorly; Estes *et al.* 1988). The retroarticular process has a subtle waist and a medial concavity unlike in limbed gekkotans, where this process is strongly waisted and spoon-like (Evans 2008). There are two foramina ventral to the articular portion of the compound bone on the lingual side: one for the chorda tympani at the base of the retroarticular process and, anterior to this, a larger one that has not been reported previously in other pygopod genera and which could be for the passage of a branch of the chorda tympani nerve. These two foramina are confluent and connected to an extensive hollow space that extends into the articular and the prearticular portions of the compound bone.

Hyoid apparatus

The hyoid apparatus is incompletely ossified and, thus, not fully revealed by the HRXCT scans. The glossohyal, basihyal, and second ceratobranchial comprise a contiguous, weakly ossified structure. The glossohyal is short and positioned entirely below the braincase. The second epibranchials are slightly divergent from one another posteriorly, unlike the condition reported for *Delma*, *Pygopus* and *Lialis* (Underwood 1957). The first ceratobranchials are fully ossified, robust, and bowed in shape, with their posterior portions inflected dorsally. The remaining elements of the hyoid are not represented by hard tissue.

Discussion

Miniaturisation is a common evolutionary process that has yielded small-bodied forms in all major clades of squamate reptiles (Vitt & Caldwell 2014). It is particularly widespread among groups of fossorial squamates, being considered one of the distinctive features of head-first burrowers, including dibamids, scolecophidian snakes, amphisbaenians, scincids, and gymnophthalmids (Rieppel 1984b; Lee 1998). Among the approximately 1500 gekkotan species, there are several groups of miniaturised lizards (Daza *et al.* 2008; Gamble *et al.* 2011); the main changes in skull structure associated with miniaturisation are the reduction of skull diameter and a posterodorsal shift in the origin of the jaw musculature (Rieppel 1984b; Daza *et al.* 2011). Miniaturisation has also been regarded as a common process in head-first burrowing forms—and strongly associated with cranial modification. Members of the genus *Aprasia* are among both the most highly fossorial and the most miniaturised of all pygopodids (Greer 1989). As a consequence, the cranial anatomy of *Aprasia* is the most highly modified among pygopodids thus far studied (Stephenson 1962) and departs strikingly from the gekkotan *Bauplan*. There are several parts of the skull that display adaptations that are paralleled in other squamates occupying similar ecological niches, most strikingly scolecophidians, with which *Aprasia* shares both small size and subsurface activity. Some of the most noteworthy of these convergences are associated with burrowing, feeding, and hearing; these are discussed in turn below.

Burrowing

The diameter of the skull of *A. repens* is greatly reduced. These lizards use a head-first burrowing style, the main adaptations for which are expressed in the snout, which is modified to facilitate digging (McCoy 1888). This region of the skull has a similar "outer-shell" design to the one described for scolecophidians, in which the prefrontal extends anteriorly all the way to the posterior margin of the naris (Cundall & Rossman 1993; Rieppel *et al.* 2009), but with two main differences. First, the prefrontal reaches the level of the naris, but is excluded from it by the maxilla (although it has been reported that the prefrontal can reach the border of the naris in some specimens of *Aprasia* and *Pletholax*; Stephenson 1962). Second, the septomaxilla is more recessed than in scolecophidians (Haas 1930, 1964; Mahendra 1936; Abdeen *et al.* 1991a, 1992; Kley 2006; Cundall & Irish 2008). Simple forward movements during burrowing might exert high loads in the snout (Gans 1974) and, in this regard, the imbricated arrangement of the nasal, premaxilla, maxilla, and prefrontal bones suggests that the relatively large snout forms a self-supporting structure that might help to distribute high loads. The anteriormost part of the skull is formed exclusively by the nasals and premaxilla; the ascending nasal process in *Aprasia* has been described as rudimentary (Evans 2008) and as having bluntly abutting contact with the nasal as in some amphisbaenas (Jollie 1960). Although this genus exhibits perhaps the most paedomorphic premaxilla among gekkotans in retaining an unfused ascending nasal process in skeletally mature specimens (in pygopodoideans and eublepharids, the premaxilla is formed from two discrete centres of ossification; Camp 1923; Kluge 1967; Daza & Bauer 2012), they also develop a complex peg-and-socket joint between the premaxilla and nasals that might contribute to the reinforcement of the snout. Carphodactylids, the sister group to pygopodids, also show some trace of the paired premaxilla, presenting a clear trace of a seam (Bauer 1990). This character might reflect an overall tendency of this clade to display paedomorphic features (e. g., two ossification centres versus one; Kluge 1967).

The skull of gekkotans is highly kinetic, especially at the mesokinetic axis or frontoparietal joint (Versluys 1912; Frazzetta 1962; Arnold 1998; Metzger 2002). Cranial kinesis has been demonstrated to be variable across species (Herrel *et al.* 1999, 2000) and to provide some advantages to geckos during jaw abduction and adduction (Herrel *et al.* 2000, 2007). In burrowing lizards (e. g., the amphisbaenian *Leposternon microcephalum* = *Amphisbaena microcephala*), force is transmitted to the head by the m. longissimus dorsi (Gans 1973; Navas *et al.* 2004). Because these forces generated by the axial muscles need to be transferred to the snout during digging, a complex rigid frontoparietal joint might be advantageous (Lee 1998). The frontoparietal joint of *A. repens* has extensive oblique facets for the articulation of the participating bones, producing a constrained hinge-like articulation (but not as elaborate as the type B interdigitations of amphisbaenians or the parietal tabs of fossorial gymnophthalmids) that might reduce skull bending at the mesokinetic axis. The frontoparietal joint is far more complex than in other gekkotans and most other fossorial squamates, such as scolecophidian snakes. Additionally, the greater extension of the parabasisphenoid rostrum and its interface with the frontal bone (Underwood 1957) might provide additional resistance to mesokinetic bending.

Additional adaptations of the skull for burrowing might be indicated by the additional walling of the braincase by the parietal, prootic, epipterygoid, parabasisphenoid, and frontal bones. In other burrowing squamates, the braincase exhibits a similar bony enclosure of the brain (Rieppel 1981; Rieppel 1984a; Montero & Gans 2008; Roscito & Rodrigues 2010, 2012). However, other adaptations seen in fossorial squamates, such as the lateral closure of the juxtastapedial recess (Rieppel 1979), are not present in *A. repens.*

Feeding

Geckos have excellent vision (Roth & Kelber 2004; Roth *et al.* 2009), good hearing (Marcellini 1977), and well-developed olfaction (Schwenk 1993). In *Aprasia,* the eyes are still comparatively large (Boulenger 1885), but, compared to other gekkotans, they show some reduction in size as indicated by the lower number of scleral ossicles (Kluge 1976; Underwood 1984). Underwood (1957) reported a specimen of *A. pulchella* lacking a lens in addition to the loss of scleral cartilage as well as having a particularly thin fibrous sclera. Unlike the eyes of many other fossorial squamates, those of *Aprasia* are not extremely reduced or rudimentary, but, based on the relative reduction of size and the asymmetrical presence of a lens in some specimens (Underwood 1957), they can be considered somewhat degenerate (Walls 1942; Parker 1956). *Aprasia* could thus rely more heavily on other senses for capturing their prey. Members of the genus *Aprasia* have been reported to be myrmecophagous (Kluge 1976; Patchell & Shine 1986b), although they also consume other prey such as termites (Worrell 1963; Kluge 1974; Webb & Shine 1994; Pianka 2011) as do typhlopid snakes (Torres *et al.* 2000; Kley 2003a). *Aprasia repens* exhibits great development of Jacobson's organ as indicated by the dorsal expansion of the septomaxilla. Vomerolfaction might be advantageous while feeding in termite or ant colonies, although other strictly myrmecophagous squamates can perform well despite poorly developed vomeronasal organs (e. g., *Phrynosoma* or *Moloch*; Schwenk 2000) by foraging on the surface. Edentulism or the reduction of teeth can be attributed to the specialised diet of *Aprasia*, although reduction in tooth number has been also correlated with fossoriality (Broschinski & Sigogneau-Russell 1996) irrespective of diet. In this regard, *A. repens* exhibits convergent tooth distribution with scolecophidians and especially with leptotyphlopids, which, among the tooth bearing bones, retain only a few teeth on the dentary (Abdeen *et al.* 1991b; Kley 2003b, 2006; Cundall & Irish 2008). These snakes likewise exhibit a much shortened lower jaw and resulting pronounced overbite.

Hearing

The ear of *Aprasia* has been described as rudimentary based on the absence of tympanum and the anatomy of the middle ear (Shute & Bellairs 1953; Manley & Kraus 2010). Although we could not identify a stapes, the internal anatomy of the ECD resembles that of other gekkotans with full auditory capabilities and indicates that *Aprasia* might have a reasonably well-developed sense of hearing. For instance, the limbic portion of the ear is fully developed in *A. repens* (Underwood 1957). A detailed account of the modified sound transmitting apparatus in *A. repens* will be provided in a separate paper but, in brief, our preliminary observations support the previous hypothesis that, although this species might have limited ability to hear airborne sounds, it might be able to hear "underground sound" (Greer 1989). Anatomical modifications in the pterygoid and quadrate are consistent with this observation. The former presents a posterior suspension and mediolateral flattening and the latter exhibits a columnar shape and paroccipital abutment. Additionally, the internal connection of the paroccipital process with the ECD suggests that the quadrate has a role in sound transmission from the jaw to the inner ear homologous to some degree to that in snakes (Rieppel 1980b; Friedel *et al.* 2008). In *A. repens,* the quadrate might assist in transmitting low-frequency vibrations intercepted by the lower jaw into the middle ear. The dissociation of the pterygoid from the quadrate would prevent vibrations from being passed into the palate.

Conclusions

The study of this extremely miniaturised gekkotan by means of HRXCT data has revealed an unprecedented level of detail about its cranial anatomy. What has been considered for more than a half century as a degenerate morphological condition is, in fact, one of the most derived architectures in the entire gekkotan clade, prompting comparisons with other squamates that exploit similar niches. Although members of the genus *Aprasia* retain many of the apomorphic characters of gekkotans as a whole, other aspects of the skull have been completely reinvented, presumably under the influence of selective forces associated with fossorial life and miniaturisation.

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Literature cited

Abdeen A.M., Abo-Taira A.M. & Zaher M.M. (1991a). Further studies on the ophidian cranial osteology: the skull of the Egyptian blind snake *Leptotyphlops cairi* (Family Leptoyphlopidae). I. The cranium. A. The median dorsal bones, bones of the upper jaw, circumorbital series and occipital ring. *J. Egypt. Germ. Soc. Zool.*, 5, 417–437.

Abdeen A.M., Abo-Taira A.M. & Zaher M.M. (1991b). Further studies on the ophidian cranial osteology: the skull of the Egyptian blind snake *Leptotyphlops cairi* (Family Leptoyphlopidae). The lower jaw and the hyoid apparatus. *J. Egypt. Germ. Soc. Zool.*, 5, 457–467.

Abdeen A.M., Abo-Taira A.M. & Zaher M.M. (1992). Further studies on the ophidian cranial osteology: the skull of the Egyptian blind snake *Typhlops vermicularis* (Family Typhlopidae). A. The median dorsal bones, bones of the upper jaw, circumorbital series and occipital ring. *J. Egypt. Germ. Soc. Zool.*, 8, 355–378.

Arnold E.N. (1998). Cranial kinesis in lizards: variations, uses, and origins. In:. *Evolutionary Biology Volume 30* (eds. Hecht M, Macintyre R & Clegg M). New York: Plenum Press. 323–357.

Baird I.L. (1970). The anatomy of the reptilian ear. In: *Biology of the Reptilia, Volume 2, Morphology B* (eds. Gans C & Parsons T). Academic Press, New York, NY, 263–284.

Bauer A.M. (1990). Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn. Zool. Monogr.*, 30, 1–217.

Bellairs A.d'A. & Kamal A.M. (1981). The chondrocranium and the development of the skull in recent reptiles. In: *Biology of the Reptilia, Volume 11, Morphology F* (eds. Gans C & Parsons T). Academic Press, New York, NY, 1–283.

Bellairs A.d'A. & Underwood G. (1950). The origin of snakes. *Biol. Rev.*, 26, 193–237.

Bever G.S, Bell C.J. & Maisano J.A. (2005). The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Palaentol. Electron.*, 8, 1–36.

Bocage J.V.B. (1873). 3. Sur quelques sauriens nouveaux de la Nouvelle Calédonie et de l'Australie. *J. Sci. Math. Phys. Nat. (Lisboa)*, (1) 4, 228–232.

Boulenger G.A. (1884). Synopsis of the families of existing Lacertilia. *Ann. Mag. Nat. Hist*., (5) 14, 117–122.

Boulenger G.A. (1885). *Catalogue of the lizards in the British Museum* (*Natural History*). *Volume I . Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae.* Trustees of the British Museum, London, UK, 436 pp, 32 pls.

Boulenger G.A. (1887). *Catalogue of the lizards in the British Museum* (*Natural History*). *Volume III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae.* Trustees of the British Museum, London, UK, xii, 575 pp, 40 pls.

Brandley M.C., Huelsenbeck J.P. & Wiens J.J. (2008). Rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. *Evolution*, 62, 2042–2064.

Broschinski A. & Sigogneau-Russell D. (1996). Remarkable lizard remains from the lower Cretaceous of Anoual (Morocco). *Ann. Paleontol.* (*Vert.-Invert.*), 82, 147–175.

Camp C.L. (1923). Classification of the lizards. *Bull. Am. Mus. Nat. Hist.,* 48, 289–307.

Comeaux R.S., Olori J.C. & Bell C.J. (2010). Cranial osteology and preliminary phylogenetic assessment of *Plectrurus aureus* Beddome, 1880 (Squamata: Serpentes: Uropeltidae). *Zool. J. Linn. Soc.,* 160, 118–138.

Conrad J.L. (2004). Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata: Anguimorpha). *Zool. J. Linn. Soc.* 141, 399–434.

Conrad J.L. (2008). Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bull. Am. Mus. Nat. Hist.,* 310, 1–182.

Cundall D. & Irish F. (2008). The snake skull. In: *Biology of the Reptilia, Volume 20, Morphology H* (eds. Gans C, Gaunt AS & Adler K). Society for the Study of Amphibians and Reptiles, Ithaca, NY, 349–692.

Cundall D. & Rossman D.A. (1993). Cephalic anatomy of the rare Indonesian snake *Anomochilus weberi*. *Zool. J. Linn. Soc.,* 109, 235–273.

Daza J.D., Abdala V., Thomas R. & Bauer A.M. (2008). Skull anatomy of the miniaturized gecko *Sphaerodactylus roosevelti* (Squamata: Gekkota). *J. Morphol.,* 269, 1340–1364.

Daza J.D. & Bauer A.M. (2010). The circumorbital bones of the Gekkota (Reptilia: Squamata). *Anat. Rec.*, 293, 402–413.

Daza J.D. & Bauer A.M. (2012). Temporal bones of the Gekkota support molecular relationships within the Pygopodoidea. *J. Herpetol.*, 46, 381–386.

Daza J.D., Aurich J. & Bauer A.M. (2012). Anatomy of an enigma: an osteological investigation of the Namibian festive gecko (*Narudasia festiva*: Gekkonidae: Gekkota). *Acta Zool.*, 93, 465–486.

Daza J.D., Bauer A.M. & Snively E. (2013). *Gobekko cretacicus* (Reptilia: Squamata) and its bearing on the interpretation of gekkotan affinities. *Zool. J. Linn. Soc.* 167:430–448.

Daza J.D., Diogo R., Johnston P. & Abdala V. (2011). Jaw adductor muscles across lepidosaurs: a reappraisal. *Anat. Rec.*, 294, 1765–1782.

Ehmann H. (1976). The reptiles of the Mt. Lofty Ranges, South Australia. Part 1. *Herpetofauna*, 8, 2–5.

Estes R., de Queiroz K. & Gauthier J. (1988). Phylogenetic relationships within Squamata. In: *Phylogenetic relationships of the lizard families. Essays commemorating Charles L. Camp* (eds. Estes R & Pregill G). Stanford University Press, Stanford, CA, 119–281.

Evans S.E. (2008*)*. The skull of lizards and tuatara. In: *Biology of the Reptilia, Volume 20, Morphology H, The skull of Lepidosauria* (eds. Gans C, Gaunt AS & Adler K). Society for the Study of Amphibians and Reptiles, Ithaca, NY, 1–347.

Frazzetta T.H. (1962). A functional consideration of cranial kinesis in lizards. *J. Morphol.*, 111, 287–319.

Freeman D.M. (1990). Anatomical model of the cochlea of the alligator lizard. *Hearing Res.*, 49, 29–38.

Friedel P., Young B.A. & van Hemmen J.L. (2008). Auditory localization of ground-borne vibrations in snakes. *Phys. Rev. Lett.*, 100, 048701-1–4.

Fry D.B. (1914). On a collection of reptiles and batrachians from Western Australia. *Rec. South Aust. Mus.* 1, 174–210, pls. xxvii-xxviii.

Gamble T., Daza J.D., Colli G.R., Vitt L.J. & Bauer A.M. (2011). A new genus of miniaturized and pug-nosed gecko from South America (Sphaerodactylidae: Gekkota). *Zool. J. Linn. Soc.*, 163, 1244–1266.

Gans C. (1973). Locomotion and burrowing in limbless vertebrates. *Nature*, 242, 414–415.

Gans C. (1974). *Biomechanics: an Approach for Vertebrate Biology.* J. B. Lippincott Company, Philadelphia, PA, x, 261.

Gauthier J., Kearney M., Maisano J.A., Rieppel O. & Behlke A. (2012). Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bull. Peabody Mus. Nat. Hist.*, 53, 3–308 .

Gray J.E. (1838). Catalogue of the slender-tongued saurians, with descriptions of many new genera and species. *Ann. Nat. Hist.* 2, 331–337.

Gray J. E. (1845). *Catalogue of the specimens of lizards in the collection of the British Museum*. Trustees of the British Museum, London, UK, xxvii, 289 pp.

Greer A.E. (1989). *The biology and evolution of Australian lizards*. Surrey Beatty & Sons Pty. Limited, Chipping Norton, New South Wales, xvi, 264 pp.

Grismer L.L. (1988). Phylogeny, taxonomy, classification, and biogeography of Eublepharid geckos. In: *Phylogenetic relationships of the lizard families. Essays commemorating Charles L. Camp* (eds. Estes R & Pregill G). Stanford University Press, Stanford, CA, 369–469.

Gugg W. (1939). Der Skleralring der plagiotremen Reptilien. *Zool. Jahrb. Abt. Anat. Ontog. Tiere*, 65, 339–416.

Haas G. (1930). Über das Kopfskelett und die Kaumuskulatur der Typhlopiden und Glauconiiden. *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere*, 52, 1–94.

Haas G. (1964). Anatomical observations on the head of *Liotyphlops albirostris* (Typhlopidae, Ophidia). *Acta Zool.*, 45, 1–62.

Hamilton D.W. (1960). Observations on the morphology of the inner ear in certain gekkonoid lizards. *Univ. Kansas Sci. Bull.*, 41, 983–1024.

Hamilton D.W. (1964). The inner ear of lizards. *J. Morphol.*, 115, 255–272.

Herrel A., Aerts P. & De Vree F. (2000). Cranial kinesis in geckoes: functional implications. *J. Exp. Biol.*, 203, 1415–1423.

Herrel A, De Vree F., Delheusy V, & Gans C. (1999). Cranial kinesis in gekkonid lizards. *J. Exp. Biol.*, 202, 3687–3698.

Herrel A., Schaerlaeken V., Meyers J.J., Metzger K.A. & Ross C.F. (2007). The evolution of cranial design and performance in squamates: consequences of skull-bone reduction on feeding behavior. *Integr. Comp. Biol.*, 47, 107–117.

Holliday C.M., Gardner N.M., Paesani S.M., Douthitt M. & Ratliff J.L. (2010). Microanatomy of the mandibular symphysis in lizards: patterns in fiber orientation and Meckel's cartilage and their significance in cranial evolution. *Anat. Rec.*, 293, 1350–1359.

Hutchinson M.N. (1997). The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. *Mem. Qld. Mus.*, 41, 355–366.

Jennings W.B., Pianka E.R. & Donnellan S.C. (2003). Systematics of the lizard family Pygopodidae with implications for the diversification of Australia temperate biotas. *Syst. Biol.*, 52, 757–780.

Jensen A.S. (1901). Om *Ophiopsiseps nasutus* du Bocage og dens stilling i reptiliernes system. *Vidensk. Medd. Naturhist. Foren. København*, 2, 317–328.

Jollie M.T. (1960). The head skeleton of the lizard. *Acta Zool.*, 41, 1–54.

Jones M.E.H., O'Higgins P., Fagan M.J., Evans S.E. & Curtis N. (2012). Shearing mechanics and the influence of a flexible symphysis during oral food processing in *Sphenodon* (Lepidosauria: Rhynchocephalia). *Anat. Rec.*, 295, 1075–1091.

Jones M.E.H., Curtis N., Fagan M.J, O'Higgins P. & Evans S.E. (2011). Hard tissue anatomy of the cranial joints in *Sphenodon* (Rhynchocephalia): sutures, kinesis, and skull mechanics. *Palaentol. Electron.*, 14, 1–92.

Jones M.E.H., Curtis N., O'Higgins P., Fagan M. & Evans S.E. (2009). The head and neck muscles associated with feeding in *Sphenodon* (Reptilia: Lepidosauria: Rhynchocephalia). *Palaentol. Electron.*, 12, 1–56.

Kinghorn J.R. (1923). Studies in Australian reptiles. No. 3. *Rec. Aust. Mus.* 14, 126–134.

Kinghorn J.R. (1926). A brief review of family Pygopodidae. *Rec. Aust. Mus.* 15, 40–64.

Kley N.J. (2003a). Blindsnakes (Typhlopidae). In: *Grzimek's animal life encyclopedia, 2nd edition. Vol. 7, Reptiles* (eds. Hutchins M, Murphy JB & Schlager N). Gale Group, Farmington Hills, MI, 379–385.

Kley N.J. (2003a). Slender blindsnakes (Leptotyphlopidae). In: *Grzimek's animal life encyclopedia, 2nd edition. Vol. 7, Reptiles* (eds. Hutchins M, Murphy JB & Schlager N). Gale Group, Farmington Hills, MI, 373–377.

Kley N.J. (2006). Morphology of the lower jaw and suspensorium in the Texas blindsnake, *Leptotyphlops dulcis* (Scolecophidia: Leptotyphlopidae). *J. Morphol.*, 267, 494–515.

Kluge A.G. (1962). Comparative osteology of the eublepharid genus *Coleonyx* Gray. *J. Morphol.*, 110, 299–332.Kluge A.G. (1967). Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Am. Mus. Nat. Hist.*, 135, 1–60, 5 pls.

Kluge A.G. (1974). A taxonomic revision of the lizard family Pygopodidae. *Misc. Pub. Mus. Zool., Univ. Michigan,* (147), i–vi, 1–221.

Kluge A.G. (1976). Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. *Misc. Pub. Mus. Zool., Univ. Michigan,* (152), i–iv, 1–72

Kluge A.G. (1987). Cladistic relationship in the Gekkonoidea (Squamata, Sauria). *Misc. Pub. Mus. Zool. Univ. Michigan,* (173), i–iv, 1–54.

Kluge A.G. (2001). Gekkotan lizard taxonomy. *Hamadryad,* 26, 1–209.

Lee M.S.Y. (1998). Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol. J. Linn. Soc.*, 65, 369–453.

Mahendra B.C. (1936). Contributions to the osteology of the Ophidia. I. The endoskeleton of the so-called “Blind snake”, *Typhlops braminus*. *Proc. Indian Acad. Sci., Ser. B*, 3, 128–142.

Manley G.A. & Kraus J.E.M. (2010). Exceptional high-frequency hearing and matched vocalizations in Australian pygopod geckos. *J. Exp. Biol.*, 213, 1876–1885.

Marcellini D. (1977). Acoustic and visual display behaviour of gekkonid lizards. *Amer. Zool.*, 17, 251–260.

McCoy F. (1888). The lined Aprasia (*Aprasia pulchella*, Gray). In: *Natural history of Victoria. Prodromus of the zoology of Victoria; or figures and descriptions of the living species of all classes of the Victorian indigenous animals*. Decade XVII. Robt. S. Brain, Government Printer and Trübner and Co, Melbourne and London. 233–234, plate 162.

McDowell S.B.J. & Bogert C.M. (1954). The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bull. Am. Mus. Nat. Hist.,*105, 1–142, 16 pls, 3 tables.

Metzger K. (2002). Cranial kinesis in lepidosaurs: skulls in motion. In: *Topics in functional and ecological vertebrate morphology* (eds. Aerts P, D’Aout K, Herrel A, Van Damme R) Shaker Verlag, Aachen, 15–46.

Miller M.R. (1966). The cochlear duct of lizards and snakes. *Am. Zool.*, 6, 421–429.

Montero R. & Gans C. (1999). The head skeleton of *Amphisbaena alba* Linneaus. *Ann. Carnegie Mus.*, 68, 15–80.

Montero R. & Gans C. (2008). An atlas of amphisbaenian skull anatomy. In: *Biology of the Reptilia, Volume 21, Morphology I, The skull and appendicular locomotor apparatus of Lepidosauria* (eds. Gans C, Gaunt AS & Adler K). Society for the Study of Amphibians and Reptiles, Ithaca, NY, 621–738.

Navas C.A., Antoniazzi M.M, Carvalho J.E., Chaui-Berlink J.G., James R.S., Jared C., Kohlsdorf T., Dal Pai-Silva M. & Wilson R.S. (2004). Morphological and physiological specialization for digging in amphisbaenians, an ancient lineage of fossorial vertebrates. *J. Exp. Biol.*, 207, 2433–2441.

Oelrich T.M. (1956). The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Pub. Mus. Zool., Univ. Michigan,* 94, 1–122.

Olori J.C. (2010). Digital endocasts of the cranial cavity and osseus labyrinth of the burrowing snake *Uropeltis woodmansoni* (Alethinophidia: Uropeltidae). *Copeia,* 2010, 14–26.

Olori J.C. & Bell C.J. (2012). Comparative skull morphology of uropeltid snakes (Alethinophidia: Uropeltidae) with special reference to disarticulated elements and variation. PLoS ONE 7, e32450, 52 pp.

Parker H.W. (1956). The Lizard Genus *Aprasia*; its taxonomy and temperature-correlated variation. *Bull. Br. Mus. (Nat. Hist) Zool.,* 3, 365–385.

Patchell F.C. & Shine R. (1986a). Feeding mechanisms in pygopodid lizards: how can *Lialis* swallow such a large prey. *J. Herpetol.*, 20, 59–64.

Patchell F.C. & Shine R. (1986b). Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). *Copeia*, 1986, 30–39.

Pianka E.R. (2011). Notes on the ecology of four species of pygopodid lizards in the Great Victoria Desert. *West. Aust. Nat.,* 27, 175–181.

Pianka E.R. & Vitt L.J. (2003). *Lizards, windows to the evolution of diversity.* University of California Press, Berkeley, CA, xiii, 333 pp.

Pritchard J.J., Scott J.H. & Girgis F.G. 1956. The structure and development of cranial and facial sutures. *J. Anat.*, 90, 73–86.

R Core Team. (2013). R: A language and environment for statistical computing. R Core Team, Vienna. Available at: http://www.R-project.org. Last accessed 30 April 2013.

Rieppel O. (1979). The braincase of *Typhlops* and *Leptotyphlops* (Reptilia: Serpentes). *Zool. J. Linn. Soc.*, 65, 161–176.

Rieppel O. (1980a). The phylogeny of anguinomorph lizards. *Denkschr. Schweiz. Naturf. Ges.*, 94, 1–86.

Rieppel O. (1980b). The sound transmitting apparatus of primitive snakes and its phylogenetic significance. *Zoomorphology*, 96, 45–62.

Rieppel O. (1981). The skull and jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *J Zool.* (*London*), 195, 493–528.

Rieppel O. (1984a). The cranial morphology of the fossorial lizard genus *Dibamus* with a consideration of its phylogenetic relationships. *J Zool.* (*London*), 204, 289–327.

Rieppel O. (1984b). Miniaturization of the lizard skull: its functional and evolutionary implications. In: *The structure, development and evolution of reptiles* (ed. Ferguson MW J). The Zoological Society of London and Academic Press, London, 503–520.

Rieppel O. (1984c). The structure of the skull and jaw adductor musculature of the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zool. J. Linn. Soc.*, 82, 291–318.

Rieppel O. (1985). The recessus scalae tympani and its bearing on the classification of reptiles. *J. Herpetol.,* 19, 373–384.

Rieppel O. & Kearney, M. (2002). Similarity. *Biol. J. Linn. Soc.*, 75, 59–82.

Rieppel O., Kley N.J. & Maisano J.A. (2009). Morphology of the skull of the white-nosed blindsnake, *Liotyphlops albirostris* (Scolecophidia: Anomalepidae). *J. Morphol.*, 270, 536–557.

Roscito J.G. & Rodrigues M.T. (2010). Comparative cranial osteology of fossorial lizards from the tribe Gymnophthalmini (Squamata, Gymnophthalmidae). *J. Morphol.*, 271, 1352–1365.

Roscito J.G. & Rodrigues M.T. (2012). Embryonic development of the fossorial gymnophthalmid lizards *Nothobachia ablephara* and *Calyptommatus sinebrachiatus*. *Zoology* (*Jena*)*,* 115, 302–318.

Roth L.S.V. & Kelber A. (2004). Nocturnal colour vision in geckos. *Proc. R. Soc. Lond., B.* (*Supplement*), 271, S485–S487.

Roth L.S.V., Lundström L., Kelber A., Kröger R.H.H., & Unsbo P. (2009). The pupils and optical systems of gecko eyes. *J. Vision,* 9, 1–11.

Schwenk K. (1993). Are geckos olfactory specialists? *J. Zool.* (*London*), 229, 289–302.

Schwenk K. (2000). Feeding in lepidosaurs. In: *Feeding: Form, function, and evolution in tetrapod vertebrates* (ed. Schwenk K). Academic Press, San Diego, 175–291.

Shute C.C.D. & Bellairs A.d'A. (1953). The cochlear apparatus of Geckonidae and Pygopodidae and its bearing on the affinities of these groups of lizards. *Proc. Zool. Soc London,* 123, 695–708.

Smith K.T. (2007). A translation of A. S. Jensen, 1900 [1901], "Om *Ophiopsiseps nasutu*s du Bocage og dens stilling i reptiliernes system,". Available at: http://paleoglot.org. Last accessed 30 April 2013.

Spaw A., Bourke J., Witmer L.M. (2013). Visible interactive iguana. Available at: http://www.oucom.ohiou.edu/dbms-witmer/3D_iguana.htm. Last accessed 30 April 2013.

Stephenson N.G. (1962). The comparative morphology of the head skeleton, girdles and hind limbs in the Pygopodidae. *J. Linn. Soc* (*Zool.*), 44, 627–644.

Stokely P.S. (1947). The post-cranial skeleton of *Aprasia repens*. *Copeia*, 1947, 22–28.

Tol P. (2012). Colour schemes. SRON (Netherlands Institute for Space Research) Technical note SRON/EPS/TN/09-002. Available at: http://www.sron.nl. Last accessed 30 April 2013.

Torres J.A., Thomas R., Leal M. & Gush T. (2000). Ant and termite predation by the tropical blindsnake *Typhlops platycephalus*. *Insects Soc.*, 47, 1–6.

Uetz P., Hošek J. & Hallermann J. (2013). The Reptile Database. Available at: http://www.reptiledatabase.org. Last accessed 30 April 2013.

Underwood G. (1957). On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the Squamata. *J. Morphol.*,100, 207–268.

Underwood G. 1970. The eye. In: *Biology of the Reptilia, Volume 2, Morphology B* (eds. Gans C & Parsons TS). Academic Press, New York, NY, 1–97.

Underwood G.. (1984). Scleral ossicles of lizards: an exercise in character analysis. In: *The structure, development and evolution of Reptiles* (ed. Ferguson MWJ) The Zoological Society of London, Academic Press, London, 483–502.

Versluys J. (1912). Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden. *Zool. Jahrb.*, 15, 545–716.

Vitt L.J. & Caldwell J.P. (2014) *Herpetology: An Introductory Biology of Amphibians and Reptiles*, 4th edition. Academic Press, London, xiv, 757 pp.

Walls G.L. (1942). The vertebrate eye and its adaptive radiation. *Cranbrook Inst. Sci. Bull.* (19), xiv, 785 pp.

Walsh S.A., Barrett P.M., Milner A.C., Manley G. & Witmer L.M. (2013). Inner ear anatomy is a proxy for deducing auditory capability and behaviour in reptiles and birds. *Proc. R. Soc. B*, 276, 1355–1360.

Webb J.K. & Shine R. (1994). Feeding habits and reproductive biology of Australian pygopodid lizards of the Genus *Aprasia*. *Copeia*, 1994, 390–398.

Weber E. G. & Gans C. (1973). The ear in Amphisbaenia (Reptilia); further anatomical observations. *J. Zool.,* 171, 189–206.

Wells R.W. (2007). Some taxonomic and nomenclatural considerations on the Class Reptilia in Australia. A review of species in the genus *Aprasia* Gray 1839 (Aprasiaidae), including the description of a new genus. *Aust. Biodivers. Rec.,* (6), 1–17.

Werner F. (1912). Reptilia. Eublepharidae, Uroplatidae, Pygopodidae. In: *Das Tierreich, Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen* (ed. Schulze FE). R. Friedländer und Sohn, Berlin, Germany, x, 33 pp.

Wever E. G. (1973). Closure muscles of the external auditory meatus in Gekkonidae. *J. Herpetol.,* 7, 323–329.

Wever E. G. (1978). *The Reptile ear: Its Structure and Function*. Princeton University Press, Princeton, NJ, xii, 1024 pp.

Wiens J.J., Brandley M.C. & Reeder T.W. (2006). Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution*, 60, 123–141.

Witmer L.M., Ridgely R.C., Dufeau D.L. & Semones M.C. (2008). Using CT to peer into the past: 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian dinosaurs. In: *Anatomical imaging:*

towards a new morphology (eds. Endo H & Frey R). Springer, Tokyo, Japan, 67–88.

Worrell E. (1963). *Reptiles of Australia*. Angus & Robertson Ltd., Sydney, NSW, xv, 207 pp, 64 pls.

Zietz F.R. (1921). Catalogue of Australian lizards. *Rec. South Aust. Mus*., 1, 181–228.

Appendix

Specimens of gekkotan lizards for which HRXCT scans have been used in a comparative context for this study. Collection abbreviations: CAS / CAS-SU, California Academy of Sciences (San Francisco, California); CM, Carnegie Museum (Pittsburgh, Pennsylvania); FMNH, Field Museum of Natural History (Chicago, Illinois); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts); USNM, United States National Museum of Natural History (Washington, D.C.); YPM, Yale Peabody Museum of Natural History (New Haven, Connecticut).

Diplodactylidae: *Eurydactylodes vieillardi* (CAS 231986), *Pseudothecadactylus australis* (MCZ R-35162), *Rhacodactylus auriculatus* (CAS 205486), *Strophurus ciliaris* (FMNH 215488).

Carphodactylidae: *Carphodactylus laevis* (MCZ R-35114), *Nephrurus asper* (CAS 74733), *Nephrurus levis* (YPM 12868), *Saltuarius cornutus* FMNH 57503.

Pygopodidae: *Aprasia repens* (CAS 104382), *Delma borea* (USNM 128679), *Lialis burtonis* FMNH 166958, *Pletholax gracilis* MCZ R-187676.

Eublepharidae: *Aeluroscalabotes felinus* (FMNH 146141), *Coleonyx variegatus* (YPM 14383), *Eublepharis macularius* CM 67524, *Hemitheconyx caudicinctus* (YPM 14381).

Sphaerodactylidae: *Aristelliger georgeensis* (CAS 176485), *Euleptes europaea* (MCZ R-4463), *Gonatodes albogularis* (FMNH 55929), *Pristurus carteri* (CAS 225349), *Pseudogonatodes barbouri* (MCZ R-14385), *Sphaerodactylus semasiops* (MCZ R-55766), *Teratoscincus przewalskii* (CAS 171013).

Phyllodactylidae: *Gymnodactylus geckoides* (CAS 49397), *Haemodracon riebeckii* (MCZ A-27255), *Phyllopezus lutzae* (MCZ R-46191).

Gekkonidae: *Afroedura karroica* (CAS 198274), *Kolekanos plumicaudus* (CAS 248782), *Afrogecko porphyreus* (CAS 175312, CAS 175308), *Agamura persica* (CAS 140562), *Calodactylodes aureus* (MCZ R-3918), *Cnemaspis boulengerii* (MCZ R-16665), *Cnemaspis gracilis* (CAS 113988), *Cnemaspis spinicollis* (CAS 103312), C*ryptactites peringueyi* (CAS 186375), *Cyrtodactylus ayeyarwadyensis* (CAS 221985), *Gekko gecko* (FMNH 186818), *Goggia lineata* (CAS 193627), *Hemidactylus frenatus* CAS 215743, *Lygodactylus capensis* (CAS 167621), *Narudasia festiva* (CAS 186278); *Pachydactylus bicolor* (CAS 223912), *Phelsuma lineata* (FMNH 260100), *Ptenopus carpi* (CAS 214548), *Rhoptropus afer* (CAS 193865), *Microgecko helenae* (CAS 120795), *Tropiocolotes tripolitanus* (CAS 123467), *Uroplatus fimbriatus* (CAS-SU 13469).

The morphology of the adult skull of the Leopard Gecko, *Eublepharis macularius*

Patrick A.D. Wise

4835 Yellowpoint Road, Ladysmith, British Columbia V9G 1H2, Canada; E-mail: padwise@gmail.com

Abstract

The gecko family Eublepharidae, formerly considered basal within Gekkota, is now recognised as deeply nested within the gekkotan clade. Nonetheless, it exhibits an array of plesiomorphic features (e. g., movable eyelids, lacrimal bone present, and lack of adhesive toepads) and remains a good model for a relatively unspecialised gekkotan body plan. *Eublepharis macularius*, in particular, is commonly kept and bred in captivity and has become a widely used model in biological investigations. A detailed description of the adult skull of *E. macularius* based on seven adult specimens is provided. Specimens were examined as unarticulated whole mounts, completely disarticulated specimens, and computed tomography (CT). The lacrimal and jugal bones, which have been considered as absent by some authors, were present in all specimens. The angular, splenial, articular, prearticular, and surangular bones were all present in the mandible, but have fused into two compound bones with no remaining trace of sutures. CT scans have been helpful in resolving aspects of cranial pattern, but embryological material is needed to further document the relative timing and order of the fusion events.

Introduction

The tetrapod skull is a composite of three structural and developmental units: the chondrocranium, splanchnocranium, and dermatocranium. These are derived from two separate embryonic tissue types, namely paraxial mesoderm

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(the sclerotomal population) and neural crest (Hall 1999; Le Douarin & Kalcheim 1999), and are integrated during ontogeny to ultimately form two structural components, the cranium and the lower jaw.

The chondrocranium originally condenses from head mesenchyme derived from paraxial mesoderm (Hall 1999) and gives rise to the following elements: occipital series (basioccipital, paired exoccipitals and the supraoccipital), basisphenoid, sphenethmoid, prootic, and opisthotic (Le Douarin & Kalcheim 1999).

The splanchnocranium ultimately originates from neural crest cells that migrate into the pharyngeal arches (Hall 1999; Le Douarin & Kalcheim 1999). From the mandibular arch (pharyngeal arch I) arise the articular, quadrate, and epipterygoid, whereas the hyoid arch (pharyngeal arch II) gives rise to the columella and extracolumella as well as part of the hyoid apparatus (Romer 1956).

The elements of the dermatocranium arise as condensations of bone from the mesenchyme and ectomesenchyme of the dermis, which is all of neural crest origin (Hall 1999; Le Douarin & Kalcheim 1999). Bones of the dermatocranium in early tetrapods are as follows: premaxilla, maxilla, nasal, septomaxilla, lacrimal, prefrontal, postfrontal, postorbital, jugal, squamosal, quadratojugal, intertemporal, supratemporal, tabular, frontal, parietal, postparietal, vomer, palatine, ectopterygoid, pterygoid, dentary, splenials (one anterior and one posterior), angular, surangular, prearticular, and coronoids (two or three arrayed linearly) (Romer 1956).

Within squamates, there is great diversity of form expressed by the skull and, even within lineages, variation among species can be substantial. Both the structure and the proportions of individual cranial elements are highly variable within Squamata (Romer 1956) as is the configuration of elements with respect to one another (Etheridge 1964). Some squamate groups retain what is held to be the primitive adult condition, with little erosion of the margins, or loss, of temporal fenestrae, whereas in others there is substantial reduction or loss (Romer 1956; Evans 2008). Cranial anatomy, therefore, has proved to be of great importance in studies of both functional anatomy and systematics (Estes & Pregill 1988; Conrad 2008; Gauthier *et al.* 2012).

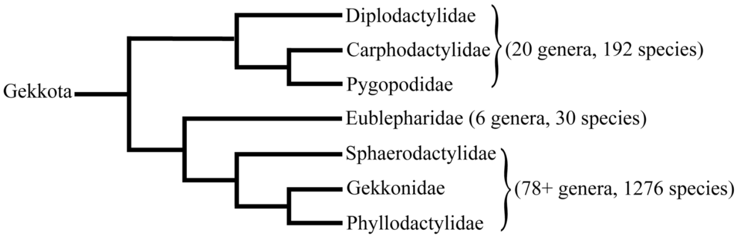

Figure 1:
Current Gekkotan phylogeny.

Within squamates, two major assemblages are recognised, the monophyletic snakes and the paraphyletic lizards (Evans 2008). Lizards exhibit a broad array of form and ecological adaptations and basal taxa provide excellent opportunities for the investigation of cranial form in this assemblage. One of the major squamate radiations is Gekkota. “Geckos” occupy all the warmer areas of the world, being found between 45° N (Bauer 2013) and 50° S (Kluge 1967). They occur on every continent except Antarctica and current estimates recognise about 1500 species (Uetz 2013) comprising seven families in total: Diplodactylidae, Carphodactylidae, Pygopodidae, Eublepharidae, Sphaerodactylidae, Gekkonidae, and Phyllodactylidae (Gamble *et al.* 2008; Fig. 1). The monophyly of Gekkota is supported by both morphological and molecular data (Evans 2003; Han *et al.* 2004; Townsend *et al.* 2004; Gamble *et al.* 2008, 2012).

Camp (1923) diagnosed Gekkota using the following skeletal features: absence of the squamosal; presence of the jugal; a strong postfronto-jugal ligament, incomplete or absent postorbital arch, vertebrae amphicoelous or procoelous with small condyles and persistent intercentra, short centra that are equal in width at both ends and constricted medially, and six cervical vertebrae. He then further defined the three extant gekkotan families recognised at the time—Gekkonidae, Uroplatidae, and Pygopodidae—and stated that they all lack temporal arches. Camp’s (1923) osteological definition of Gekkota still holds today with a few modifications (Kluge 1987; Estes & Pregill 1988; Evans 1994; Conrad 2008), although familial disposition has changed. Whereas Camp did not employ synapomorphies and symplesiomorphies as we currently understand them, he calculated the total “Paleotelic weight” for a given clade based on a hierarchy of primitiveness to arrange his phylogeny. Camp (1923) considered Gekkota to be an ancient and primitive clade, and current estimates recognise fossil taxa considered to be stem gekkotans, such as *Gobekko* from the Cretaceous (Daza *et al.* 2013) and *Eichstaetisaurus* from the Jurassic (Gauthier *et al.* 2012). This places the origin of the gekkotan "trunk" earlier still. A review of gekkotan synapomorphies furnished by Estes and Pregill (1988) listed the following features as being defining attributes of Gekkota: vertebrae amphicoelous or procoelous, and absence of the postorbital bar and the supratemporal arch. These diagnostic features agree with those advocated by Camp (1923) except for his claim for the absence of the squamosal (see below). The features relating to the jugal differ between Estes & Pregill (1988) and Camp (1923) in that Camp states that it is present in Gekkota whereas Estes & Pregill describe it as being reduced or lost. More recently, its presence has been confirmed by Daza & Bauer (2010) in all 105 Gekkotan taxa that they examined. As well as the aforementioned synapomorphies of Gekkota, Estes & Pregill (1988) and Conrad (2008) also list ontogenetic fusion of the frontals and fused crista cranii of the frontals. Estes & Pregill (1988) further list the loss of the lacrimal (except for some eublepharids). Kluge (1987) described two additional features as being unique to Gekkota: paired egg teeth and a large, wing-like hyoid cornu.

Gekkotan skulls exhibit strong trends toward miniaturisation (Rieppel 1996; Daza *et al.* 2008, 2012; Gamble *et al.* 2011) and reduction of certain elements; it is believed that differential developmental timing (Stephenson & Stephenson 1955; Stephenson 1960; Rieppel 1996; Barahona & Barbadillo 1998; Donnellan *et al.* 1999; Evans 2003) is responsible for the differential levels of expression of cranial elements in these lizards. Understanding the development of the gekkotan skull is likely to be of significance in the unravelling of the causes of systematic differences and in interpreting systematic data. Many bones common in the skulls of other squamates ostensibly fail to appear at all during the ontogeny of gekkotans. Developmental studies can assist in determining what actually occurs in such instances. Gekkota specifically exhibits loss of the following: postorbital, upper and lower temporal bars, parietal foramen, and palatal teeth. The angular is often fused or absent and the lacrimal and jugal might or might not be present (Evans 2008).

Historically, higher-level classification of gekkotans and all squamates has been based on comparative osteology of adult specimens (Noble 1921; Stephenson & Stephenson 1955; Stephenson 1960; Cogger 1964) and cranial

Figure 2:
Adult female leopard gecko (*Eublepharis macularius*).

anatomy has figured prominently in many of these studies (Wellborn 1933; Webb 1951; Kluge 1962, 1967). Many studies using morphological data have combined information from both hard and soft tissues (Grismer 1988; Conrad 2008), and there have also been purely descriptive studies of gekkotan skeletons (Kluge 1962; Häupl 1980). Recent investigations into gekkotan systematics have shown a shift towards the use of molecular data in place of, or to supplement, morphological characters (Zug & Moon 1995; Good *et al.* 1997; Donnellan *et al.* 1999; Ota *et al.* 1999; Macey *et al.* 2000; Han *et al.* 2004; Gamble *et al.* 2008, 2012).

The bulk of Gekkota are assignable to the three lineages Sphaerodactylidae, Gekkonidae and Phyllodactylidae (Fig. 1). Diplodactylidae, Carphodactylidae and Pygopodidae are restricted to the New Guinea/Australia region along with some South Pacific islands. Eublepharidae, the focus of the current study, consists of six genera and approximately 30 species (Uetz 2013), with representatives in both the Palearctic, tropical Asia, Africa, and North and Central America. Long considered to be a basal taxon within Gekkota, Eublepharidae is currently regarded as more closely related to Sphaerodactylidae + (Gekkonidae + Phyllodactylidae) than it is to Diplodactylidae + (Carphodactylidae + Pygopodidae) (Fig. 1). Nonetheless, Eublepharidae exhibits an array of archaic gekkotan features (e. g., they retain eyelids, the notochord, the lacrimal and the jugal, but lack adhesive toe pads) and is generally considered to exhibit a body plan reflective of that of stem gekkotans (Grismer 1988). For this reason, this taxon was selected for investigation of the form of cranial skeletal anatomy. From among its ranks, *Eublepharis macularius* (Fig. 2) was selected as a target taxon because of its ease of maintenance and captive propagation as well as its widespread use in a diversity of studies (Whimster 1978; Coomber *et al.* 1997; Crews *et al.* 1998; Rhen *et al.* 2000; Vallely *et al.* 2001; Gamble *et al.* 2006; Janes *et al.* 2007).

To this end, in this work, I furnish a detailed description of the adult skull of *E. macularius* and briefly review how its structure compares to what is known of cranial structure in gekkotans in general. This chapter is purely descriptive to establish the form of and terminology for the skull of the Leopard Gecko.

Materials and methods

For this chapter, one cleaned, dried and prepared skull, one completely disarticulated skull, two cleared and double-stained specimens, and computed-tomography (CT) scans of four intact, preserved specimens were used. The articulated, cleaned specimen provides the basis for considering dermal elements in their articulated context with no soft tissue obstructing the view. Chondrocranial elements, however, are not easily seen in such specimens nor are any of the internal surfaces of the dermal elements. The disarticulated specimen therefore enabled a thorough inspection of each individual element, including the joint surfaces. The two cleared and double-stained whole mounts enabled observation of the dermal elements *in situ*, with less potential for shrinkage of the elements during preparation (Filipski & Wilson 1985). The CT-scanned specimens enable all the elements to be viewed without physical disruption. But, because analysing CT data and building 3-D reconstructions are very time consuming, I have limited my foray in this medium to areas of the skull for which the other methods of preparation and observation were inadequate. In this instance, features of the lower jaw and chondrocranium are the main foci of my CT data analysis. CT data were imported into the program Amira® (Pro Medicus Ltd.), which stacks and concatenates the individual images to create a composite image. Each image is analysed and elements are colour-coded to distinguish one from another.

Descriptive format

Historically, various approaches have been employed to subdivide the skull of lizards for the purpose of their description. Major contributions in this regard are those of Wellborn (1933), Oelrich (1956), Romer (1956), Jollie

(1960), Kluge (1962), Daza *et al.* (2008), and Evans (2008); these are summarised in Table 1. I herein employ the framework established by Evans (2008), further subdividing the cranial elements into the developmental clusters of the dermatocranium and the splanchnocranial and chondrocranial derivatives. This results in a slight rearrangement of the order of treatment of some of the elements. Terminology for the names of the component parts of the elements is the same as that used by Evans (2008) except where noted. In cases where different terms have been used for the same process or structure, I list these upon first mention in the text.

My description begins with an overview of the intact skull, including the major openings. This is followed by a description of the dermatocranial elements in the following order: skull-roofing bones (nasals, frontal, and parietal), tooth-bearing bones of the upper jaw (premaxilla and maxillae); circumorbitals (prefrontals, lacrimals, jugals, postfrontals, and postorbitals), temporal bones (squamosals and supratemporals), palatal elements (vomers, septomaxillae, palatines, pterygoids, ectopterygoids, and parasphenoid), and lower-jaw bones (dentaries, splenials, coronoids, angulars, surangulars, articulars, and prearticulars). Note that the prearticulars are rarely described, possibly because they fuse very early with the articulars (which are splanchnocranial in origin) in embryological development and are thereafter indistinguishable from them (Jollie 1960) such that they cannot be recognised in post-hatching material. The ossified splanchnocranial elements are then described, namely the palatoquadrate derivatives (quadrates and epipterygoids) and stapedes. Lastly, the ossified chondrocranial elements of the braincase (prootics, epiotics, basisphenoid, occipitals, and opisthotics) are described.

Table 1:
Variation in descriptive formats employed by different authors for describing squamate skulls.

Author	Format of description	
Wellborn (1933)	Skull	Basioccipital, exooccipital, supraoccipital, prootic, opisthotic, epiotic, parasphenoid, basisphenoid, orbitosphenoid, squamosal, supratemporal, parietal, frontal, nasal, premaxilla, maxilla, prefrontal, lacrimal, jugal, postfrontal, postorbital, quadrate, pterygoid, epipterygoid, ectopterygoid, palatine, vomer, septomaxilla, sclerotic ring, stapes and columella
	Mandible	Dentary, coronoid, surangulare, articulare, prearticulare, angulare, and splenial
Romer (1956)	Dermal roof shield	(1) Tooth-bearing elements: premaxilla and maxilla
		(2) Median roofing elements: nasal, frontal, parietal, and postparietal
		(3) Circumorbital elements: prefrontal, postfrontal, postorbital, jugal, lacrimal, and septomaxilla
		(4) Temporal series: intertemporal, supratemporal, and tabular
		(5) Cheek region: squamosal
	Palatal complex	(1) Marginal palatal elements: vomer, palatine, and ectopterygoid
		(2) Remaining palatal elements: pterygoid, epipterygoid, and quadrate
	Braincase	Parasphenoid, Basal tubera, basioccipital, exoccipital, supraoccipital, prootic, opisthotic, and basisphenoid
	Mandible	(1) Endochondral: articular
		(2) Dermal: dentary, splenial, angular, surangular, prearticular, and coronoid
Oelrich (1956)	Occipital segment	(1) Otico-occipital part: basisphenoid, basioccipital, prootic, exoccipitals, and supraoccipital
		(2) Orbitotemporal part: orbitosphenoid
	Maxillary segment	(1) Palate: pterygoid, ectopterygoid, vomer, palatine, premaxilla, and maxilla
		(2) Nasal capsule: prefrontal, lacrimal, and septomaxilla
		(3) Orbit: frontal, postfrontal, and jugal
		(4) Temporal region: parietal, supratemporal, postorbital, squamosal, quadrate, and epipterygoid
	Jaws	Articular, supra-angular, angular, splenial, dentary, and coronoid
Jollie (1960)	Skull	Basioccipital, exoccipital, supraoccipital, pro-otic, opisthotic, epiotic, parasphenoid, basisphenoid, orbitosphenoid, squamosal, supratemporal, parietal, frontal, nasal, premaxilla, maxilla, prefrontal, supraciliary, lacrimal, jugal, quadratojugal and intercalare, postfrontal, postorbital, quadrate, pterygoid, epipterygoid, ectopterygoid, palatine, vomer, septomaxilla, sclerotic ring, and stapes and columella

Table 1: Continued.

Author	Format of description	
	Mandible	Dentary, coronoid, supra-angular, articulare, prearticulare, angulare, and splenial
Kluge (1962)	Cranium	Premaxilla, maxilla, prefrontal, jugal, lacrimal, palatine, pterygoid, prevomer (vomer), septomaxilla, ectopterygoid, nasal, frontal, postfrontal, parietal, squamosal, epipterygoid, quadrate, sphenoid, basioccipital, prootic, opisthotic, exoccipitals, and supraoccipitals
	Lower jaw	Dentary, splenial, coronoid, surangular, angular, and articular
Daza *et al*. (2008)	Dermatocranium	Premaxilla, maxilla, nasal, prefrontal, postorbitofrontal, jugal, frontal, parietal, squamosal, septomaxilla, vomer, palatine, pterygoid, and ectopterygoid
	Splanchnocranium	Epipterygoid, quadrate, and stapes
	Neurocranium	Sphenoid, basioccipital, prootic, supraoccipital, and otooccipital
	The jaw	Dentary, coronoid, surangular, and compound bone (articular, prearticular and angular)
Evans (2008)	Major openings	Paired: exterrnal naris, orbit, upper and lower temporal fenestra, post-temporal fenestra, fenestra exochoanalis, suborbital fenestra, and sub-temporal fenestra Unpaired: interpterygoid vacuity and foramen magnum
	Skull-roofing bones	Nasal, frontal, and parietal
	Tooth-bearing bones of upper jaw	Premaxilla and maxilla
	Circumorbitals	Prefrontal, lacrimal, jugal, and postorbitofrontal
	Temporal bones	Squamosals and supratemporals
	Palatoquadrate derivatives	Quadrate and epipterygoid
	Palatal elements	Vomer, septomaxilla, palatine, pterygoid, and ectopterygoid
	Braincase	Prootic, epiotic, basispheenoid, occipitals, opisthotic, and stapes
	Lower jaw	Dentary, splenial, coronoid, angular, surangular, and articular

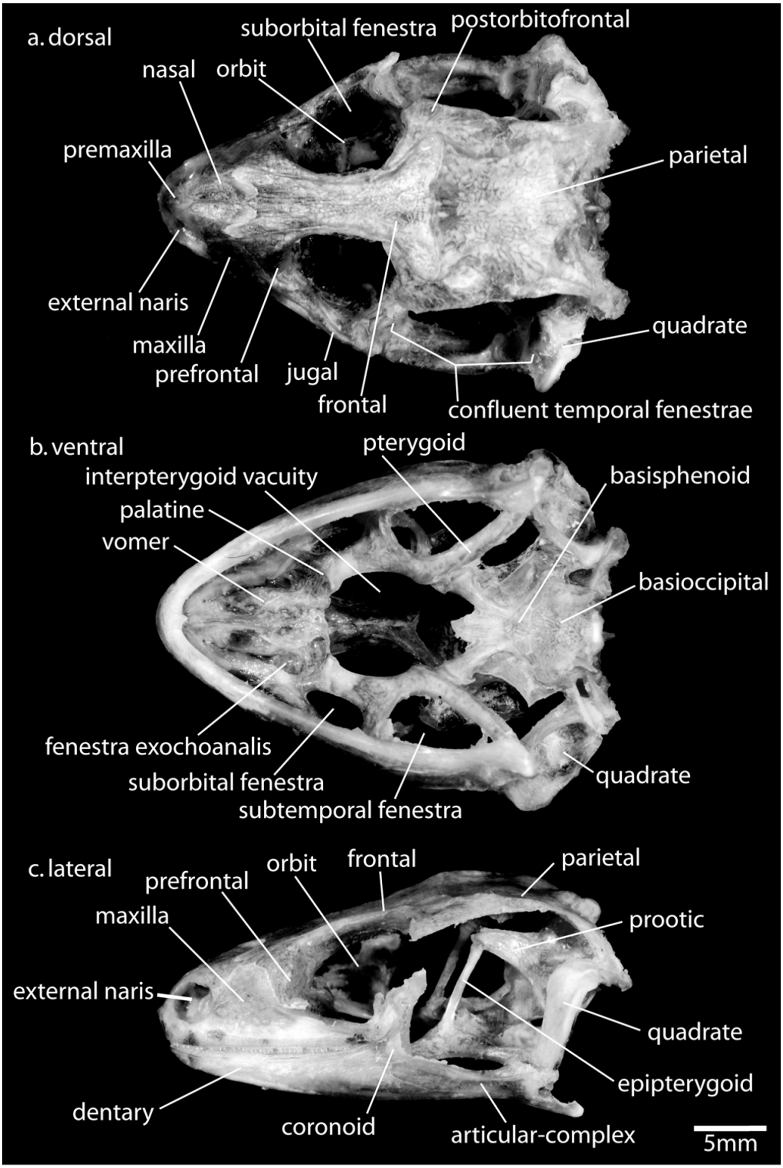

Figure 3: Skull and lower jaw of an adult *Eublepharis macularius* in three views.

Results

General features

The cranium of *E. macularius* is composed of seven unpaired and 21 paired elements, and the mandible is composed of seven paired elements, although some of these might be fused one to another with no trace of a suture. The overall shape of the skull in dorsal view is roughly that of an isosceles triangle (Fig. 3a) with the base represented by the occiput. In lateral view (Fig. 3c), the skull is depressed compared to that of many other lizards (such as *Lacerta*). Overall, when compared to the skull of other squamates, that of gekkotans exhibits a reduction in the number of elements and is generally paedomorphic (Rieppel 1992).

Openings of the skull

Paired openings of the skull

There are eight paired openings in the skull of *E. macularius* (Figs. 3–5) (exclusive of the foramina for nerves and blood vessels) that involve multiple elements in their boundaries. These are described here separately and are considered in greater detail than when they are mentioned in the descriptions of the individual elements that border them.

External naris (Apertura narium externa of Wellborn 1933) (Figs. 3a and c, 4a and c, and 5a)

This is oval in shape, faces dorsolaterally and slightly rostrally, and is bounded in almost equal proportion by three elements. The premaxilla delimits its anterior margin, extending as far dorsally as the curvature of its dorsorostral edge where it meets the nasal; the nasal bounds the dorsal and dorsocaudal edges; the maxilla constitutes the remainder of the border, occupying the remaining caudal and most of the ventral border. The septomaxilla (Fig. 5a and b) forms the floor of the nasal meatus.

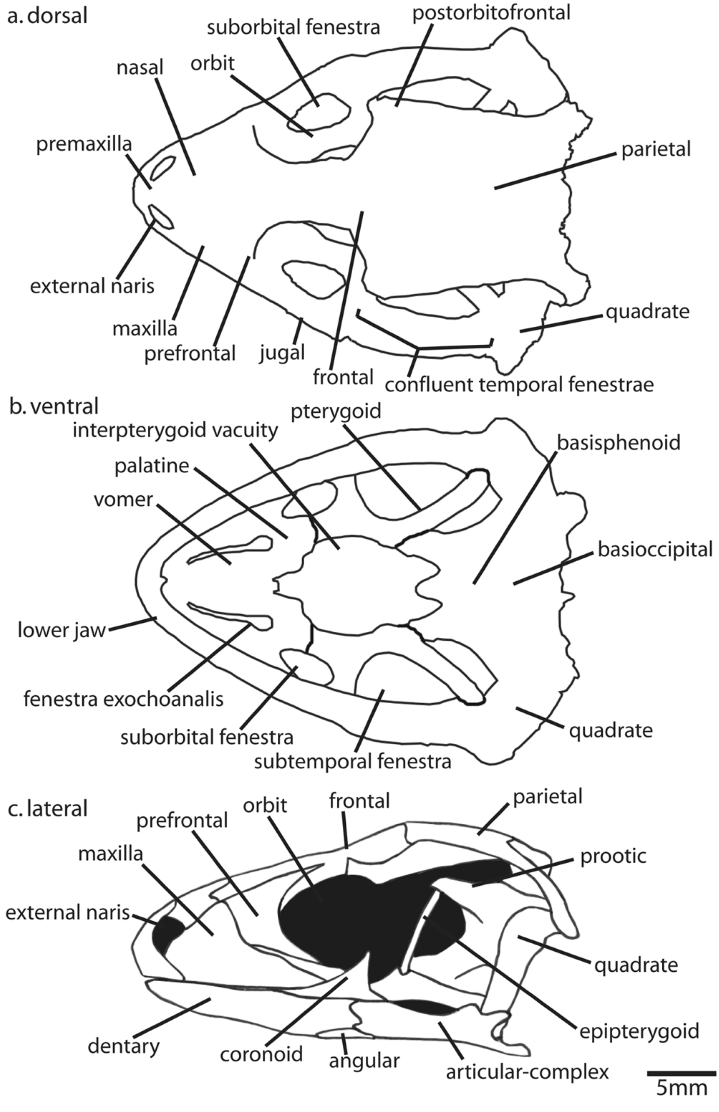

Figure 4:
Diagrammatic representation of the skull and lower jaw of an adult *Eublepharis macularius* in three views.

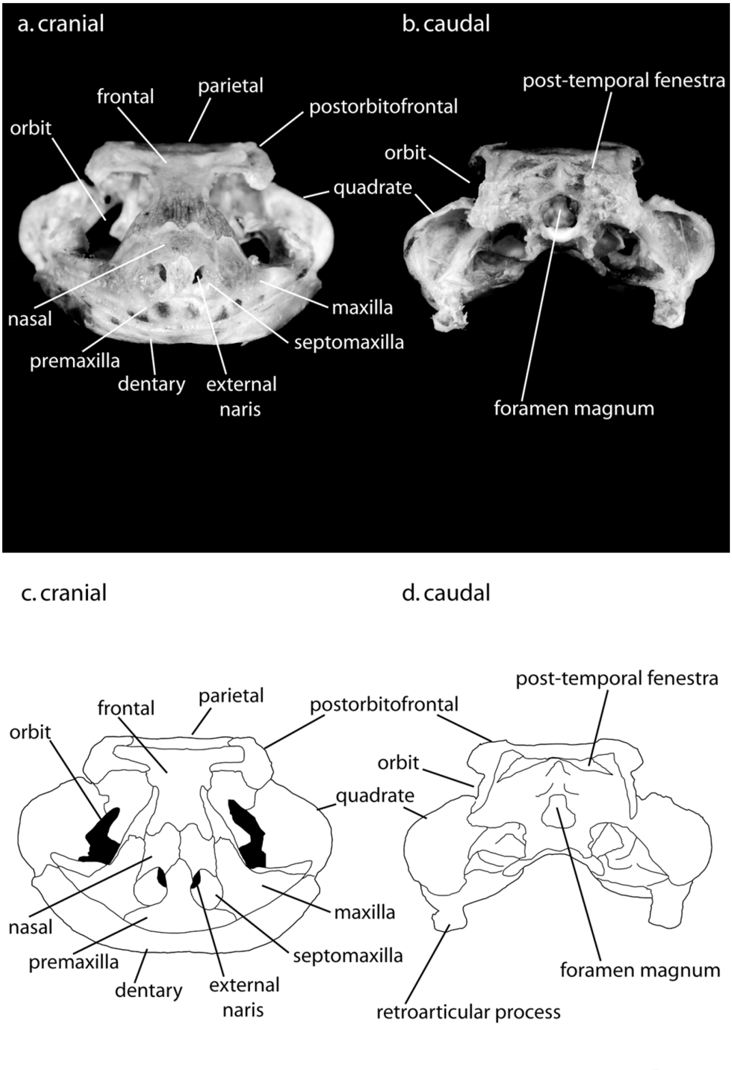

Figure 5:
a and b Adult skull and lower jaw of an adult *Eublepharis macularius* in two views with c and d as complimentary diagramatic representations.

Orbit (Figs. 3a and c and 5a and b)

This is a large opening that is approximately equal in anteroposterior length to that of the preorbital portion of the snout. As for all geckos, the postorbital bar is reduced and the orbit is thus confluent with both the upper and lower temporal fenestrae. The orbit is bounded rostrally by the prefrontal, dorsomedially by the frontal, and caudodorsally by the postorbitofrontal. The ventral margin is made up almost exclusively by the jugal, with a minor contribution from the maxilla anteroventrally at the orbital boundary of the lacrimal duct.

Upper and lower temporal fenestrae (Fig. 3a)

These openings are confluent with the orbit as well as with one another as a result of reduction and loss of various temporal elements (see below). Unlike the condition in *Sphenodon* and basal lepidosaurs, the upper temporal fenestra is partially confluent with the lower temporal fenestra because the postorbital and the squamosal do not contact one another. The lower temporal arch is also incomplete, in part, because of the relative reduction in size of the jugal and squamosal (compared to the condition in basal lepidosaurs) and, in part, because of the absence of the quadratojugal. These modifications result in an enlarged temporal vacuity that is bounded rostrodorsally by the postorbitofrontal, dorsally by the parietal, caudodorsally by the squamosal, caudally by the quadrate, and that is open ventrally.

Post-temporal fenestra (Fig. 5b)

This is a narrow, slit-like opening that faces caudally and is obliquely oriented from dorsomedial to ventrolateral. Its dorsal margin is bounded entirely by the parietal, whereas its ventral border is formed by the supraoccipital medially and the otooccipital laterally.

Fenestra exochoanalis (Fig. 3b)

E. macularius exhibits the palaeochoanate condition of the fenestra exochoanalis, characterised by confluence of the internal naris and the opening of the vomeronasal organ. Widest caudally, the choana narrows abruptly to a slit-like opening that curves medially at its rostral-most end. The lateral border is made up of the maxilla, the medial border by the vomer, and the caudal border by the palatine.

Suborbital fenestra (Fig. 3a and b)

This is an oblong opening, wider caudally than rostrally. It is less than half the length of the orbit, is positioned equidistant between the rostral and caudal borders of the orbit, and is bordered caudomedially by the pterygoid, rostromedially by the palatine, and laterally by the ectopterygoid.

Subtemporal fenestra (Fig. 3b)

This is a large oblong opening that is roughly the same shape as the suborbital fenestra, but about twice its size. It is bounded rostrolaterally by the ectopterygoid, rostromedially and medially by the pterygoid, and caudolaterally by the quadrate. Its lateral border is bounded by the lower jaw when the mouth is closed.

Unpaired openings in the skull

There are two unpaired openings (Figs. 3 and 5) that involve multiple elements in their boundary, the interpterygoid vacuity (Fig. 3b) and the foramen magnum (Fig. 5b). The interpterygoid vacuity is a large, roughly elliptical opening that occupies the majority of the central area of the roof of the mouth. It is roughly one-third the length of the entire skull. It is bounded caudally by the basisphenoid, laterally by the pterygoids and palatines, and rostrally by the caudomedial margins of the vomers. The foramen magnum is somewhat pentagonal in shape, with rounded corners and an apex oriented dorsally. This opening is bounded by the basioccipital ventrally, the exoccipitals laterally, and the supraoccipital dorsally.

Individual skull elements: the dermatocranium

Skull-roofing bones

Nasal (paired) (Fig. 6) The nasals are paired, unfused elements and are anvil-shaped in dorsal view. The main body of each is sub-rectangular and four processes project from it: two rostrally (one larger and medial and one smaller and lateral) and two caudally (again, one larger and medial and one smaller and lateral). The nasal forms the rostral part of the roof of the snout and the two rostrally-projecting processes form the dorsal and dorsolateral border of the external naris. The medial processes are flat in dorsal view,

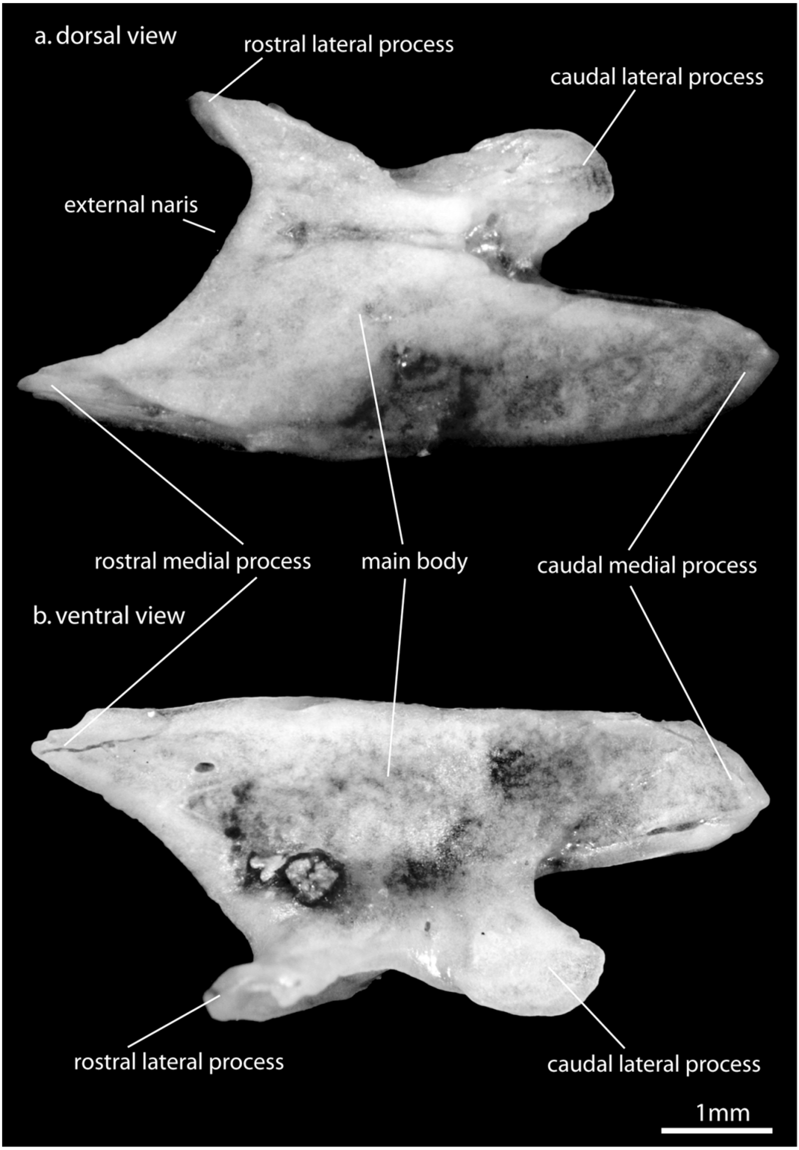

Figure 6:
Nasal (right) of an adult *Eublepharis macularius* in two views.

whereas both lateral processes and the lateral edge of the nasal curve slightly ventrally as they extend laterally. The two nasals abut each other in the sagittal plane for most of their length by way of a slight alternating tongue-and-groove articulation on the rostral half and a butt-joint on the caudal half of the articulation. The nasals are, however, separated both rostrally and caudally along the midline by the intervening nasal process of the premaxilla, which forms a short wedge between the nasals at their rostral margin, as well as by the median rostral projection of the frontal at their caudal margin. Between the anterior medial and anterior lateral projections of the frontal is a shelf that projects ventral to the caudal medial projection of the nasal, forming an overlapping scarf joint between these two elements. The caudal edge of the caudal lateral process is subsumed beneath an overlapping process of the anterior lateral process of the frontal, resulting in an irregular scarf joint.

Caudolaterally, the nasal contacts the anterior lateral process of the frontal, and, laterally, the facial process of the maxilla. The lateral surface of the nasal is slightly indented, with the apex of the indentation lying at about the midpoint of the length of the lateral border. This indentation receives the apex of the ascending facial process of the maxilla. The lateral edge of the rostral lateral process of the nasal is grooved to receive the rostral edge of the facial process of the maxilla. The lateral edge of the caudal lateral process of the nasal is slightly scalloped and fits beneath the caudal edge of the facial process of the maxilla, forming an irregular scarf joint.

Frontal (unpaired) (Fig. 7) The single, median frontal is a relatively large cranial bone. It has an hourglass shape in dorsal and ventral aspect (Fig. 7a and b) and forms the roof of the skull between the dorsal border of the orbits (Jollie 1960). Anteriorly, it is drawn out into three processes, one median and two lateral. The midline anterior median process (Fig. 5a) intrudes slightly between the caudal extremes of the medial borders of the nasals, separating them for a short distance. Laterally on each side is a strong, wedge-shaped anterior lateral process (Fig. 5a) that borders the nasal on its caudal aspect and just makes contact with the maxilla on the caudolateral aspect of the facial process of the latter. This contact precludes contact between the nasal and prefrontal. Caudal to the anterior lateral processes of the frontal, the prefrontals border the lateral edges of the frontal for half the length of the orbital opening, articulating with the frontal for one-third of its length along its rostral-most dorsolateral edge by a shallow tongue-and-groove joint. The

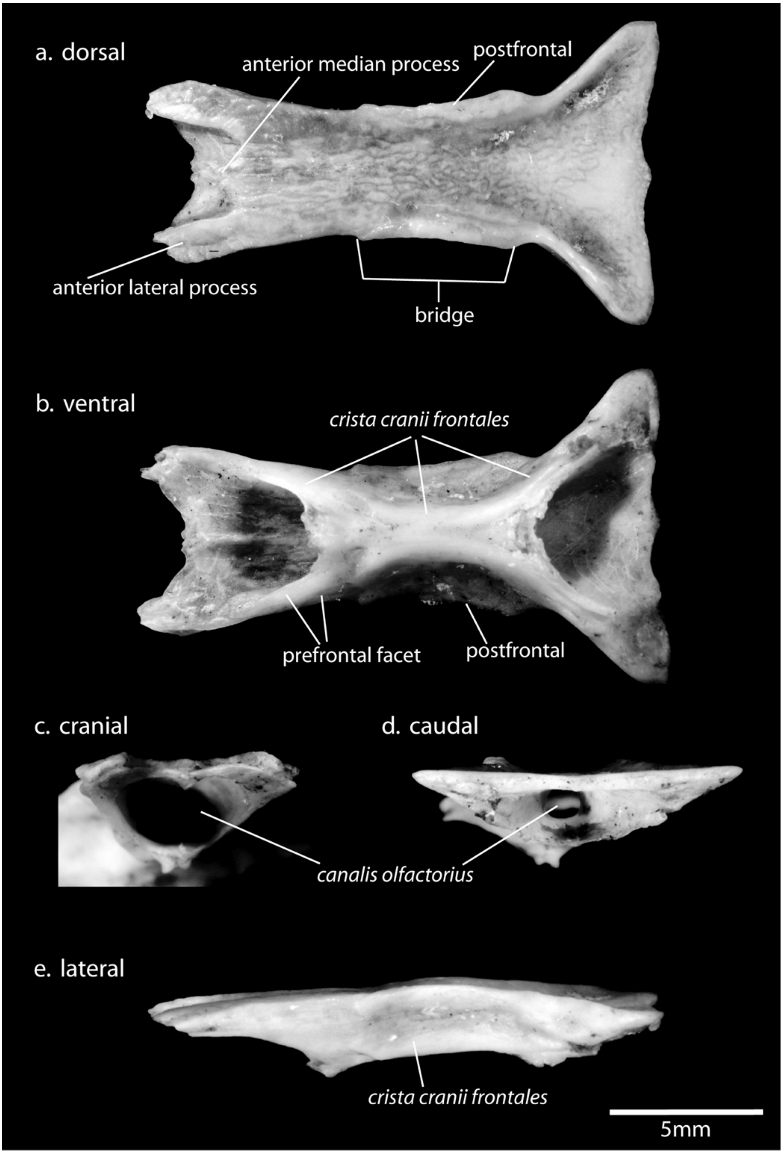

Figure 7:
Frontal of an adult *Eublepharis macularius* in five views and postfrontal in two views.

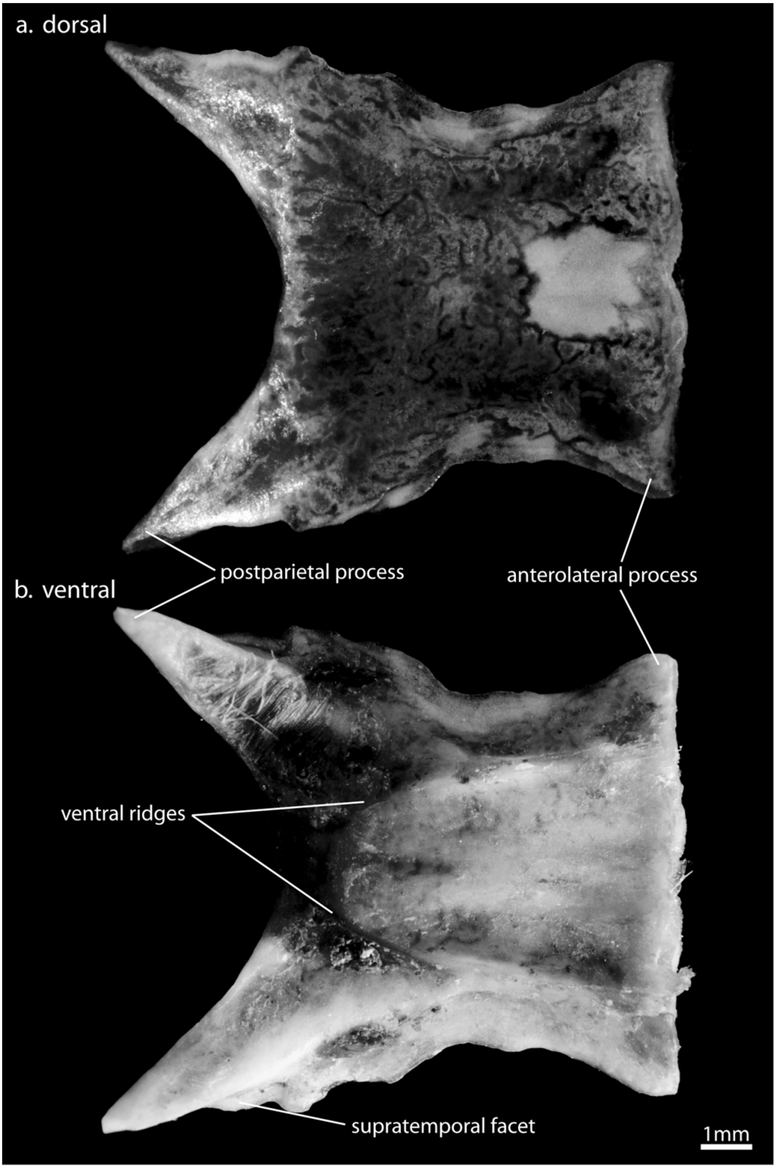

Figure 8:
Parietal of an adult *Eublepharis macularius* in two views.

entire caudal border of the frontal abuts the rostral border of the parietal via a shallow tongue-and-groove joint. The frontal achieves its greatest width along this caudal edge. Laterally, the suture between the frontal and parietal is bounded by the postorbital (Rieppel 1984), which extends rostrally along the dorsolateral-most edge of the frontal, angling medially to the caudal portion of the bridge of the frontal. There are two ventromedially directed descending processes that originate along the ventrolateral edge of the frontal (Fig. 7b and e; = the crista cranii frontales of Wellborn 1933). These run the entire length of the ventral surface, meeting and fusing for the middle one-third of their length to form a canal (Fig. 7c and d; = the canalis olfactorius of Wellborn 1933) through which the olfactory tracts pass. Caudally, the canal is circular in cross section (Fig. 7d), but its rostral opening is weakly bipartite (Fig. 7c). The ventral and lateral surfaces of the anterior unfused portion of the crista cranii frontales (the prefrontal facets; Fig. 7b) abut the medial edge of the prefrontal.

Parietal (unpaired) (Fig. 8) This is a single, large, roughly square bone from which two long, ventrolaterally tapering, caudally directed postparietal processes (Evans 2008) project from its caudolateral borders (Fig. 8a and b). The parietal constitutes a major portion of the roof of the cranium. Its lateral edges are slightly concave ventrally (Fig. 8b) and are relatively thin dorsoventrally along their dorsolateral edges. They thicken towards the ventromedial edge. Medial to these lateral shelves, the middle portion is about twice as thick as the lateral edges.

The postparietal processes (Fig. 8a and b) curve progressively ventrally as they extend caudally, ultimately contacting the squamosals caudolaterally. The supratemporals wedge between the squamosal and the parietal at the caudal-most lateral edges of the postparietal process.

Flush with its dorsal-most surface, the parietal articulates along the first third of its rostrolateral edge with the caudal portion of the postorbitofrontal via a shallow tongue-and-groove articulation, the tongue being borne by the parietal. The dorsal surface of the parietal is relatively flat, but its ventral surface bears two ridges that span from the rostral border one quarter of its width in from the lateral edge to the ventral midline of the caudal border, curving gently medially. The medial ventrocaudal edge articulates via a small notch (the pit for the processus ascendens; = the fossa parietalis of Romer 1956) with the supraoccipital.

Tooth-bearing bones of the upper jaw

Premaxilla (unpaired) (Fig. 9) The single premaxilla forms the rostral-most portion of the snout and constitutes the entire medial and rostral one-third of the entire ventral border of the external naris. In cranial view, this element has the form of an inverted T (Fig. 9a). There are two portions of the premaxilla: the alveolar lamina (= pars dentalis of Jollie 1960; Fig. 9a), which is the main body of the element and forms the rostral tip of the snout, and the ascending, nasal process (Fig. 9a–c and e). On the caudal surface, at the junction between the alveolar plate and the nasal process, is the palatal process (Fig. 9b), a caudally directed shelf that gives rise to three projections along its caudal-most edge. There is a single median, ventrally directed peg-like incisive process (or tubercle; = ventromedian spine of Wellborn 1933), and a lateral process (Romer 1956) on each posterolateral edge (Fig. 9b and d; Oelrich 1956). The latter is a triangular projection with its apex directed caudolaterally and slightly ventrally, and the dorsal surface of which is curved convexly.

Dorsocaudally, the premaxilla contacts the paired nasals via its nasal process, intervening between them at their rostromedial extremity via a triangular, wedge-shaped, distal extremity that curves caudally as it ascends. This ex tremity is slightly bevelled on the caudolateral edges of its dorsal-most portion, yielding scarf joints between it and the underlying processes of the nasals, which it overlaps. The caudal aspect of the nasal process bears a septonasal crest (Fig. 9b and c) that ascends to half of its height and bears a fissure along the median line for the dorsal-most three quarters of its length, possibly representing incomplete fusion of the two primitively paired premaxillae. This fissure continues beyond the dorsal tip of the septonasal crest as far as the dorsal-most tip of the caudal surface of the nasal process.

The rostroventral edge of the body of the premaxilla curves gently caudolaterally from the midline (Fig. 9d and e). The entire lateral edge of the alveolar plate of the premaxilla curves medially as it ascends, contacting the maxilla along this entire edge. Ventrolaterally, a vertical section ascends one-third of the height of the alveolar plate and articulates via a butt joint with the corresponding surface on the maxilla. The lateral process of the premaxilla interdigitates between the two rostromedially oriented premaxillary processes of the maxilla (one labial and one lingual; see below) that demarcate the lateral and medial aspects, respectively, of the lateral process of the premaxilla, partially overlapping its downwardly curved outer edges.

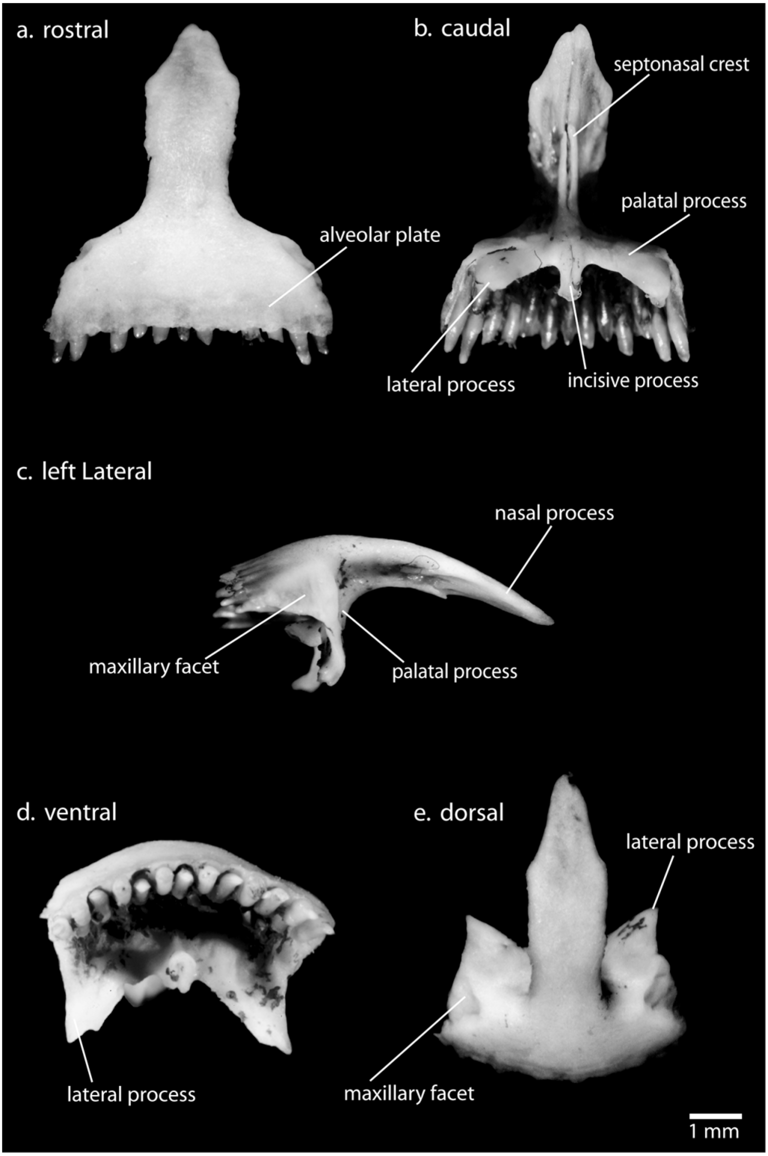

Figure 9:
Premaxilla of an adult *Eublepharis macularius* in five views.

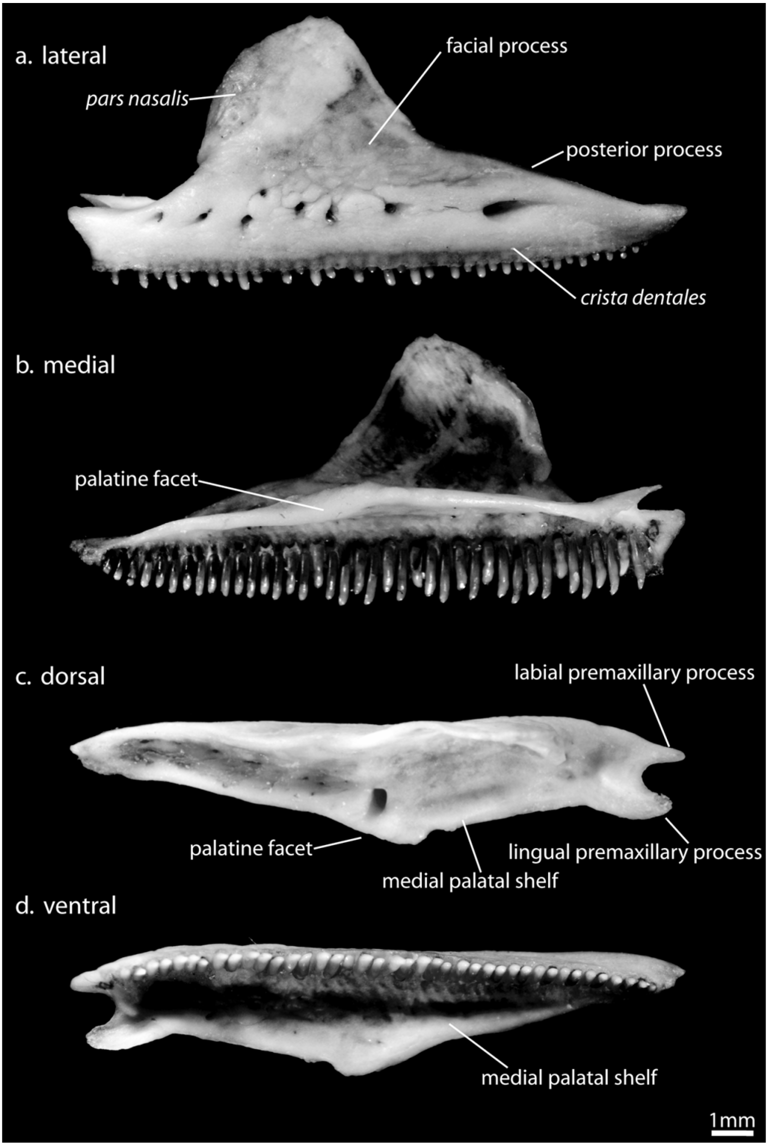

Figure 10:
Left maxilla of an adult *Eublepharis macularius* in four views.

The palatal process (Fig. 9b) of the alveolar plate of the premaxilla abuts the vomers only along its caudomedial-most margin via the peg-like, incisive process that articulates via its caudal-most surface with short corresponding vertically oriented flanges of the rostromedial-most aspects of the vomers. Thirteen pleurodont teeth (Fig. 9a–d) are carried by the ventral half of the caudal aspect of the alveolar plate (= the pars dentalis of Kluge 1962) of the premaxilla.

Maxilla (paired) (Fig. 10) The maxilla is the main tooth-bearing bone of the skull, forming a large portion of the side wall of the snout. It contributes the caudolateral and the caudal one-third of the ventral border of the external naris.

The maxilla consists of two main regions, a vertically oriented lateral side wall (the facial process) and a medially directed horizontal shelf (the medial palatal shelf; = lamina horizontalis of Wellborn 1933), that run the full length of the element. The facial process is roughly triangular in lateral view, with a narrow, caudally-projecting, posterior process and is comprises the ascending pars nasalis (Kluge 1962) and the tooth bearing crista dentales (Wellborn 1933; cf. pars dentalis of Kluge 1962). As the pars nasalis ascends, it curves slightly medially and contacts the nasals dorsorostrally, articulating via its leading dorsorostral edge, which inserts into an adjacent groove on the nasal. Dorsally and along its caudal aspect, the pars nasalis meets the prefrontal in a scarf joint along the entire length of the contact. Dentition is pleurodont and ca. 41 teeth occur in a single row along the lingual surface of the crista dentales. The teeth are straight for four-fifths of their length with the distal tips curved slightly caudally.

At one-third of the height of the lateral side wall (pars nasalis plus crista dentales), as measured from its ventral edge, the medial palatal shelf extends the entire length of the maxilla and contributes to the lateral portion of the roof of the mouth. This shelf articulates rostrally with the premaxilla via the prong-like labial and lingual premaxillary processes that curve in a rostromedial direction, surrounding and slightly overlapping the lateral process of the premaxilla. The medial palatal shelf is separated from the vomer and palatine for most of its length by the choana; however, it does contact the vomer and the septomaxilla at its rostromedial-most edge along the caudal edge of the lingual premaxillary process. The vomer makes contact ventromedially with the lingual premaxillary process and the septomaxilla contacts the lingual premaxillary process dorsomedially. Contact is made with the palatine starting at the widest point of the medial palatal shelf along its caudomedial-most and dorsomedial aspects. The caudomedial edge and caudodorsal surface of the medial palatal shelf of the maxilla contacts the ectopterygoid on the lateral-most and ventrolateral surface of the latter via a butt joint. The posterior half of the medial palatal shelf of the maxilla is bounded dorsally by the lacrimal and the jugal, which lie in the partial trough created by the medial palatal shelf and the pars nasalis.

Circumorbital bones

Prefrontal (paired) (Fig. 11) The prefrontal is a wide, wedge/tent-shaped bone that forms the rostrodorsal and rostral borders of the orbit. It is crescent shaped in articulated lateral view and consists of two main components, a lateral lamina (the lateral side wall) that contributes, in part, to the caudal portion of the side wall of the snout, and, at a right angle to this, facing caudally, a concave curved sheet (orbitonasal flange) that forms the rostral border of the orbit. The ventral caudolateral corner of the prefrontal is drawn out into a pair of ventrocaudally directed processes, the lateral and medial infraorbital processes (Kluge 1962) that contribute to the boundary of the medial, rostral, and lateral margins of the lacrimal foramen.

The dorsocaudal-most edge of the prefrontal articulates via an irregular contour along a scarf joint with the rostral-most edge of the crista cranii of the frontal. Medial to this, there is a prong-shaped process that is directed medially and articulates with the corresponding prong of the other prefrontal. In the articulated skull, the lateral wall is only partially visible because its rostral-most third underlies the pars nasalis of the maxilla, which it contacts via a lap joint. It contacts the frontal dorsally along the dorsal edge of the lateral sheet and articulates via a scarf joint with the rostrolateral dorsal edge of the frontal. It barely contacts the anteromedial half of the lacrimal via the ventrolateral edge of the medial infraorbital processes, whereas, ventrally and medial to the point of lacrimal contact, it meets the rostrodorsal margin of the body of the palatine along almost the entire width of the latter. The lateral side wall and the orbitonasal flange help enclose the nasal cavity by contributing to its lateral and caudal walls, respectively.

Lacrimal (paired) (Fig. 12) The lacrimal is a small triangular bone when viewed in articulated dorsal aspect. It is nested between the lacrimal foramen rostrally (of which it forms the entire caudal border and variably part or none

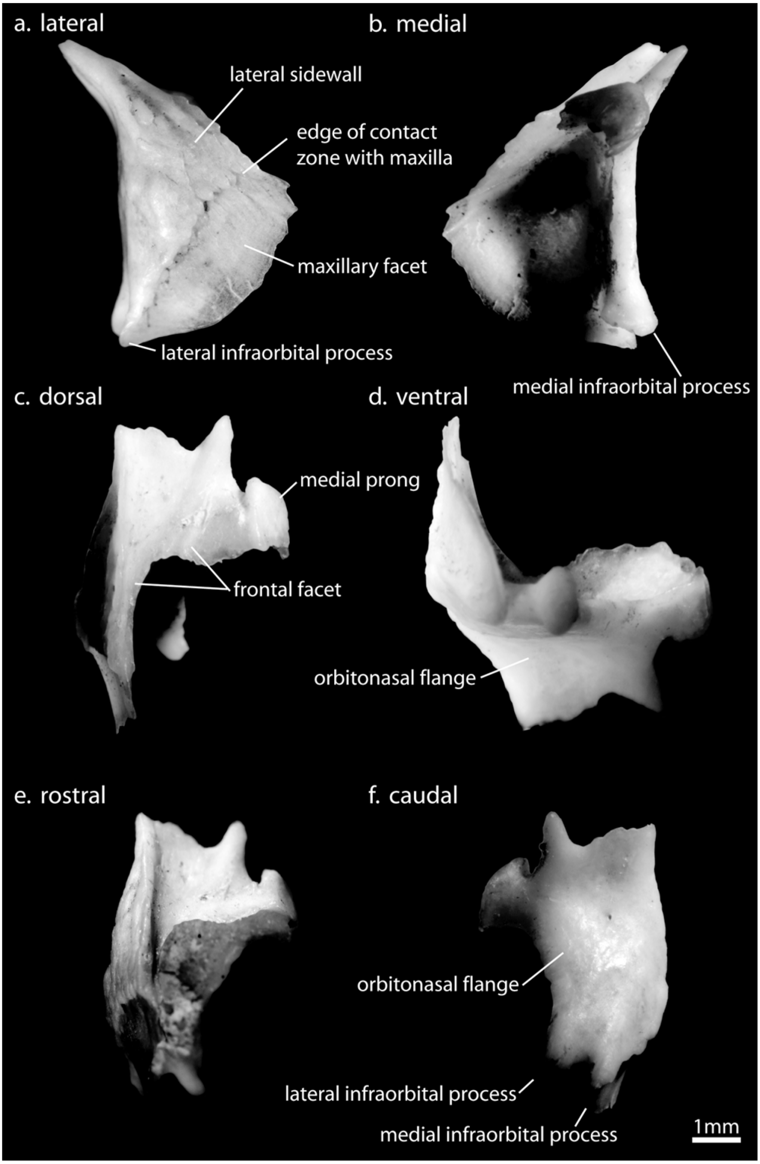

Figure 11:
Right prefrontal of an adult *Eublepharis macularius* in six views.

of its medial border), the jugal laterally, the prefrontal rostromedially and the anterior tip of the ectopterygoid caudomedially. Although small, the lacrimal has a complex shape, comprising a sub-square, flat sheet of bone that is bent at 90° along its horizontal midline. The rostral edge angles from dorsorostral to ventrocaudal, whereas the dorsal and ventral edges are roughly parallel to one another. The caudal edge is bifurcated into two scallops, the lateral surfaces of which articulate with the craniomedial edge of the jugal. The craniomedial edge of the lacrimal contacts the prefrontal.

Jugal (paired) (Fig. 13) The jugal is a slender splint of bone forming the lower margin of the orbit. As in all gekkotans, the maxillary process is the only part represented, with the postorbital process being absent and no longer contacting the postfrontal. In dorsal view (Fig. 13a), the jugal is a long thin element that deflects medially, both cranially and caudally. When the skull is viewed laterally, the jugal is visible for its entire length, at least in part, but the majority of its cranial half is obscured by the maxilla. The cranial edge is scalloped and its medial surface is concave, creating a vertically-oriented flange where it articulates with the lacrimal. The cranial three quarters of the jugal is laterally compressed and carries a groove along its lateral edge for articulation with the dorsomedial edge of the corresponding part of the posterior process of the maxilla. The caudal-most quarter of the jugal is somewhat rounded in cross section. The middle third of the length of the ventral surface is flattened for the entire width of the element, creating a triangular cross section in this part of the jugal. The jugal lies dorsal to, and contacts, the medial palatal shelf of the maxilla. Rostromedially, the jugal is bounded by the lacrimal and it variably contributes to the lateral wall of the lacrimal foramen. Progressing caudally, the jugal curves up and over the posterior process of the maxilla and sits dorsal to it. Farther caudally, it projects slightly beyond the maxilla and becomes the caudal-most element of the lower margin of the orbit. Medially, the jugal contacts the ectopterygoid for almost the entirety of its own length.

Postfrontal (paired) (Fig. 7) This is a thin, curved, splinter-like bone fused to the bridge of the frontal on its dorsolateral-most edges and is delineated from the frontal by a faint sutural boundary (Wise & Russell 2010). These elements stand out from the dorsolateral edges of the frontal and demarcate the rostral and caudal extent of the bridge of the frontal.

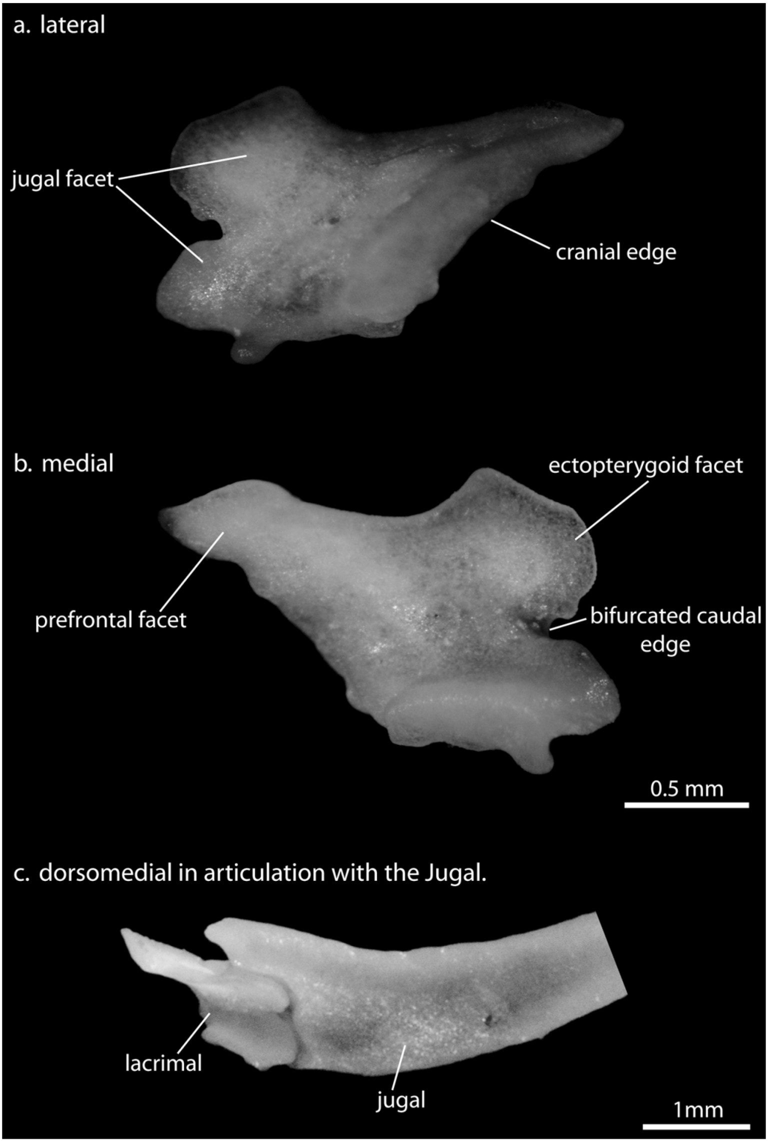

Figure 12:
Right lacrimal of an adult *Eublepharis macularius* in three views.

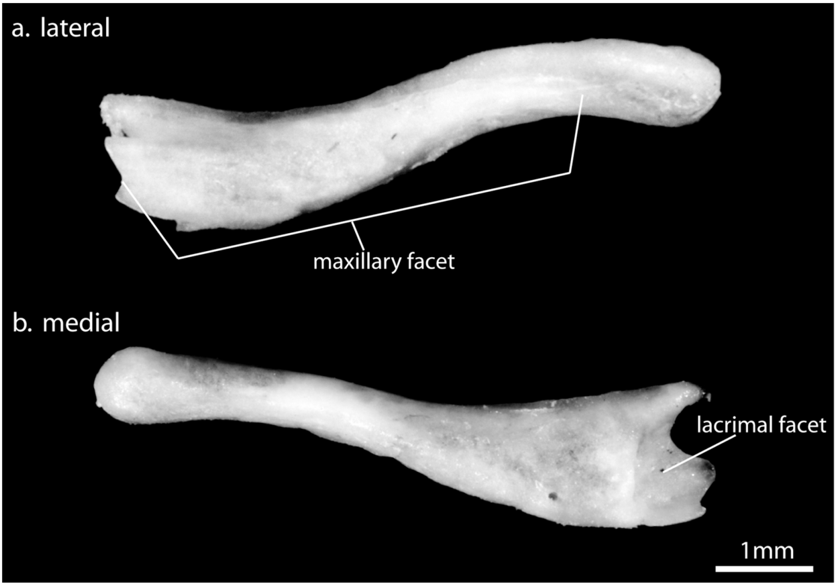

Figure 13:
Left jugal of an adult *Eublepharis macularius* in two views.

Postorbital (paired) (Fig. 14) This is a chevron-shaped bone when viewed in dorsal aspect. The apex of the chevron is positioned midway along the length of the postorbital and is oriented laterally. The postorbital forms the caudodorsal bony margin of the orbit and is believed to be a composite that arises from two centres of ossification representing the ancestral postorbital and the postfrontal (Rieppel 1984) because of the apparent lack of these two discrete elements. The thin lamina of the postorbital lies laterally to both the caudal part of the frontal and the rostral-most part of the parietal. The medial edge of the apex of the postorbital bounds the lateral edge of the frontoparietal suture. The rostrolateral corner of the postorbital curves ventrally, dipping slightly below the plane of the dorsal aspect of the frontal. A small shelf projects medially from the middle third of the ventromedial edge of the postorbital and underlies, and helps form the articulation with, the frontal and the parietal via a lap joint. The postorbital is hollow and there is an irregularly-shaped foramen on its craniolateral edge, just beyond the apex of the chevron.

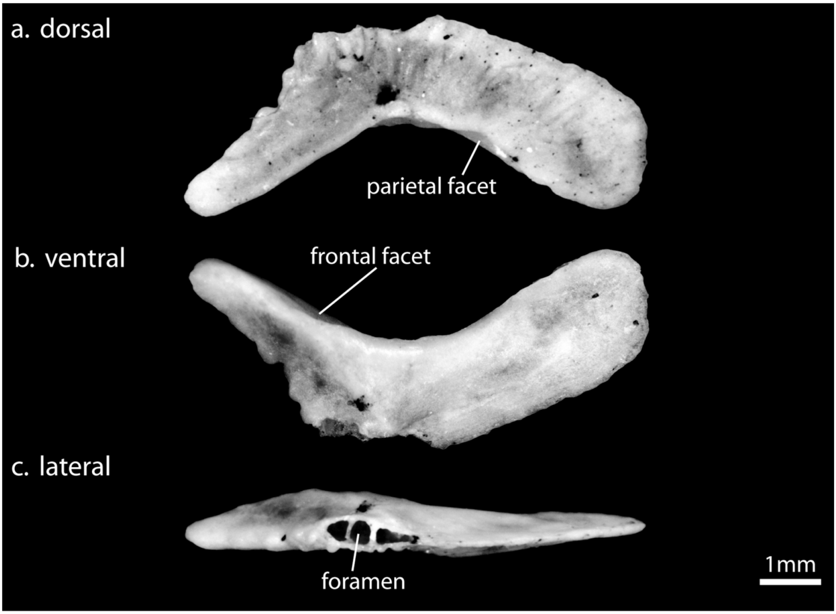

Figure 14:
Right postorbital of an adult *Eublepharis macularius* in three views.

Temporal bones

The squamosal and the supratemporal (Figs. 15 and 16) are both paired elements and, as previously mentioned, are difficult to distinguish in an intact skull, not only from one another, but also from the postparietal process of the parietal. Both of these elements are similar in shape, although the rostral portion of the squamosal is about twice as long as its counterpart on the supratemporal. Closely apposed to one another, these elements articulate with the quadrate via their posterior processes (Oelrich 1956). The posterior processes of the squamosal and the supratemporal each contribute equally to a cotyle. Along with the paraoccipital process of the otooccipital, these posterior processes receive the cephalic condyle of the quadrate.

Squamosals (paired) (Fig. 15) The shape of the squamosal is elongate, slender, and slightly curved, with a cotyle at its caudal end. The apex of the chevron points dorsally and the bone is very thin mediolaterally. In its articulated state, the dorsal surface of the rostral half of the squamosal is oriented horizontally along its long axis and lies flush with the ventrolateral-most edge of the postparietal process of the parietal. The rostral-most quarter of the squamosal is twisted and, relative to its caudal portion, its medial side faces dorsally to meet the ventral surface of the postparietal process of the parietal. The caudal half of the squamosal angles caudoventrally at about 45º below the horizontal to meet the cephalic condyle of the quadrate.

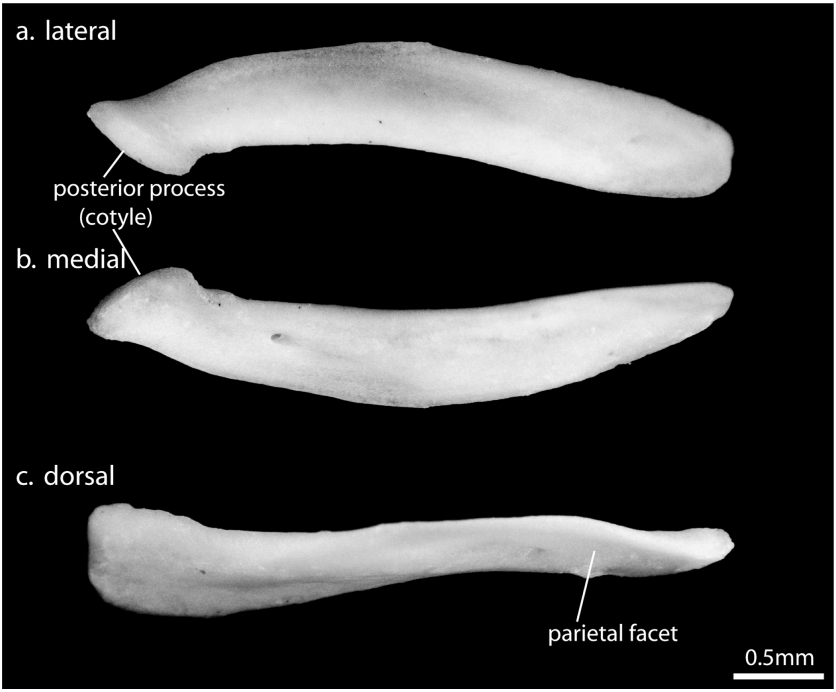

Figure 15:
Left squamosal of an adult *Eublepharis macularius* in three views.

Supratemporal (paired) (Fig. 16) In the articulated state, the supratemporal lies medial to the squamosal and is very similar to it in overall morphology, but has a much shorter rostral process (Fig. 16). The entire lateral surface of the supratemporal contacts the apposing medial surface of the squamosal, with alignment starting from the cotyles at their caudal ends. The caudoventrally directed posterior process makes tight contact on its medial surface with the paroccipital process of the otooccipital (a composite bone formed from the fused exoccipital and opisthotic) via a ligament.

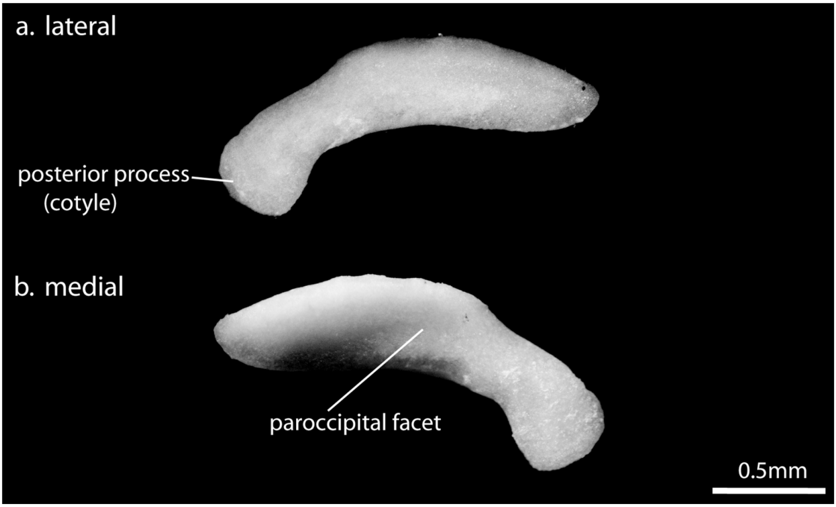

Figure 16:
Left supratemporal of an adult *Eublepharis macularius* in two views.

Palatal elements

Vomer (paired) (Fig. 17) In ventral view, the vomer resembles a thin, elongate parallelogram with a notch in its caudal end (Fig. 17a and b). The rostral end of the vomer is deflected laterally and the caudal end is deflected medially. The vomers form the anteromedial portion of the palate, adjoining one other along the median line. Each vomer contacts the premaxilla rostromedially, the maxilla rostrolaterally, and the septomaxilla dorsally. The lateral edge of each vomer forms the medial border of the fenestra exochoanalis. Posterolaterally, each vomer contacts the palatine.

Each vomer consists of three portions, a rod and two thin laminae. The rod lies horizontally and is oriented rostrocaudally. Extending laterally from the rod along its entire length is a thin, horizontal lamina that is deflected slightly ventrally at both its rostral and caudal ends. The dorsal surface of the horizontal lamina bears two shallow depressions separated by an elevated area of bone, a smaller, round vomeronasal fossa rostrally and a larger, ellipsoid

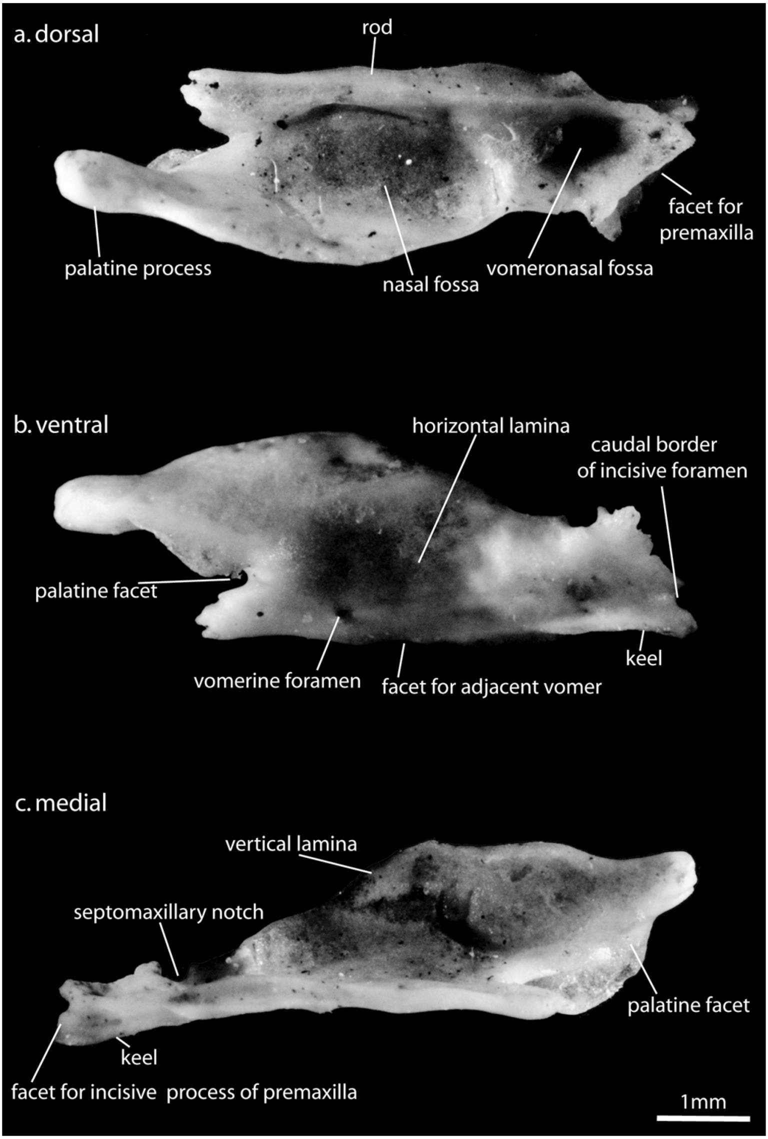

Figure 17:
Right vomer of an adult *Eublepharis macularius* in three views.

nasal fossa caudally (Daza 2005). The lateral edge of the horizontal lamina curves dorsally, forming a second, vertically oriented lamina. Starting flush with the horizontal lamina at its rostral end, the vertical lamina ascends as it progresses caudally until, at the mid-length of the vomer, the dorsal edge ofthe vertical lamina levels out in the horizontal plane and then proceeds caudally. The vertical lamina is convex laterally. There is a U-shaped septomaxillary notch (Oelrich 1956) in the dorsorostral edge of the vertical lamina.

The dorsocaudal tip of the vomer forms a caudally directed palatine process, the medial surface of which receives the lateral edge of the vomerine flange of the palatine. The dorsorostral edge of the horizontal lamina is grooved, with this recess receiving the medial edge of the maxillary process of the premaxilla.

The medial edge of the rostral end of the vomer is keeled. The keel ascends caudally at a shallow angle to become flush with the ventral surface of the rod at a point one-fifth of the length of the rod from its rostral end. The anterior process (Evans 2008) of the keel abuts the incisive process of the premaxilla. Lateral to the anterior process, there is a small notch in the rostral edge of the horizontal lamina of the vomer and, together, they form the medial and caudal borders, respectively, of the incisive foramen.

The vomerine foramen (Oelrich 1956) lies just lateral to the rod at a point one-third of the length of the element from its caudal end.

Septomaxilla (paired) (Fig. 18) The septomaxilla is a complex element that roofs over Jacobson's organ and forms the floor of the external naris. It contacts the premaxilla anteriorly, the maxilla laterally, and the vomer ventrally.

The main body of the septomaxilla consists of a rectangular lamina, with the rostral third (anterior process) deflected ventrally at a right angle to the caudal two-thirds (posterior lamina), which lie in the horizontal plane; the anterior process abuts the palatal process of the premaxilla. The posterior lamina is convex dorsally, with the ventral concavity roofing over Jacobson's organ. There are three processes emanating from the body of the septomaxilla, a dorsally oriented eminence on the rostromedial edge of the posterior lamina and two caudal projections, a medial septal process and a lateral posterior process. The two caudal projections form the ventrolateral side walls of the nasal passage as far back as the rostral edge of the fenestra exochoanalis.

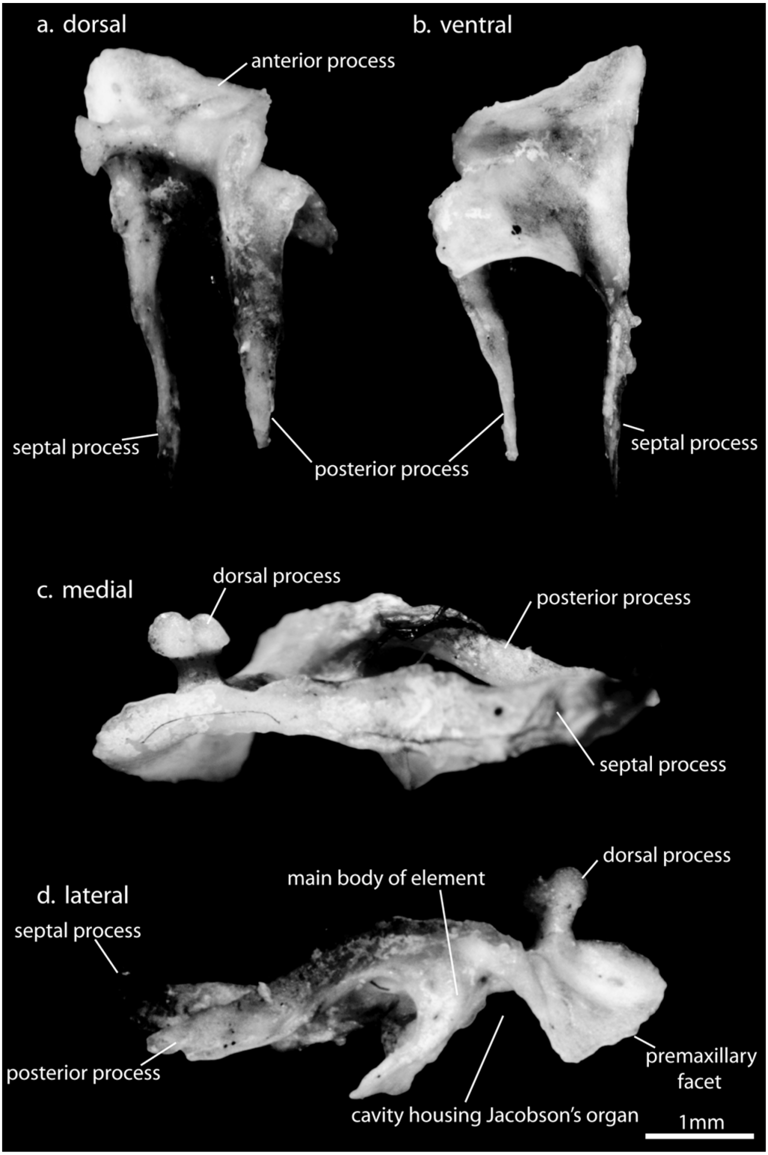

Figure 18:
Right septomaxilla of an adult *Eublepharis macularius* in four views.

When viewed laterally, the rostromedial, dorsal process originates as a narrow neck that flattens out laterally and forms two rounded lobes. These processes of the left and right septomaxilla are closely apposed to one another, separated only by the thin nasal septum.

The septal process originates on the caudomedial edge of the septomaxilla, curves sharply dorsally until it is vertically oriented, and then projects caudally as a shallow fin that is equal in length to the body of the septomaxilla. The posterior process originates as a narrow, lateral sheet projecting rostrally from the rostrolateral edge of the dorsal surface of the ventral process. From this point, it curves sharply dorsally and finally caudally, extending back fora distance almost equal in length to that of the septal process. This posterior process rests upon the dorsal surface of the medial palatal shelf of the maxilla.

Palatine (paired) (Fig. 19) This is a square sheet of bone that is slightly concave ventrally and presents two prominent anteriorly directed processes, the maxillary process and the vomerine flange. The palatine contributes to the middle region of the palate and forms the rostromedial border of the suborbital fenestra; the rostrolateral border of the interpterygoid vacuity; and the caudal, caudolateral, and caudomedial borders of the fenestra exochoanalis. It articulates with the pterygoid caudally and is sutured to the vomer rostromedially and the maxilla rostrolaterally.

The entire caudal border of the pterygoid process of the palatine forms a suture with the rostral end of the anterior process of the pterygoid. The lateral half of the caudal edge of the palatine forms a simple butt joint with the adjacent part of the pterygoid. The medial half, however, is eroded ventrally, forming a shelf that is underlain by the adjoining edge of the pterygoid and forming a lap joint.

The maxillary process of the palatine is situated on the rostrolateral edge of the bone; it curves ventrally and laterally and then projects rostromedially and caudolaterally. Both projections of the maxillary process narrow to spike-like points. The entire lateral edge of the maxillary process slots into the medial palatal shelf of the maxilla. This, along with the thickened lateral edge of the body of the palatine, forms a sturdy strut between the pterygoid and the maxilla.

The vomerine flange is a long, depressed, rod-like process that slots into the caudally oriented palatine notch of the vomer, forming a solid brace between the main bodies of these two elements.

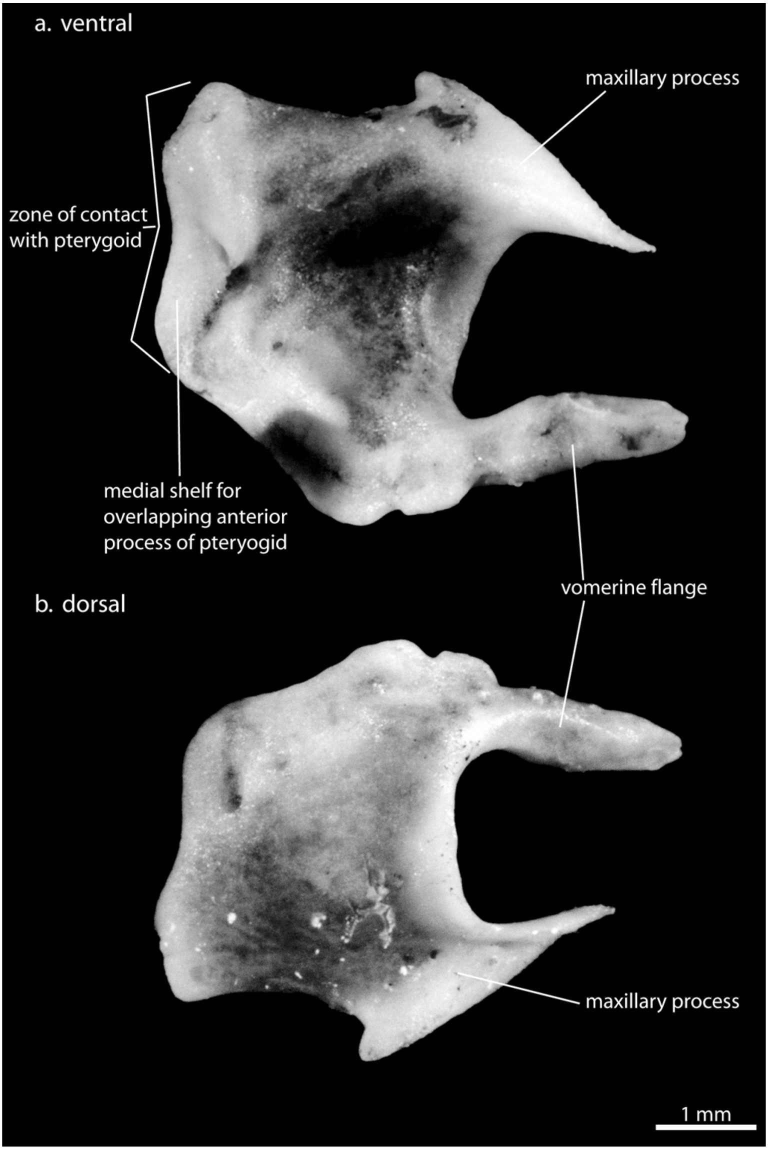

Figure 19:
Right palatine of an adult *Eublepharis macularius* in two views.

Pterygoid (paired) (Fig. 20) The pterygoid of *E. macularius* is tri-radiate, with a prominent, caudal “posterior” process (= processus quadratus of Wellborn 1933) and two smaller, less prominent extensions, an anterior process (= palatine process of Wellborn 1933) and a laterally directed pterygoid flange (= processus lateralis of Wellborn 1933, transverse process of Romer 1956, and ectopterygoid process of Oelrich 1956) (Fig. 20a, b and d).

The pterygoid comprises the posterior portion of the palate and contacts the palatine rostrally, the ectopterygoid rostrolaterally, the quadrate caudolaterally, and the basipterygoid process of the sphenoid medially. The pterygoid forms most of the lateral boundary of the interpterygoid vacuity and the entire medial border of the subtemporal fenestra. It is the longest individual skeletal element in the skull.

There are two topographical portions of the pterygoid, one rostral and one caudal; they are demarcated from one other by the fossa columellae (Fig. 20a), a deep, oval depression for receipt of the base of the epipterygoid. In dorsal view, the rostral half of the pterygoid comprises a triangular sheet of bone, with the base of the triangle forming the medial edge and the apex being oriented laterally (Fig. 20a). The caudal half of the pterygoid, the posterior process, is a long rod of bone that curves gently laterally as it progresses caudally. The distal half of the posterior process is compressed along its medial margin so that, in cross section, this portion of the bone takes the form of a capital T lying on its side. There are dorsal and ventral ridges on the lateral margin.

On the medial surface adjacent to the fossa collumellae, resides the deep, oblong pterygoid notch (Oelrich 1956). It is deepest rostrally, becoming shallower as it progresses caudally until it is flush with the medial side of the posterior process. In life, this fossa houses a cartilaginous pad that articulates with the cartilage of the basipterygoid process of the basisphenoid.

Rostral to the fossa collumellae and the pterygoid notch, the pterygoid is slightly constricted and then flares out, forming the anterior triangular lamina. Both medial and lateral edges are concave when viewed dorsally. Adorning the rostromedial corner of the anterior process is an ascending process that curves gently dorsally. Lateral to this, along the dorsorostral edge of the anterior process, is the shallow palatine fossa by which the pterygoid articulates with the palatine.

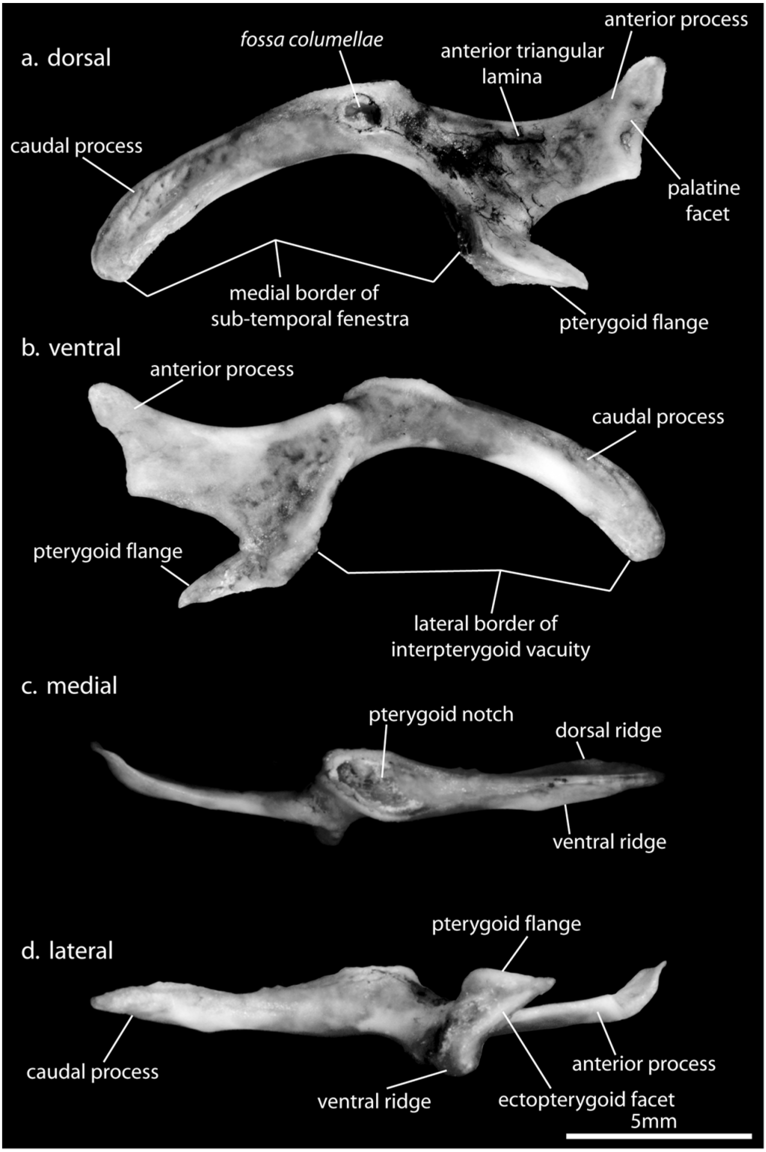

Figure 20:
Left pterygoid of an adult *Eublepharis macularius* in four views.

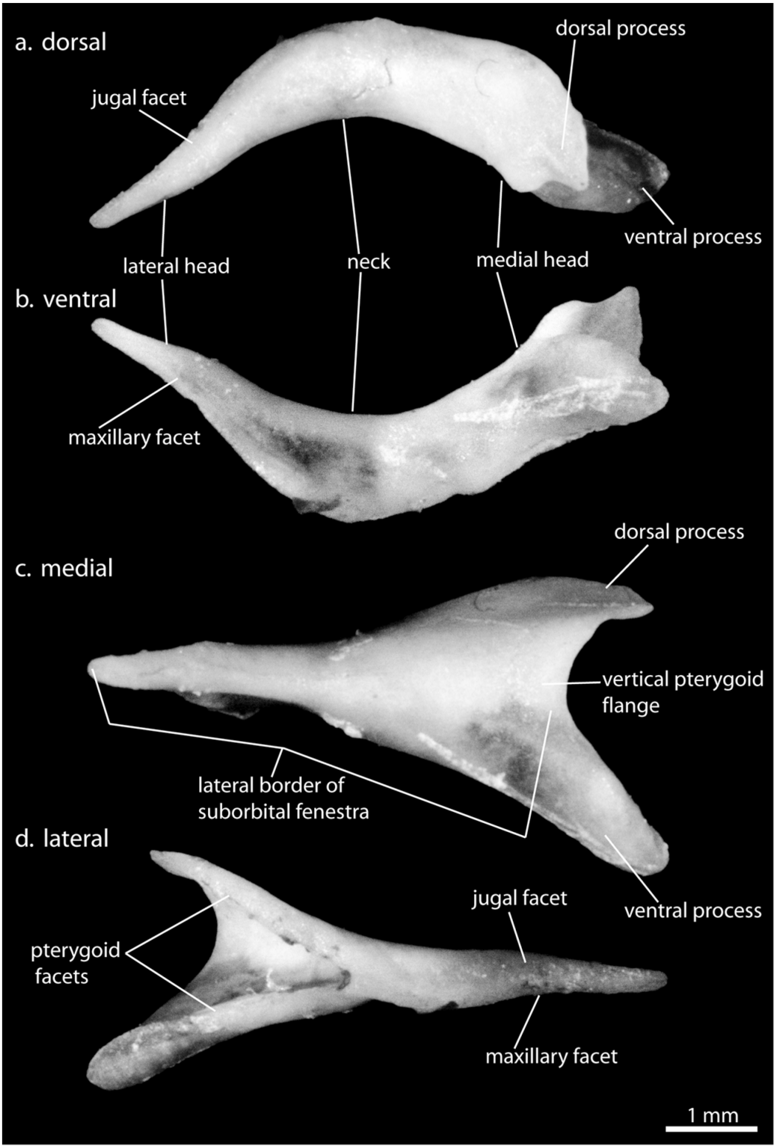

Figure 21:
Right ectopterygoid of an adult *Eublepharis macularius* in four views.

Along the caudal edge of the pterygoid flange, a ventrally directed ridge of bone originates just lateral to the neck (i.e., on the ventral surface of the pterygoid immediately opposite the fossa collumellae) and descends to a form a point as it progress laterally. Along the dorsal edge of the lateral-most portion of the pterygoid flange, the dorsal fin originates and sweeps rostrodorsally as it ascends from the body of the flange. There is a continuous sheet of bone between the ventral and dorsal ridges, creating a lateral vertical surface that bears a groove oriented caudoventral to dorsolateral that itself forms the articulation surface for the ectopterygoid.

Ectopterygoid (paired) (Fig. 21) This is a short, curved element that forms a caudolateral brace between the palate and the posterior side wall of the snout. It articulates with the pterygoid medially, the jugal dorsolaterally, and the maxilla ventrolaterally, and forms the lateral border of the suborbital fenestra (Fig. 3a). It can be described as having three parts: a medial head, a lateral head, and the neck that connects the two. The rostral-most end of the lateral head tapers to a point and, in life, is sutured to the ventromedial edge of the jugal and the medial palatal shelf of the maxilla. On its caudomedial aspect, the ectopterygoid flares out to form the medial head, a conical process that is open caudally and laterally. The medial head can be further subdivided into dorsal and ventral processes of the vertical pterygoid flange that, according to Evans (2008), is absent in gekkotans. This process articulates with the lateral fin groove of the pterygoid flange of the pterygoid in a tongue-and-groove fashion.

Parasphenoid (unpaired) This element apparently rarely occurs in Gekkota. When it does occur, it is little more than a fragment fused onto the cranial end of the basisphenoid (Evans 2008). It does occur in *E. macularius*, but is indistinguishable from the basisphenoid in the mature braincase. The vidian canal marks the plane of fusion between these two elements (Evans 2008).

The lower jaw (Fig. 22 and 23)

Six of the seven elements of the lower jaw are of dermal origin. Only the articular displays a different pattern of development, being an endochondral element of splanchnocranial origin that arises as an ossification around Meckel's cartilage. My description of the lower jaw, however, includes all seven elements described together in one section because the lower jaw functions as a single unit and is more easily understood when described as an integrated structure.

The skeletally mature lower jaw of adult *E. macularius* consists of two easily distinguished and separable elements, the dentary and the coronoid, as well as two fused element complexes that leave little or no trace of sutures, the splenial-angular complex (Fig. 24) and the surangular-articular-prearticular complex (Fig. 25). Because of the inability to dissociate the constituent elements of the latter two complexes, further resolution of their extent and form was explored via fully articulated specimens that were CT scanned.

Four foramina of the lower jaw involve multiple elements in their boundaries, the anterior surangular foramen laterally as well as the anterior inferior alveolar foramen, the anterior mylohyoid foramen, and the mandibular foramen medially (Fig. 22). The anterior surangular foramen is bounded dorsally by the coronoid and ventrally by the surangular. The anterior inferior alveolar foramen is bounded cranodorsally, dorsally, and ventrally by the dentary as well as caudally and dorsocaudally by the splenial. The anterior mylohyoid foramen is bounded laterally by the dentary, whereas the cranial, medial, and caudal edges are demarcated by the splenial. The mandibular foramen is enclosed fully within the surangular-articular-prearticular complex, being laterally, ventrally, and ventromedially walled by the articular and dorsomedially by the prearticular.

Dentary (paired) (Fig. 26) The dentary is the only tooth-bearing bone of the lower jaw and comprises a little over half of the length of the latter. The dentary constitutes the entire cranial ramus of the lower jaw and resembles a compressed tube that curves medially as it progresses cranially. The cranio medial surface is the symphysial surface that fuses to the contralateral dentary. Medially, there is a splenial recess (Oelrich 1956) that tapers to a point cranially into which the splenial slots. The caudal end bears individual dorsal, ventral, and laterally positioned caudal processes. At its caudal end, the den tary slots into the coronoid dorsally, is overlapped by the surangular laterally at the surangular facet, interdigitates with the angular-splenial complex ven trally and medially, and forms a sleeve around the ossified anterior-most projections of Meckel’s cartilage (the articular). Its lateral surface bears five foramina for the passage of nerves and blood vessels (Oelrich 1956) and the medial surface bears the alveolar shelf upon which sit ca. 45 conical, pleurodont teeth.

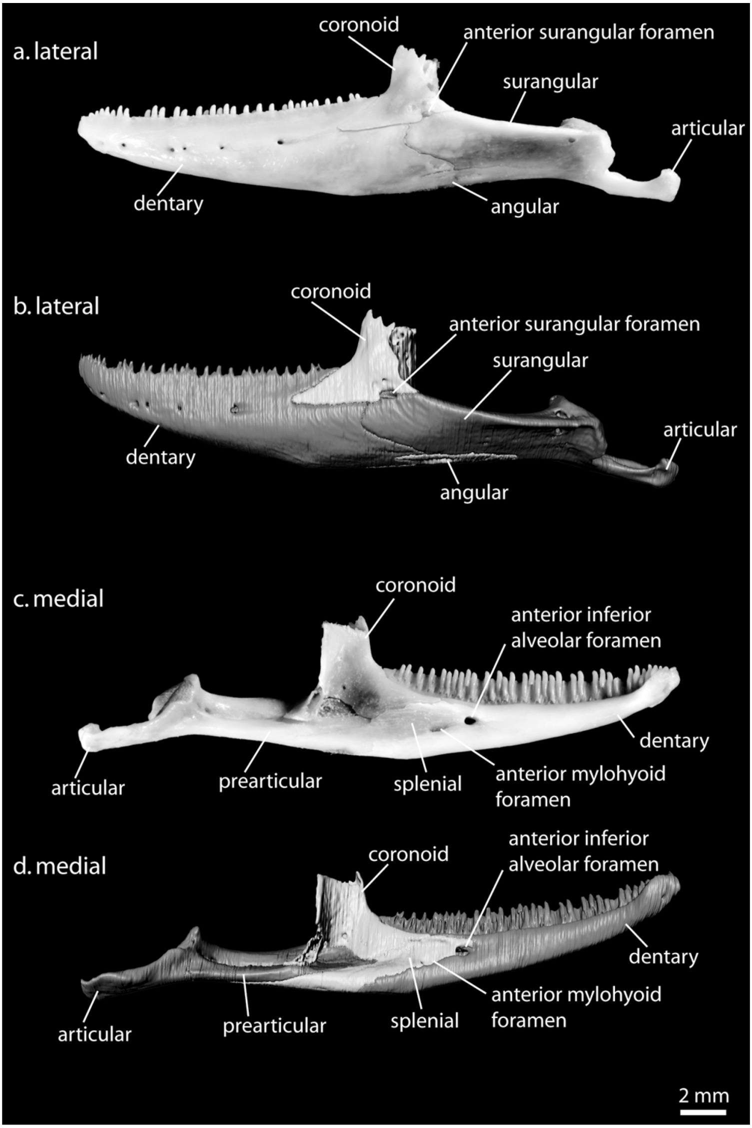

Figure 22:
Left lower jaw of an adult *Eublepharis macularius* in two views, with complimentary images of the actual bones (a and c) and Amira-rendered CT scans (b and d).

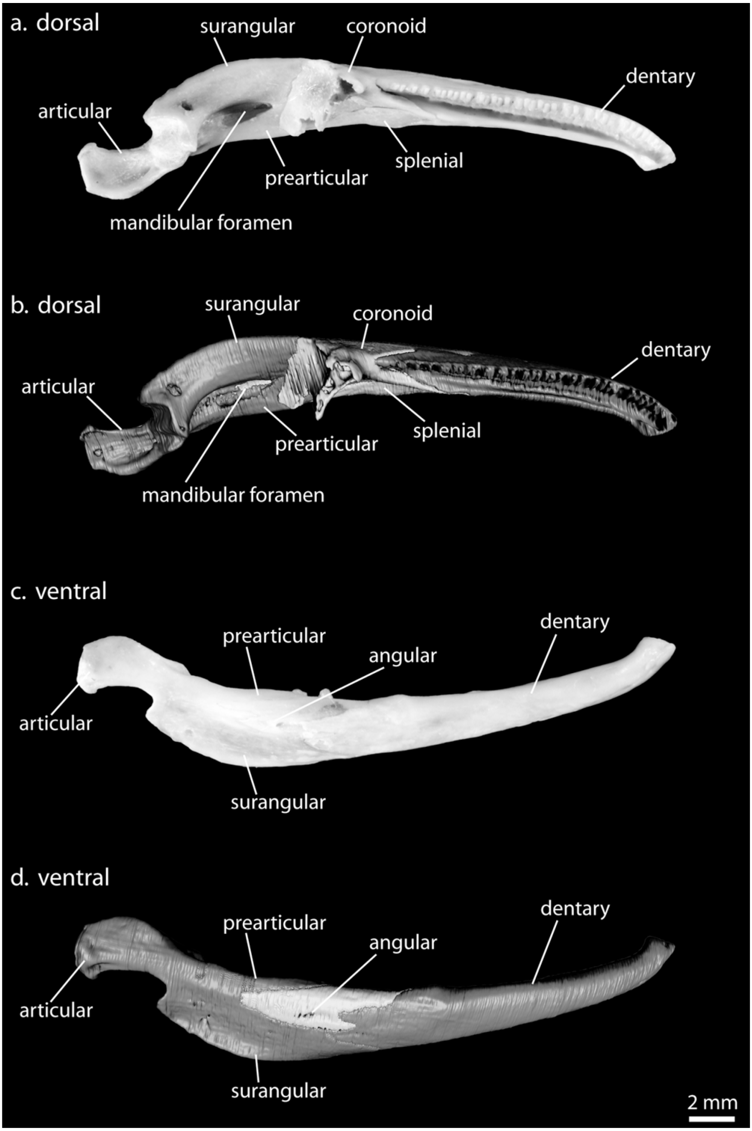

Figure 23:
Left lower jaw of an adult *Eublepharis macularius* in two views, with complimentary images of the actual bones (a and c) and Amira-rendered CT scans (b and d).

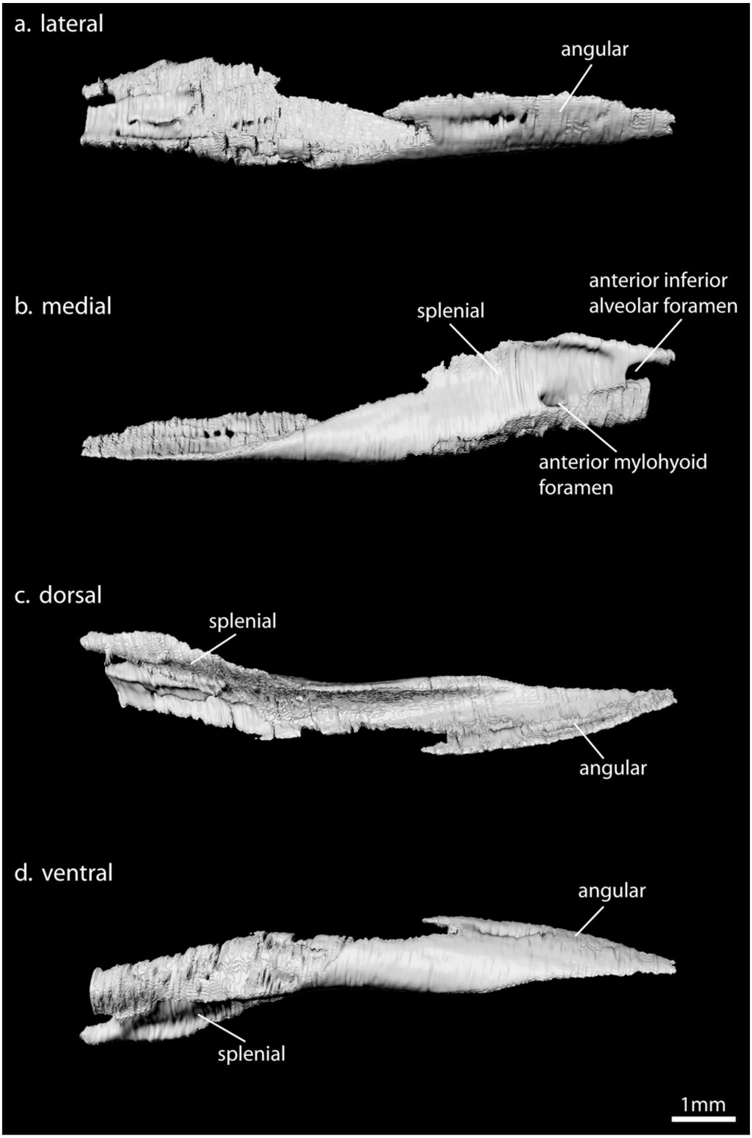

Figure 24:
Amira-rendered and isolated CT scans of the left splenial and angular of an adult *Eublepharis macularius* in four views.

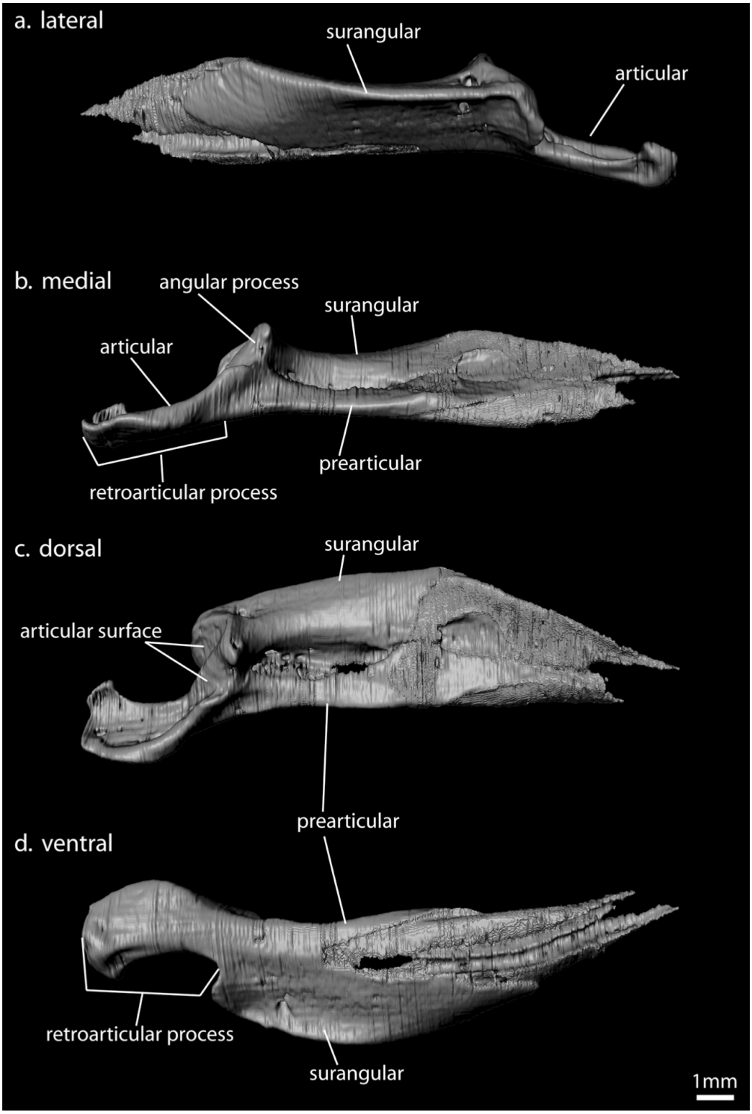

Figure 25:
Amira-rendered and isolated CT scans of the left surangular-articular-prearticular complex of an adult *Eublepharis macularius* in four views.

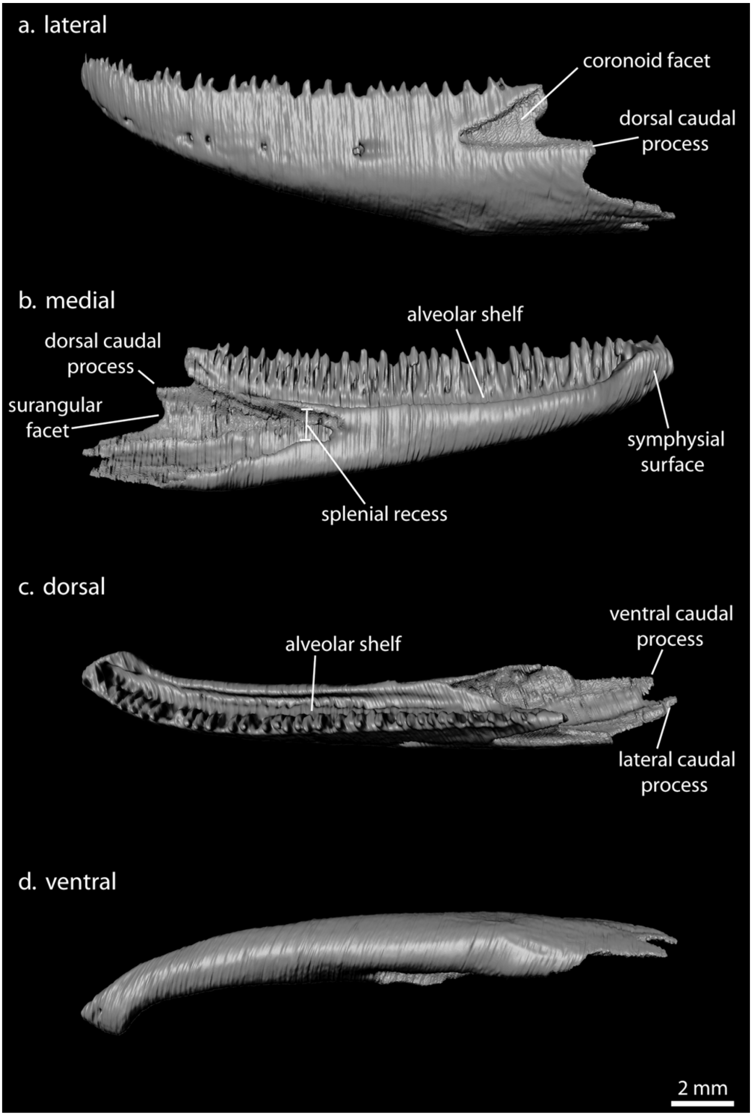

Figure 26:
Amira-rendered and isolated CT scans of the left dentary of an adult *Eublepharis macularius* in four views.

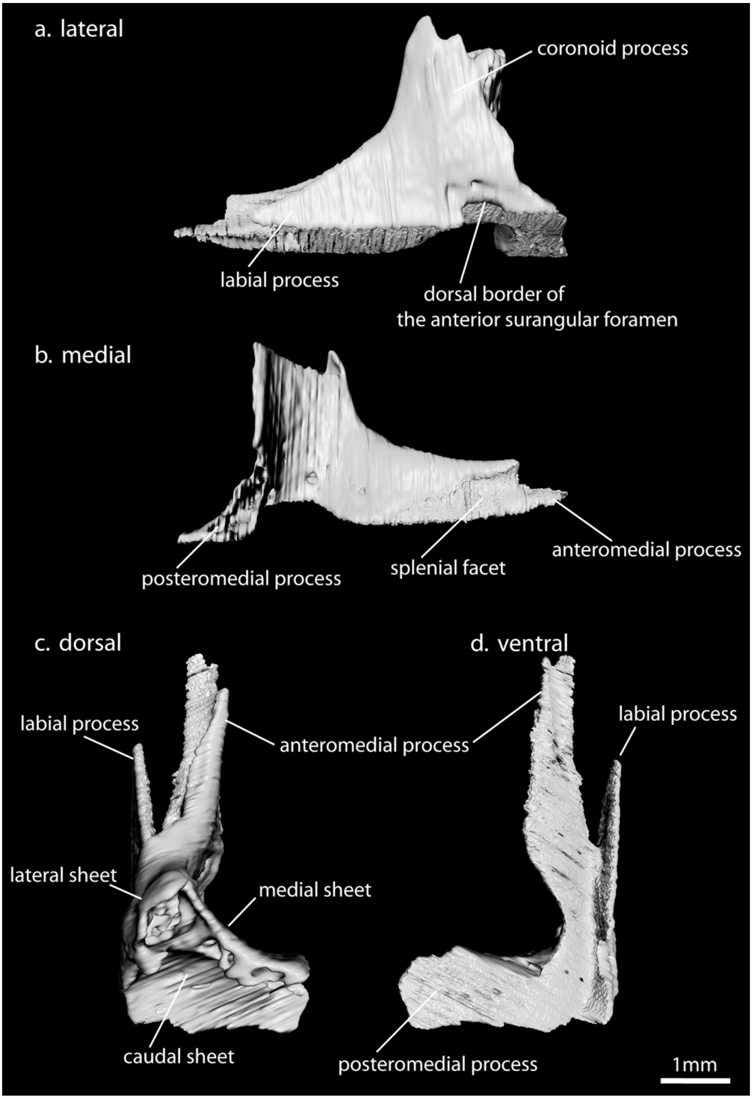

Figure 27:
Amira-rendered and isolated CT scans of the left coronoid of an adult *Eublepharis macularius* in four views.

Coronoid (paired) (Fig. 27) This is a tall, complex element consisting of the dorsal coronoid process and the ventral labial, anteromedial, and posteromedial processes. The coronoid process can be further subdivided into a lateral, medial sheet, and caudal sheets. The cranial edge of the lateral sheet curves gently craniomedially to a point in line with the lateral edge of the anteromedial process, where it bends sharply caudally to form the medial sheet. The medial sheet angles caudomedially and curves gently more medially as it sweeps caudally until its caudal edge faces medially. The caudal sheet connects the previous two and, together, all three form a hollow structure traversed by trabeculae throughout. The medial side of the labial process bears the dentary facet and overlaps the dentary. Caudally, the ventral edge of the labial process is emarginated as the anterior surangular foramen. The lateral side of the anteromedial process also overlaps the dentary and this, together with the labial process, forms a wedge into which the dentary slots. The medial side of the anteromedial process bears the splenial facet, which is overlapped by that element. Ventrally, the anteromedial process flares out to form a triangular foot that runs along its length and is firmly wedged in place by the dentary laterally and the splenial medially. The posteromedial process forms a bridge over the fused craniodorsal aspect of the articular and prearticular, which pass underneath and then beyond it.

Splenial-angular complex (paired) (Fig. 24) The splenial and the angular are fused indistinguishably to one another in the adult jaw and form a trough that curls around the jaw from craniomedial to ventral and then to caudolateral. Ventrally, the posterior mylohyoid foramen is completely enclosed in what is presumed to be the angular section of this composite element. This is little more than a thin sheet of dermal bone that wraps around Meckel's cartilage.

Laterally, the splenial-angular complex is just visible ventral to the surangular and caudal to the dentary between which it resides. Medially, the splenial-angular complex is bounded by the prearticular caudally and the dentary ventromedially and cranially on its dorsomedial aspect, whereas the coronoid bounds it caudally on its dorsomedial aspect.

Surangular-articular-prearticular complex (paired) (Fig. 25) This is a complex, composite structure consisting of two dermal bones fused to the craniolateral and craniomedial aspects of ossified components of Meckel's cartilage comprising the articular. This element complex makes up almost the entire caudal half of the lower jaw in lateral view and bears a slight ventral embayment adjacent to the angular. The articular bears the angular process, the retroarticular process, and the articular surface that receives the mandibular condyle of the quadrate to form the hinge of the lower jaw.

Dorsally, the complex resembles two depressed lateral and medial tubes, each equal in length but with the lateral one offset rostrally relative to the medial one by one quarter of its length. The rostral ends of both tubes taper to points and curve towards the midline of the element. In ventral view, the complex strongly resembles a machete, with the retroarticular process forming the handle and the medial surface forming the curve of the blade. The lateral side is twice the depth of the medial side, and, in lateral view, the topography rises to two peaks, one at the articular surface and the other at the point of fusion to the coronoid.

Individual skull elements: the splanchnocranium

Palatoquadrate derivatives

The quadrate and the epipterygoid are derived from the palatoquadrate cartilage and are the only two ossified elements from this source known to remain in extant squamates.

Quadrate (paired) (Fig. 28) This is a large element that plays an integral role in the streptostylic pattern of jaw suspension. It forms the anterior border of the middle ear. For descriptive purposes, the quadrate can be broken into two main regions, the medial column and the lateral conch.

In lateral view, the quadrate angles slightly from cranioventral to caudodorsal, and the medial column is curved, with the concavity of the curvature facing caudally. In anterior and posterior view, the medial column appears straight. The dorsal end of the medial column bears the relatively wide and dorsally flat cephalic condyle, the caudal edge of which bears a slight, ventrally oriented, caudal tongue.

On the craniomedial edge of the dorsal-most quarter of the medial column is the dorsomedial crest. The ventromedial crest is located just dorsal to the mandibular condyle and ascends one-sixth the height of the medial column.

At the ventral end of the medial column is the primary bipartite mandibular condyle and a secondary, more dorsocaudally positioned, bipartite caudal mandibular condyle. The medial component of the bipartite condyle is and less prominent than the lateral part, which is rounded, ventrally directed,

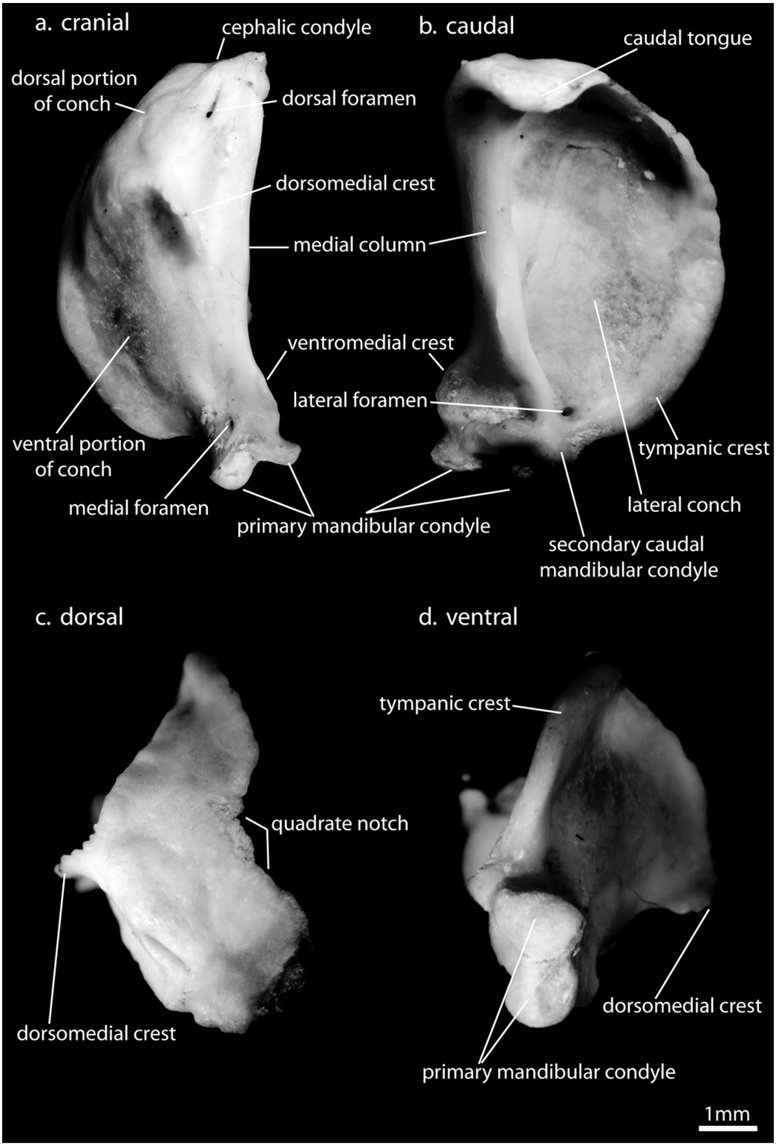

Figure 28:
Right quadrate of an adult *Eublepharis macularius* in four views.

and projects farther ventrally than does the medial component. The medial component projects medially at a right angle to the lateral component.

The lateral conch can be further subdivided into two components, the dorsal convex rostral portion and a ventral flat, sheet-like portion. On the rostral face, these two components are separated by a curved ridge that begins flush with the conch laterally before gradually elevating away from the surface of the conch, with the apex of the curvature pointing dorsally. The ridge becomes more prominent as it descends medioventrally to form a serrated edge pointing rostroventrally. The quadrate notch disrupts the otherwise straight dorsal caudolateral edge. The conch is widest at mid-height, other than for the tympanic crest, which flares out along the ventrolateral edge, widening as it descends, before curving to merge into the dorsolateral edge of the mandibular condyle.

Three small foramina occur on the quadrate, one positioned dorsally and two positioned ventrally. The rostrocaudally oriented, oblong, groove-like dorsal foramen is located on the rostromedial surface of the cephalic condyle. Both of the ventral foramina are round. The medial one is located just dorsal to the notch of the mandibular condyle. The lateral foramen is located at the junction of the tympanic crest with the mandibular condyle.

The quadrate is not sutured to any other element, but is held in place by ligamentous attachments. The dorsocaudal aspect of the cephalic condyle is closely apposed to the bipartite cotyle created by the squamosal and supratemporal, and the caudal tongue of the cephalic condyle rests against the paraoccipital process of the otooccipital, a condition termed “paraoccipital abutting” (Rieppel 1984). The mandibular condyle is received by the articular surface of the articular.

Epipterygoid (paired) (Fig. 29) This is a long, slender, tripartite, columnar element that flares out slightly at both ends. Sutures between the shaft and the epiphyses are evident in skeletally mature specimens. This element forms a brace between the pterygoid and the alar process of the prootic. In articulated lateral view, the epipterygoid is angled approximately 15° from the vertical in a dorsocaudal to ventrorostral direction. The dorsal three quarters are straight, but the ventral quarter curves ventrally. In anterior view, the epipterygoid appears relatively straight, with the dorsal third of the shaft being about twice the diameter of the ventral third, with the middle third tapering from the dorsal, thicker portion to the ventral, thinner portion.

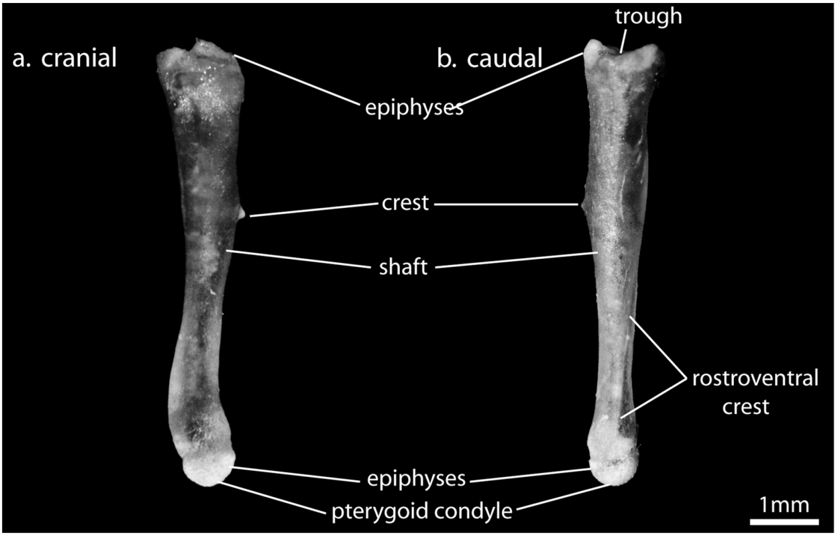

Figure 29:
Right epipterygoid of an adult *Eublepharis macularius* in two views.

On the lateral side, one-third of the way from the dorsal tip, are two chevron-like projections forming a shallow V-like crest. Located just above the pterygoid condyle is a small, horizontal shelf on the rostromedial half of the shaft. Also located just dorsal to the pterygoid condyle, but extending from the centre of the rostral surface, is the rostroventral crest that ascends one-third the length of the shaft and angles medially to become flush with the medial edge of the shaft.

The dorsal end of the epipterygoid is divided to form a rostrocaudally oriented trough into which the ventral edge of the alar process of the prootic fits. The ventral end of the epipterygoid is a rounded condyle somewhat greater in diameter than the shaft immediately dorsal to it. This ventral condyle articulates with the pterygoid via the deep fossa collumellae, into which it fits so deeply that it is not visible in the articulated skull.

Hyoid arch derivatives

Stapes (= columella) (paired) (Fig. 30) The stapes is a long, thin rod that is intimately associated with the chondrocranium and abuts the fenestra ovalis. The proximal portion of the shaft is compressed and the lateral portion is depressed, with the inflection from compressed to depressed occurring about midway along the length of the stapes. The proximal end of the stapes is perforated for passage of the stapedial artery. Beyond this, the proximal edge flares slightly to extend a rounded process ventrally and a smaller one dorsally. The dorsal side of the bone, enclosing the stapedial foramen, is very thin and fragile in appearance, whereas the ventral side is much more robust.

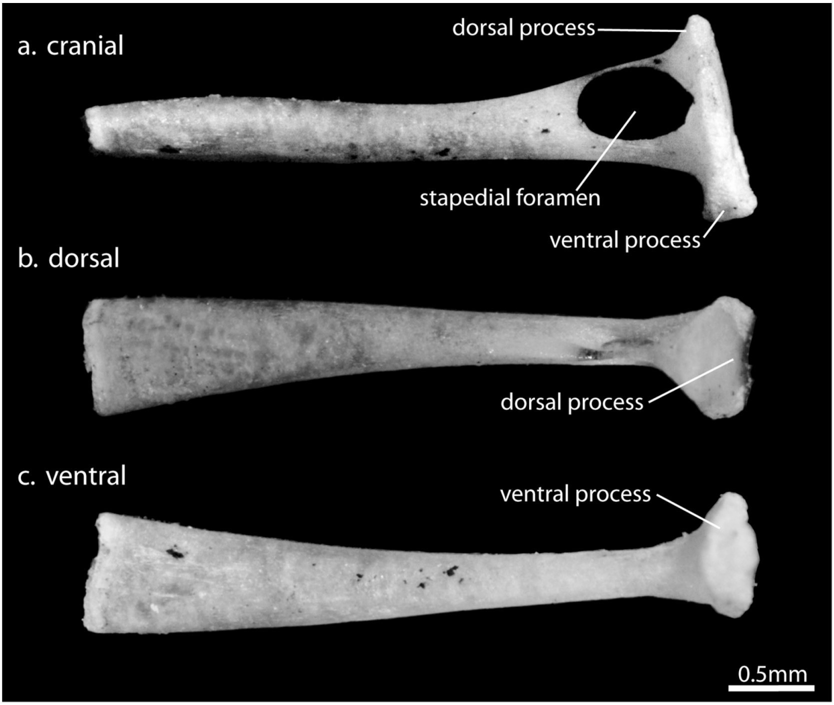

Figure 30:
Right stapes of an adult *Eublepharis macularius* in three views.

Individual skull elements: the chondrocranium

The osseous adult chondrocranium (Figs. 31 and 32) of *E. macularius* is a single fused structure with no trace of sutures in the specimens I examined. For this reason, I describe only the general regions of the prootics, basisphenoid, basioccipital, supraoccipital, and the otooccipitals. The exact locations of sutural boundaries between these elements have not yet been discerned.

Prootic (paired) (Figs. 31a and c and 32b)

The prootic contributes the craniodorsal side wall of the braincase and lies lateral to the vestibule. It is composed of four primary processes (alar, inferior, supratrigeminal, and posterior) that fuse with the basisphenoid rostroventrally, the basioccipital caudoventrally, the otooccipital caudolaterally, and the supraoccipital caudomedially. The alar process (= crista alaris of Romer 1956) is a large, vertically oriented flange located rostrodorsally. Ventrolaterally and pointing rostrally is the inferior process; ventromedially and also pointing rostrally is the supratrigeminal process, which fuses to the crista sellaris of the basisphenoid, enclosing the incisura prootica (= trigeminal notch of Romer 1956) to form the trigeminal canal. Pointing caudally is the posterior process, the medial face of which fuses to the lateral face of the otoocipital.

Epiotic (paired)

The epiotics are incorporated into the supraoccipital (Evans 2008) and are not distinguishable from it in mature specimens; hence, they are not described as separate elements.

Orbitosphenoid (paired)

These elements do not ossify in any gekkotan studied to date (Wellborn 1933; Daza 2005; Evans 2008). Similarly, I have found no evidence of them in the Leopard Gecko.

Basisphenoid (unpaired) (Figs. 31c and 32)

This element forms the rostral braincase floor, giving rise to large, rostrolaterally oriented basipterygoid processes, paired parasphenoid processes that are also rostrally oriented, and the dorsally oriented alar process. A thin horizontal sheet of bone follows the contour of the element and connects the alar and basipterygoid processes. The parasphenoid processes are little more than rostrally oriented, truncated cones mirroring one another just on either side of the midline between the basipterygoid processes. The latter processes form an acute angle at the confluence of their long axes and are long, slender columns that extend craniolaterally. Their dorsal edge is deflected medially and their ventral edge is deflected laterally. They flare out distally into hatchet-head-shaped terminations. The alar process of the basisphenoid ascends to meet and fuse with the inferior process of the prootic. The high-rimmed crista sellaris meets the supratrigeminal process of the prootic.

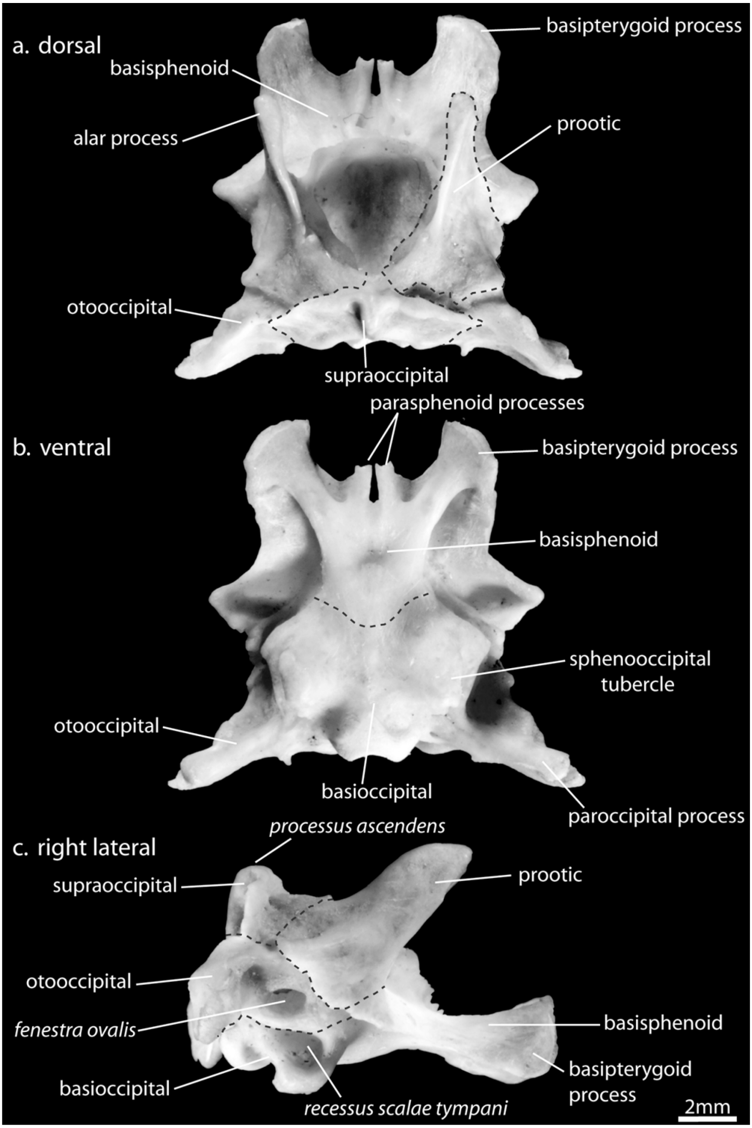

Figure 31:
Chondrocranium of an adult *Eublepharis macularius* in three views. Dashed lines represent likely boundaries between elements.

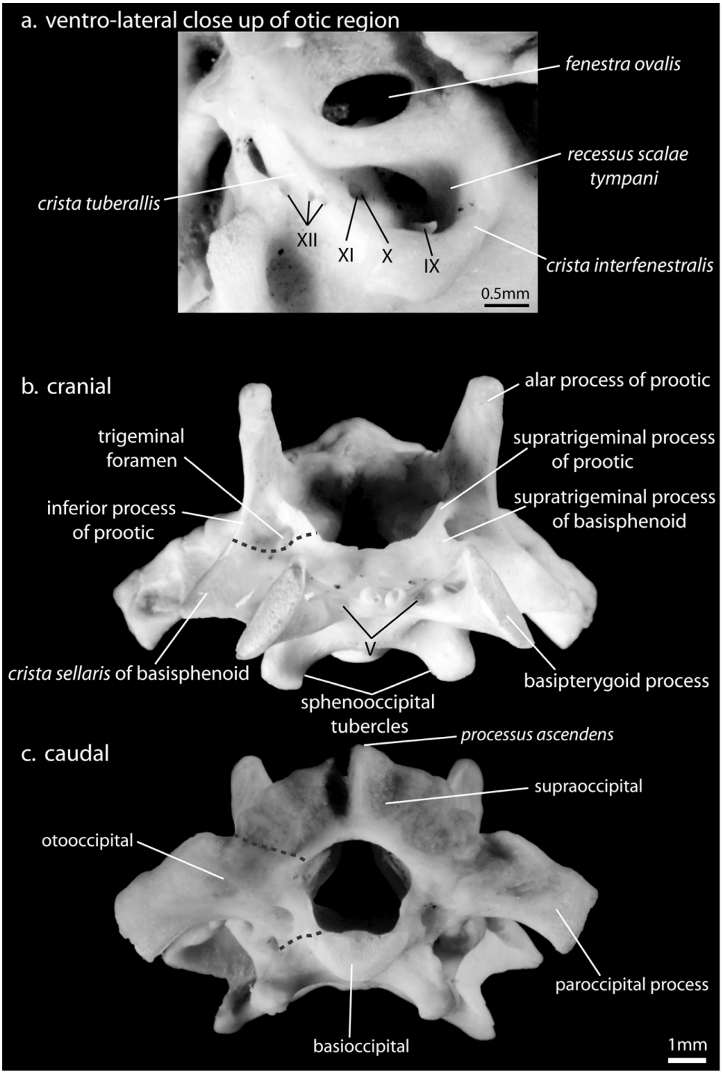

Figure 32:
Chondrocranium of an adult *Eublepharis macularius* in three views. Dashed lines represent likely boundaries between elements. Roman numerals indicate the cranial nerve passing through a given foramen. Scale bar for (a) is inset in the picture; the scale bar for (b) and (c) is located in the bottom right corner of the illustration.

Basioccipital (unpaired) (Figs. 31 and 32)

This bone forms the caudal floor of the braincase and contributes to the ventral margin of the foramen magnum (Evans 2008). The dorsal surface bears two laterally oriented occipital recesses that contribute to the floor of the recessus scalae tympani. The medial portion of the caudal face forms the occipital condyle and the ventrolaterally descending keel-like flanges, the sphenooccipital tubercles.

Supraoccipital (unpaired) (Figs. 31 and 32)

This wing-like element forms the roof of the braincase and the dorsal rim of the foramen magnum. There is a rostromedially directed processus ascendens that fits into a pit located caudally on the midline on the ventral surface of the parietal.

Otooccipital (paired) (Figs. 31 and 32)

This is a composite bone formed by fusion of the exoccipital and the opisthotic to form the caudolateral wall of the braincase and the ventrolaterally projecting paroccipital processes. The ventrolateral wall is perforated by the fenestra ovalis and forms the roof of the recessus scalae tympani as well as its caudal wall via the crista tuberalis and its cranial walls via the crista interfenestralis.

Discussion

The preceding description of the skull of *E. macularius* furnishes more detail about the structure of many of the cranial elements of gekkotans than has appeared previously. Such detail is important for studies of phylogenetic relationships among taxa as well as for an understanding of the development of form, a work that I will undertake following this one.

In compiling this description of the cranial elements of *E. macularius*, I have endeavoured to compare my descriptions with other accounts available in the literature. In so doing, I have found that there are inconsistencies between authors. Some of these are likely because of phylogenetic variation between taxa, whereas others result from the inconsistent application of descriptive terminology or are due to mistaken identity. The remainder of this discussion summarises the differences encountered. My commentary about individual elements follows the same sequence as that employed in the description of the elements of *Eublepharis* above. Only elements purported to display differences are discussed.

The dermatocranium

Skull roofing bones

Nasal

Within Gekkota, nasals can be paired or unpaired (Kluge 1962; Häupl 1980) and variation in this character state has been used in taxonomic analysis. Grismer (1988) describes the nasal within Gekkota as having two distinct character states, wide or thin. In *E. macularius*, the nasals are paired and most closely accord with the character state "wide" of Grismer (1988).

Frontal

Kluge (1962) and Bauer & Good (1996) used variation in the anterior median process of the frontal to help diagnose differences between species, whereas Häupl (1980) documented differences in the anterior lateral processes. In *Eublepharis,* the latter are well developed and blunt-ended, and preclude contact between the prefrontals and the nasals.

Parietal

The primitive condition of the parietal in Gekkota is the paired state, with the fused condition in adult eublepharids thus being considered to be derived via reversal (Estes & Pregill 1988). Grismer (1988) documented variation in three regions within the parietals of eublepharids. He noted that the posterior margin can be "unemarginate" or "emarginated", the ventral parietal surface can be depressed or not, and the ventrolateral margin ridges can bear a ventrally directed process. The parietal of *Eublepharis* is emarginated and depressed and lacks the ventrally directed process, such that my observations fit within the scheme of Grismer (1988).

Tooth-bearing bones of the upper jaw

Premaxilla

Stephenson (1960) noted three separate states of the premaxilla among the diplodactylid genera he studied: fused, partly fused, and paired. All three parts of the premaxilla have been employed as sources of characters by different researchers. Additionally, Wellborn (1933) used the presence or absence of a spine on the palatine process as a diagnostic character, whereas Häupl (1980) described variation in the shape of this process and the height of the nasal process among species. *Eublepharis* exhibits the fused condition and possesses the incisive process (= spine of Wellborn 1933); the palatal shelf does not contact the vomer except through the incisive process and the nasal process, although tall, does not intrude significantly between the nasals.

Maxilla

For the maxilla, it appears that few authors have used the number of teeth present as a source of systematic characters, with exceptions including Wellborn (1933) and Bauer & Russell (1990). Later authors (e. g., Kluge 1962; Häupl 1980) have used variation in the processes of the maxilla as a source of systematic data. Wellborn (1933) also noted variation in the total number of nerve foramina and in the number of rows of nerve foramina on the labial surface of the maxilla. In *Eublepharis*, there are two rows of nerve foramina, with one foramen in the top row and seven in the bottom, with the single foramen of the top row located near the rostral end of the bottom row of foramina.

Circumorbital bones

Prefrontal

Grismer (1988) described varying degrees of contact between the medial processes of the paired prefrontals as a diagnostic character for eublepharids. Bauer & Good (1996) as well as Webb (1951) described differences in the structure of the posterior portion of this element in the species they studied. Contact in *Eublepharis* is described as being half as wide as the extreme seen in *Hemitheconyx* and *Holodactylus* (Grismer 1988).

Postfrontal

Originally believed to be absent in geckos (Camp 1923), it was later suggested that this element had been subsumed within the postorbital (Rieppel 1984). Almost a decade later, and after examining some recent post-hatchling material in another gekkotan (*Cyrtodactylus pubisulcus*), Rieppel (1992) recanted his earlier statements, calling the single element the postorbital and listing the postfrontal as being absent. This could well be the derived condition in most Gekkota and the presence of the albeit rudimentary splint of the postfrontal in *E. macularius* (Wise & Russell 2010) probably represents the ancestral state for gekkotans.

Postorbital

For such a simple bone, the postorbital has received a great deal of attention, with much variation being described. Differences between the anterior and posterior parts have been documented (Wellborn 1933; Kluge 1962; Grismer 1988; Bauer & Good 1996) and the lack of a perforation compared to that found in pygopods has been noted (Stephenson 1960). In *Eublepharis*, the element is asymmetrical with respect to its rostral and caudal halves. The rostral portion is narrow and tapers cranially to a pointed end, whereas the caudal half is wide, flat, and shelf-like.

Temporal bones

Squamosal

This element is present in at least some Gekkota and, contrary to Camp (1923), not lost. Kluge (1967) used the presence or absence of the squamosal as a character state diagnosing higher taxa of Gekkota, with its shape and length being used to distinguish between taxa at the species level (Kluge 1962). Häupl (1980) described variation in the shape of this bone in different species. Wellborn (1933) and Häupl (1980) both used the points of contact between the posterior end of the squamosal and other bones (e. g., the quadrate and parotic process of the otooccipital) as diagnostic features of different gekkotan clades. The posterior cotyle of the squamosal in *Eublepharis* is in contact with the quadrate and is held in place via a short ligament that must be cut to separate these elements in dissections.

Palatal elements

Vomer

Several features of the vomer have been used in gecko phylogenetics. Kluge (1962) and Häupl (1980) both used variation in the palatine process, whereas Wellborn (1933) and Häupl (1980) used points of contact with the maxilla and/or the premaxilla as characters. The palatine process in *E. macularius* is rounded and club-like, and the vomer is separated from the maxilla by the fenestra exochoanalis and contacts the premaxilla only via the incisive process of the latter.

Septomaxilla

Few authors have considered variation in the septomaxilla as a source of characters. Häupl (1980) and Webb (1951) reported the absence or presence between species of the mediolateral ridge on the dorsal surface of the septomaxilla. The complete absence of this bone in *Pristurus carteri collaris* was noted by Häupl (1980). *Eublelpharis* has both the element and the mediolateral ridge.

Pterygoid

Wellborn (1933) and Häupl (1980) both described variation in the contact patterns between the pterygoid and various other cranial elements. Grismer *et al.* (1999) noted variation in its anterior processes in *Goniurosaurus* spp. Wellborn (1933) noted that the caudal end of the pterygoid is either forked or unforked, whereas Kluge (1962) and Häupl (1980) discussed variation in length and width as variable features. The caudal end of this bone is unforked in *Eublepharis* and this element only articulates with the basisphenoid, ectopterygoid, palatine, and epipterygoid.

The lower jaw

Dentary

Variation of the dentary with respect to the number (Wellborn 1933; Kluge 1962; Häupl 1980) and pattern (Wellborn 1933) of nerve foramina has been noted for geckos. Häupl (1980) documented differences in Meckel's canal between *Uroplatus fimbriatus* and all other species he studied, and Kluge (1962) noted variation in the infraorbital alveolar foramen within *Coleonyx variegatus.* Wellborn (1933) as well as Müller and Mödden (2001) listed tooth counts on the dentary as possibly aiding in diagnosis. In *E. macularius*, I recorded six nerve foramina.

Coronoid

Several authors have commented on the outer flange of the coronoid as a source of features that are collectively diagnostic of various taxa of geckos (Kluge 1962; Häupl 1980; Grismer 1988). Kluge (1995) considered variation in height of this element in his cladistic analysis of sphaerodactyline geckos. In *E. macularius*, the coronoid process is well developed and high.

Surangular-articular-prearticular complex

For the surangular-articular-prearticular complex, Wellborn (1933) documented variation of the retroarticular process in a variety of gekkotans, commenting on its length and width as well as the shape of the caudal end. With respect to the surangular portion, some variation in structure has been described and employed in systematic analysis, including the angle of the lower margin (Kluge 1962), its fusion to the articular (Häupl 1980), the shape of the retroarticular process (Häupl 1980), and the position of the mylohyoid foramen (Grismer 1988). The retroarticular process of *E. macularius* is wide and depressed in overall profile and bowl-shaped dorsally with rounded lateral and caudal margins; it has a deeply eroded medial border.

The splanchnocranium

Quadrate

Variation between species in the shape of the quadrate was noted by Häupl (1980) and Grismer (1988) documented variation in the anterodorsal margin and the condyle. Wellborn (1933) discussed the variability in the region dorsal to the mandibular condyle, with three patterns being described: presence of an incision or with one or two perforations. The *Eublepharis* specimens that I have examined have two perforations (foramina).

Hyoid-arch derivatives

Stapes

Häupl (1980) recorded perforated versus unperforated states of the stapes in the gecko species he studied. Given how thin the dorsal strut over the foramen is, it is easy to imagine the absence of a foramen and the presence of a notch. Grismer (1988) recorded a difference in the cross-sectional shape for *Aeluroscalabotes* (round) compared to other eublepharids (compressed or depressed). In *Eublepharis*, the stapes is perforated.

The chondrocranium

Prootic

Wellborn (1933) noted variation between species in the anterior inferior process of the prootic, this being related to the presence or absence of a spine. Häupl (1980) noted that a small notch occurs on the dorsorostral edge of the prootic, dividing it into upper and lower anterior processes. He noted that there is considerable variability in the smaller (lower) anterior process. Grismer (1988) described characters of the prootic relating to the trigeminal foramen and the topography of the dorsal margin as being either deeply emarginated or flat to convex. He lists the character states for *Eublepharis* as flat to convex.

Basisphenoid

Wellborn (1933) and Häupl (1980) both mentioned differences in the basipterygoid process of the basisphenoid with respect to its length and diameter as well as the shape of its ends. These processes are well developed in *Eublepharis*, being long and hatchet-head-shaped at their ends. Wellborn (1933) also documented variation in the amount that the basisphenoid contributes to the formation of the sphenooccipital tubercle. Because sutures are difficult to delineate in mature specimens, this could not be assessed in this study.

Basioccipital

Wellborn (1933) described two character states for the shape of the basioccipital: pentagonal or square. It is pentagonal in *Eublepharis*. The sphenoccipital tubercle is a ventrolateral projection that varies in size (Kluge 1962) and shape (Wellborn 1933). Grismer (1988) proposed that the variable shape of the ventral surface of this element would be a useful source of systematic data and considered the nearly flat shape seen in *Eublepharis* to be derived within Eublepharidae.

Supraoccipital

Wellborn (1933) employed the sagittal crest of the supraoccipital as a source of variation worthy of note, listing the states as being weakly developed, absent or variable. Rieppel (1984) stated that geckos lack the ascending process altogether and, instead, develop a sagittal crest from the parietal. These contradictory statements regarding the sagittal crest mean that further investigation is required. The processus ascendens is well developed in *E. macularius.*

Otooccipital

With regard to the otooccipital, Wellborn (1933) listed variation among gekkotan species in the recessus scalae tympani, the parotic processes, and the ampulla of the frontal semicircular canal. Häupl (1980) discussed several variants of the parotic process and listed two other features for which he documented variation: the occipital ridge and the jugular foramen. The crista tuberalis can be large, in which case it contributes to the posterior border of the recessus scalae tympani, or small, in which case it does not (Wellborn 1933). The paroccipital process has been described as being small or nonexistent (Wellborn 1933) or as short or long, with various shapes described for its ends (Häupl 1980). In *Eublepharis*, the ends are well developed and wing-like. The exoccipital has been stated to either border the jugular foramen or to carry a jugular incision upon it (Häupl 1980), but this cannot be determined without examining embryonic material because of the complete fusion of all chondrocranial elements in mature skulls.

Conclusions

The abundance and complicated relations of many of the bones of the skull to one another necessitates care and attention to detail in their study. Most previous studies have had limited access to material, with few specimens having been examined per species so that variation within species, variation between and within the sexes, and ontogenetic variation are not accounted for. This chapter lays the foundation for future work on variation within *E. macularius* by establishing a description based on seven adult specimens and description of anatomical detail for all elements.

There have also been questions about the presence or absence of elements in eublepharid skulls that have proven difficult to answer based on skeletally mature material. I have definitely found the lacrimal and the jugal to be present in all the specimens I have examined. As for the element complexes of the angular-splenial and the articular-prearticular-surangular, it does appear as though all the potentially contributory elements are present, but there is no trace of the location of suture or fusion within each complex. CT scans have been helpful in resolving pattern, but embryological material is needed to clarify the situation more fully.

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Literature cited

Barahona F. & Barbadillo L.J. (1998). Inter- and intraspecific variation in the post-natal skull of some lacertid lizards. *J. Zool. Lond.*, 245, 393–405.

Bauer A.M. (2013). *Geckos: The Animal Answer Guide*. Johns Hopkins University Press, Baltimore.

Bauer A.M. & Good D.A. (1996). Phylogenetic systematics of the day geckos, genus *Rhoptropus* (Reptilia: Gekkonidae), of south-western Africa. *J. Zool. Lond.*, 238, 635–663.

Bauer A.M. & Russell A.P. (1990). Dentitional diversity in *Rhacodactylus* (Reptilia: Gekkonidae). *Mem. Qld. Mus.*, 29, 311–322.

Camp C.L. (1923). Classification of the lizards. *Bull. Am. Mus. Nat. Hist.*, 48, 289–481.

Cogger H.G. (1964). The comparative osteology and systematic status of the gekkonid genera *Afroedura* Loveridge and *Oedura* Gray. *Proc. Linn Soc. NSW*, 89, 364–372.

Conrad J.L. (2008). Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bull. Am. Mus. Nat. Hist.*, 310, 1–182.

Coomber P., Crews D. & Gonzales-Lima F. (1997). Independent effects of incubation temperature and gonadal sex on the volume and metabolic capacity of brain nuclei in the Leopard Gecko (*Eublepharis macularius*), a lizard with temperature-dependent sex determination. *J. Comp. Neurol.*, 380, 409–421.

Crews D., Sakata J. & Rhen T. (1998). Developmental effects of intersexual and intrasexual variation in growth and reproduction in a lizard with temperature-dependent sex determination. *Comp. Biochem. Physiol. C*, 119, 229–241.

Daza J.D. (2005). *The skull of the gecko* Sphaerodactylus roosevelti *(Reptilia: Squamata).* MSc thesis, University of Puerto Rico, Rio Piedras, 1–352.

Daza, J.D., Abdala, V., Thomas, R. & Bauer, A.M. (2008). Skull anatomy of the miniaturized gecko *Sphaerodactylus roosevelti* (Squamata: Gekkota). *J. Morphol.*, 269, 1340–1364.

Daza J.D. & Bauer A.M. (2010). The circumorbital bones of the Gekkota (Reptilia: Squamata). *Anat. Rec.*, 293, 402–413.

Daza J.D., Aurich J. & Bauer A.M. (2012). Anatomy of an enigma: an osteological investigation of the Namibian festive gecko (*Narudasia festiva*: Gekkonidae: Gekkota). *Acta Zool.*, 93, 465–486.

Daza J.D., Bauer A.M. & Snively E. (2013). *Gobekko cretacicus* (Reptilia: Squamata) and its bearing on the interpretation of gekkotan affinities. *Zool. J. Linn. Soc.*, 167, 430–448.

Donnellan S.C., Hutchinson M.N. & Saint K.M. (1999). Molecular evidence for the phylogeny of Australian gekkonoid lizards. *Biol. J. Linn. Soc.*, 67, 97–118.

Estes,R. & Pregill G. (eds.) (1988). *Phylogenetic Relationships of the Lizard Families*. Stanford University Press, Stanford.

Etheridge R. (1964). The skeletal morphology and systematic relationships of sceloporine lizards. *Copeia,* 1964, 610–631.

Evans S.E. (2008). The skull of lizards and Tuatara. In: *Biology of the Reptilia, Volume 20, Morphology H: The Skull of Lepidosauria* (eds. Gans C, Gaunt AS & Adler K). SSAR Ithaca, New York, 1–347.

Evans S.E. (2003). At the feet of the dinosaurs: the early history and radiation of lizards. *Biol. Rev.*, 78, 513–551.

Evans S.E. (1994). The Solnhofen (Jurassic: Tithonian) lizard genus Bavarisaurus: New skull material and a reinterpretation. *N. Jahrb. Geol. Paläont. Abh.*, 192, 37–52.

Filipski G.T. & Wilson M.V. (1985). Staining nerves in whole cleared amphibians and reptiles using Sudan Black B. *Copeia*, 1985, 500–502.

Gamble T., Aherns J.L. & Card V. (2006). Tyrosine activity in the skin of three strains of albino gecko (*Eublepharis macularius*). *Gekko* 5, 39–44.

Gamble T., Bauer A.M., Greenbaum E. & Jackman T.R. (2008). Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). *Zool. Scr.*, 37, 355–366.

Gamble T., Daza J.D., Bauer A.M., Vitt L.A., Colli G., & Simons A. (2011). A new genus of miniaturized and pug-nosed gecko from South America (Sphaerodactylidae: Gekkota). *Zool. J. Linn. Soc*., 163, 1244–1266.

Gamble T., Greenbaum E., Jackman T.R., Russell A.P. & Bauer A.M. (2012) Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, 7, e39429.

Gauthier J.A., Kearney M., Maisano J.A., Rieppel O. & Behlke A.D.B. (2012). Assembling the squamate Tree of Life: perspectives from the phenotype and the fossil record. *Bull. Peabody Mus. Nat. Hist.*, 53, 3–308.

Grismer L.L. (1988). Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. In: *Phylogenetic Relationships of the Lizard Families* (eds. Estes R & Pregill G). Stanford University Press Stanford, 369–469.

Grismer L.L., Viets B.E. & Boyle L.J. (1999). Two new continental species of Goniurosaurs (Squamata: Eublpharidae) with a phylogeny and evolutionary classification of the genus. *J. Herpetol.*, 33, 382–393.

Good D.A., Bauer A.M. & Sadlier R.A. (1997). Allozyme evidence for the phylogeny of giant New Caledonian geckos (Squamata: Diplodactylidae: *Rhacodactylus*), with comments on the status of *R. leachianus henkeli*. *Aust. J. Zool.*, 45, 317–330.

Hall B.K. (1999). *The Neural Crest in Development and Evolution*. Springer, New York.

Han D., Zhou K. & Bauer A.M. (2004). Phylogenetic relationships among higher taxonomic categories of gekkotan lizards inferred from C-mos nuclear DNA sequences. *Biol. J. Linn. Soc.*, 83, 353–368.

Häupl V.M. (1980). Das Schadelskelett einiger Arten der Fam. Gekkonidae. *Ann. Naturhist. Mus., Wien*, 83, 479–518.

Janes D.E., Bermudez D., Guillette L.J. & Wayne M.L. (2007). Estrogens induced male production at a female-producing temperature in a reptile (leopard gecko, *Eublepharis macularius*) with temperature-dependent sex determination. *J. Herpetol.*, 41, 9–15.

Jollie M.T. (1960). The head skeleton of the lizard. *Acta Zool. Stockholm*, 41, 1–54.

Kluge A.G. (1962). Comparative osteology of the Eublepharid lizard genus *Coleonyx* Gray. *J. Morphol.*, 110, 299–332.

Kluge A.G. (1967). Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Am. Mus. Nat. Hist.*, 135, 1–60.

Kluge A.G. (1987). Cladistic relationships in the Gekkonoidea (Squamata, Sauria). *Misc. Publ., Mus. Zoology, Univ. Michigan*, 173, 1–54.

Le Douarin N.M. & Kalcheim C. (1999). *The Neural Crest*. Cambridge University Press, Cambridge.

Macey J.R., Ananjeva N.B., Wang Y. & Papenfuss T.J. (2000). Phylogenetic relationships among Asian gekkonid lizards formerly of the genus *Cyrtodactylus* based on cladistic analysis of allozymic data: monophyly of *Cyrtopodion* and *Mediodactylus*. *J. Herpetol.*, 34, 258–265.

Müller J. & Mödden C. (2001). A fossil leaf-toed gecko from the Oppenheim/Nierstein Quarry (Lower Miocene, Germany). *J. Herpetol.*, 35, 529–532.

Noble G.K. (1921). The bony structure and phyletic relations of *Sphaerodactylus* and allied lacertilian genera, with the description of a new genus. *Am. Mus. Novit.*, 4, 1–16.

Oelrich T.M. (1956). The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Pub., Mus. Zool., Univ. Michigan*, 94, 1–122.

Ota H., Honda M., Kobayashi M., Sengoku S. & Hikida T. (1999). Phylogenetic relationships of eublepharid geckos (Reptilia: Squamata): a molecular approach. *Zool. Sci.*, 16, 659–666.

Rhen T., Sakata J.T., Zeller M. & Crews D. (2000). Sex steroid levels across the reproductive cycle of female leopard geckos, *Eublepharis macularius*, from different incubation temperatures. *Gen. Comp. Endocrinol.*, 118, 322–331.

Rieppel O. (1984). The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zool. J. Linn. Soc.*, 82, 291–318.

Rieppel O. (1992). Studies on skeleton formation in reptiles. III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata). *Fieldiana Zool. New Ser.*, 68, 1–25.

Rieppel O. (1996). Miniaturization in tetrapods: consequences for skull morphology. *Symp. Zool. Soc. Lond.*, 69, 47–61.

Romer A.S. (1956). *Osteology of the Reptiles*. University of Chicago Press, Chicago.

Stephenson N.G. (1960). The comparative osteology of Australian geckos and its bearing on their morphological status. *J. Linn. Soc. Lond., Zool.*, 44, 278–299.

Stephenson N.G. & Stephenson E.M. (1955). The osteology of the New Zealand geckos and its bearing on their morphological status. *Trans. Roy. Soc. N. Z.*, 84, 341–358.

Townsend T.M., Larson A., Louis E. & Macey J.R. (2004). Molecular phylogenetics of squamata: the position snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Syst. Biol.*, 53, 735–757.

Uetz P. (ed.) (2013). *The Reptile Database*. http://www.reptile-database.org. Accessed April 3, 2013.

Vallely E.M.A., Cartwright E.J., Croft N.J., Markham A.F. & Coletta P.L. (2001). Characterization and expression of Sox9 in the leopard gecko, *Eublepharis macularius*. *J. Exp. Zool.*, 291, 85–91.

Webb M. (1951). The cranial anatomy of the South African geckoes *Palmatogecko rangei* (Andersson), and *Oedura karroica* (Hewitt). *Ann. Univ. Stellenbosch*, 27, A (5), 131–166.

Wellborn V. (1933). Vergleichende osteologische Untersuchungen an Geckoniden, Eublephariden und Uroplatiden. *Sber. Ges. Naturf. Freunde Berlin*, 1933, 126–199. [Translated by Russell A.P., Bauer A.M. & Deufel A. (1997). *Comparative Osteological Examinations of Geckonids, Eublepharids and Uroplatids. With an Introduction by A.M. Bauer and A.P. Russell*. Breck Bartholomew, Salt Lake City.]

Whimster I.W. (1978). Nerve supply as a stimulator of the growth of tissues including skin. II. Animal evidence. *Clin. Exp. Dermatol.*, 3, 389–410.

Wise P.A.D. & Russell A.P. (2010). Development of the dorsal circumorbital bones in the leopard gecko (*Eublepharis macularius*) and its bearing on the homology of these elements in the Gekkota. *Anat. Rec.*, 293, 2001–2006.

Zug G.R. & Moon B.R. (1995). Systematics of the pacific slender-toed geckos, *Nactus pelagicus* complex: Oceania, Vanuatu, and Solomon Islands populations. *Herpetologica*, 51, 77–90.

The evolution of the snake ear and its restricted frequency response range

Bruce A. Young

Department of Anatomy, Kirksville College of Osteopathic Medicine, A.T. Still University of Health Sciences, 800 W. Jefferson, Kirksville, MO 63501–1497; E-mail: byoung@atsu.edu

Abstract

The absence of an external ear is one of the most recognised features of snakes. The evolutionary modifications of the snake ear go far beyond the loss of the tympanum and have resulted in an auditory system characterised by a very narrow range of frequency response. The present contribution will explore the functional basis for the restricted frequency-response range in snakes as well as the selective pressures that may have led to the evolution of the snake ear.

Introduction

Despite the popular belief that snakes are “deaf”, ample neurophysiological (e. g., Hartline 1971a, b; Wever 1978) and behavioural (e. g., Young & Morain 2002; Young & Aguiar 2002) evidence exists that snakes can respond to acoustic stimuli. For a “typical” terrestrial reptile, an acoustic stimulus moving through the air is a pressure wave. This external wave can exceed the pressure within the middle-ear cavity, in which case the tympanic membrane might be deformed and this deformation is ultimately transferred to the cochlea (resulting in what is called pressure-difference audition). Depending on its physical characteristics, the external pressure wave can also induce a vibration on the surface of the animal that can, in turn, be transferred to the cochlea (resulting in what is properly called vibration detection). An acoustic

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stimulus can also move through a substrate. Depending on their physical characteristics, these substrate pressure waves can be "picked up" if the organism is in direct physical contact with the substrate (resulting, again, in vibration detection). A recent experimental analysis demonstrated that the Ball Python (*Python regius*) is far more sensitive to vibration detection than it is to pressure differences. Indeed, the magnitude of the difference between the modalities is enough to argue that all acoustic stimuli would be experienced by this snake through vibration detection (Christensen *et al.*, 2012).

Auditory frequency-response range

For the purposes of this contribution, I will assume that the results of Christensen *et al.* (2012) can safely be extrapolated to all snakes and all acoustic stimuli (for additional treatments of audition versus vibration detection in snakes, see Young 2003, 2010). Regardless of the mode of stimulus detection or presentation or even the taxon being studied, all snakes share a relatively consistent and limited frequency response range. Among squamate reptiles, the auditory frequency-response range varies considerably (Table 1), but, even among squamates, the response range of the snakes is notably restricted. Noteworthy, however, is that these response ranges were determined physiologically whereas it is common in sensory studies to obtain wider frequency-response ranges using behavioural rather than physiological criteria (e. g., Ebert & Westhoff 2006). Indeed, Young and Harris (2006) found a slightly wider frequency-response range for rattlesnakes (*Crotalus*) using behavioural criteria.

The narrow auditory frequency-response range of snakes has been well documented (e. g., Wever & Vernon 1960; Wever 1978). To date, no functional explanation for the reduced auditory frequency range in snakes has been offered. Simplistically, there are (at least) three possible explanations: (1) impedance matching, (2) cochlear fluid mechanics, and (3) neural circuitry.

Table 1:
Auditory-frequency ranges for a variety of reptiles. All data taken from Wever (1978).

Taxon	Frequency range (Hz)	Peak sensitivity (dB)
“Typical” reptiles		
Hemidactylus	300–10.000	38
Iguana	200–7.000	32
Caiman	50–4.000	34
Varanus	100–5.000	26
Ameiva	150–9.500	9
Gerrhosaurus	150–5.000	15
Eumeces	150–10.000	30
Lacerta	250–6.000	19
Taxa with reduced or absent tympani		
Acontias	100–3.000	66
Anguis	200–5.000	62
Anniella	40–5.500	69
Ceratophora	150–5.500	69
Chamaeleo	100–2.500	44
Cophosaurus	300–3.500	24
Draco	250–4.000	63
Holbrookia	100–4.500	66
Phrynocephalus	150–4.000	59
Phrynosoma	200 - 6.000	49
Taxa with “re-entrant” perilymphatic systems		
Chelydra	100–1.500	13
Chrysemys	30–1.500	23
Testudes	40–1.500	18
Sphenodon	90–900	48
Blanus	100–3.000	63
Chamaeleo	100–2.500	44
Snakes	**100–650**	**45**

Impedance matching

Impedance matching means there is little or no difference in the resistance to wave propagation between the perilymphatic fluid at the oval window and the medium (air or substrate) through which the vibration was originally propagating. An impedance mismatch (a significant difference in resistance) could produce the relatively restricted frequency range observed in snakes.

Impedance matching will depend on the structures between the external environment and the oval window. For the purposes of this treatment, this means the external and middle ears. The lizard ear is bordered superficially by the tympanic membrane, a thin sheet of connective tissue and epithelium that is anchored to the quadrate anteriorly, to the retroarticular process of the mandible inferiorly, and bordered by a connective-tissue band and the depressor mandibulae on the posterior and superior surfaces. The deep, or medial, surface of the tympanic membrane is attached to several processes of the extracolumella (or extrastapes), a body of hyaline cartilage that extends from the tympanic membrane into the middle-ear cavity. The internal process of the extracolumella forms a direct contact with the quadrate (Fig. 1). The extra columella fuses to the distal tip of the osseous columella (or stapes), which spans the remainder of the middle-ear cavity before terminating in an expansive footplate that rests in the oval window (fenestra ovalis).

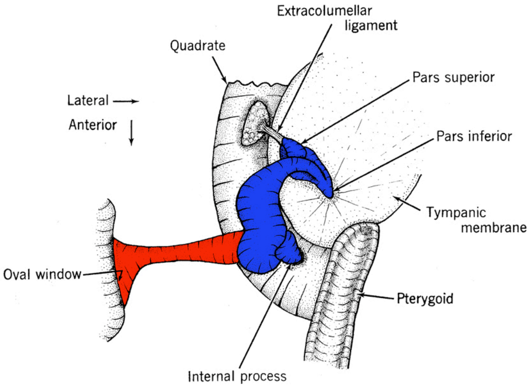

Figure 1:
Internal view of the lizard middle ear showing the columella (red), extracolumella (blue), and the diversity of the extracolumellar connections (modified from Wever 1978).

The lizard ear exhibits a wide range of structural variation. The tympanic membrane is completely lost in many species, particularly, although not exclusively, in smaller fossorial forms (e. g., Toerien 1963; Greer 2002). In other species, the tympanic membrane, although present, is covered with scalation (e. g., Wever 1978; Cogger 1986). The appearance of the tympanic membrane is dynamic in some lizards, particularly in some geckos (e. g., see Baird 1970), where contraction of a sphincter-like closure muscle can pull the adjacent scalation over (at least a portion of) the tympanic membrane (Weber 1973a). The tympanic membrane can lie flush with the surface of the scalation or deeper in the integument, thereby forming a shallow depression on the surface of the head.

Both the number and contacts of the extracolumellar processes are highly variable. In lizards lacking a tympanic membrane, the extracolumellar processes form connections with the inner surface of the integument, adjacent skeletal muscle, or the surface of isolated air-filled connective-tissue sacs (Wever & Gans 1973; Wever 1978). The processes can also form a direct link with the intercalary cartilage, a body of hyaline cartilage typically located adjacent to the proximal articulation of the quadrate (e. g., Wever 1973b). In some species, ligaments bind the extracolumella and/or the extracolumellar processes to adjacent structures (most commonly the intercalary cartilage and tympanic membrane) and, whereas the extracolumella and columella are typically fused, the nature of the contact varies and permits considerable mobility in some lizards (Wever 1978).

The middle-ear vibration-transmitting rod in snakes is the osseous columella (with an expanded footplate medially) (Fig. 2). As the columella extends laterally toward the quadrate, the bone gives way to hyaline cartilage. This portion of the columella has been homologised with the internal process. In snakes, there is commonly an additional cartilaginous element between the distal (cartilaginous) end of the columella and the quadrate that has been homologised with the stylohyal. In many snakes, there are additional isolated cartilaginous elements in addition to the stylohyal in this series; these have been homologised with the intercalary cartilage (e. g., de Beer 1937; Kamal & Hammouda 1965; Ludicke 1978). Rieppel (1980, 1993) has challenged many of these earlier homologies, but is in agreement that there are cartilaginous elements between the columella and the quadrate. Whether or not the stylohyal is present in snakes, the junction between the quadrate and the columellar complex resembles a synovial joint (Fig. 2) and is highly mobile, including, at least in some species, translational movements (Kley 2001). Although the vibration-transmitting rod of snakes has a composition distinct from that of lizards, the two systems functionally share cartilaginous ties to the quadrate, a transition from cartilage (distally) to bone (proximally), and a termination in the oval window.

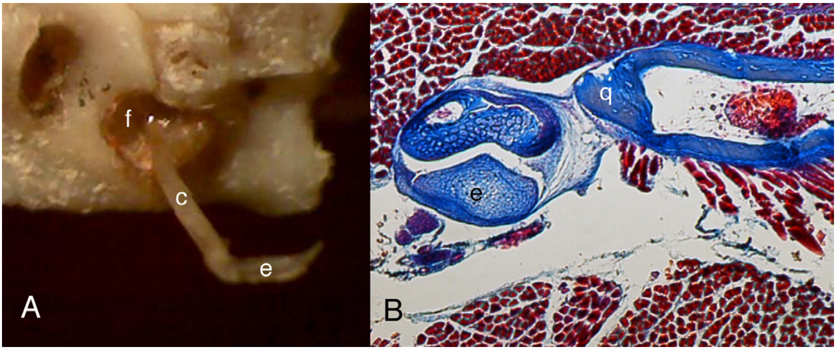

Figure 2:
The middle ear of the snake. A) Skull of *Thamnophis elegans* showing the columella (c), the expanded footplate (f) filling the oval window, and the distal extracolumella (e). B) Transverse section through the head of *Hypnale hypnale* showing the linkage between the extracolumella (e) and the quadrate (q).

Although the vibration-transmission components of the middle ear are similar in lizards and snakes, the external ear is different in that all snakes have lost the tympanic membrane entirely. As noted above, the tympanic membrane has also been lost in several lizard taxa and, if the frequency-response range of snakes is a reflection of impedance mismatches resulting from the absence of a tympanic membrane, similar frequency-response ranges would be expected in lizards that lack a tympanum. However, the lack of a tympanum is not closely associated with a reduced frequency-response range in lizards (Table 1). Although the tympanum, or its absence, is the logical place to start looking for impedance matching, it remains that any part of the auditory system can form the limiting agent (Manley 1972; Wever 1978; Ruggero & Temchin 2002; see also below).

Differences in cochlear-fluid mechanics are a second potential cause for a decreased auditory-frequency range. In most vertebrates, the perilymphatic pressure waves generated by columellar displacement of the oval window ultimately dissipate into the middle-ear cavity by way of the round window. In snakes, both the middle-ear cavity and the round window are lost (Wever 1978), necessitating a different mechanism for the dissipation of perilymphatic pressure waves. A perilymphatic duct extends from the scala tympani to the lateral surface of the braincase where it expands to form the juxtastapedial sinus, which surrounds the lateral (outer) surface of the columellar footplate (de Burlet 1934; Wever 1978). Wever (1978) called this type of perilymphatic circulation a "re-entrant fluid circuit" and noted that it should have two functional consequences for snakes: (1) the columella has to displace a greater mass of perilymphatic fluid (an impedance-matching problem) and (2) the pressure waves in the juxtastapedial sinus would dampen the vibrations of the columella.

A re-entrant fluid circuit is not unique to snakes and also occurs in some lizards and other reptile groups in which the round window has been lost. The exact course of the perilymphatic duct varies, however: in some taxa, it remains within the braincase, whereas, in others, it extends through a foramen to dissipate energy among the soft tissue of the head. If the frequency-response range of snakes is compared to that of lizards and other reptiles that have re-entrant fluid circuits (Table 1), it can be seen that all these taxa have frequency-response ranges that are narrower than those of a "typical" lizard. But, even within this comparative group, the frequency range of the snake is narrow.

Neural-circuit changes form a third potential cause for a decreased auditory-frequency range. The pressure waves within the perilymphatic fluid created by the displacement of the columella are ultimately transduced by the hair cells of the cochlear basilar papilla. The structure of the basilar papilla and cochlear duct of snakes has received relatively little attention (but see Miller 1966; Wever 1978). In lizards, the basilar papilla exhibits a wide range of morphological variation including separation into low- and high-frequency areas and the presence or absence of a tectorial membrane (e. g., Manley 2000). As Manley (2002) has noted, many of these morphological variants are not closely related to physiological performance and this also appears to be the case with snakes.

Within squamate reptiles, there are multiple neural pathways for audition. Not only have distinct low- and high-frequency pathways been described, but the first-order nuclei (e. g., Nucleus Magnocellularis) can receive either ipsi- or bilateral input and the second-order nuclei (e. g., Superior Olivary Nucleus) likely play varying roles in auditory processing (Christensen-Dalsgaard & Carr 2008).

The nature of both the first- and second-order cochlear nuclei is poorly known in snakes. Early workers provided contradictory reports for the same species, arguing about the presence of both the Nucleus Angularis and Nucleus Magnocellularis (for a review, see Young 2003). The comparative study performed by Miller (1980) reported that snakes posses a small Nucleus Angularis, a subdivided Nucleus Magnocellularis, and a Nucleus Laminaris that is larger than that found in most lizards. Unfortunately, the criteria used to distinguish these nuclei suggest that the results were strongly influenced by examining the snakes using a lizard template, a problem that is more prominent in the subsequent work of Defina and Kennedy (1983). To date, there has not been a complete description of the auditory pathway in any snake. The functional implications of these nuclei in snakes are unclear. Although previous workers have identified the Nucleus Angularis in snakes, this nucleus in lizards is associated primarily with higher-frequency stimuli outside of the auditory range of snakes.

There is much less structural variation in the auditory system of snakes than is known from the lizard ear (Wever 1978). Furthermore, the frequency response of the ear exhibits little variation among snakes; the variation that is known does not correlate well with body size, ecological habitat, or phylogeny (Wever 1978). This would be consistent with the hypothesis that the reentrant fluid circuit of snakes represents a functional constraint that limits frequency response. Because this means of perilymphatic fluid circulation coupled with the loss of a tympanic membrane is common to all snakes, it could explain the shared restricted auditory response of snakes as well as the relatively reduced morphological variation within the snake ear. The (slight) interspecific variations in auditory performance that have been documented among snakes might reflect the range of morphological variation in characters like the relative size of the columellar footplate (for an exploration of these ideas in gekkonoid lizards, see Werner & Igic 2002).

Evolution of the snake ear

In a functional sense, the snake ear can best be seen as a simplification of the "typical" lizard ear. The evolution of the snake ear entailed pronounced alterations including the loss of the tympanic membrane, the middle-ear cavity, the Eustachian tube, and the round window; the formation of a novel linkage between the columella and the quadrate; and the development of the juxtastapedial sinus (see above).

Historically, the morphological transitions associated with the snake ear have been ascribed to one of two selective pressures: fossoriality or increased gape. The fossoriality argument is predominately an argument from analogy. Because many of the lizards that lack a tympanic membrane are ground dwelling or fossorial, and because snakes lack a tympanic membrane, workers have frequently ascribed the evolution of the snake ear to fossoriality (e. g., Bellairs & Underwood 1951). There are, however, at least two major difficulties with this theory. First, it is not clear how many snakes truly qualify as being fossorial if fossorial is taken to mean “burrowing”. There are snakes that use their snout to displace soil (e. g., Deufel & Bruce 2004), but other snakes that move through the soil do so primarily, if not exclusively, by exploiting existing crevices and spaces. Functionally, this is very different from the burrowing locomotion observed in some squamates in which the head is used as a ram to create a tunnel in the substrate (e. g., Gans 1974). Aspects of the skull morphology of basal snakes have also been interpreted as specialisations for fossoriality (e. g., Rieppel & Maisano 2007), but the mechanics of burrowing (and the magnitude of forces acting on the skull) in these groups remains poorly known.

Second, whereas repeated exposure to soil and other surface matter might favour the covering or elimination of the relatively delicate tympanic membrane, how can this adaptation explain the losses of the Eustachian tube and other components of the middle ear? The loss of the tympanic membrane is fairly common in small ground-dwelling (or even fossorial) lizards, but almost all these species retain the remainder of the “typical” lizard ear. It is difficult to envision an external force acting on the head of a snake that would lead to the loss of a soft-tissue space like the middle-ear cavity, while favouring the retention of a relatively rigid coupling between the quadrate and the oval window.

The hypothesis that the snake ear evolved in response to selective pressures favouring a large gape (macrostomy) has also been advanced previously (e. g., Berman & Regal 1967). There are at least three major difficulties with this theory. First, molecular- and morphologically-based phylogenies have (with a reasonable degree of consistency) divided snakes into three major groups: Scolecophidia (or blind snakes), basal Alethinophidia, and Macrostomata

(Wilcox *et al.* 2002; Lee *et al.* 2007; Pyron & Burbrink 2012). As their name implies, it is only the derived macrostomatans that have a large gape, yet the other two groups also have "typical" snake ears. This point is not as decisive as it might initially appear. There remains some debate about how to divide the basal Alethinophidia from Macrostomata, and it has been proposed that the scolecophidians have secondarily lost macrostomy, which, if supported, would lend support to a link between macrostomy and the snake ear (e. g., Lee & Scanlon 2002; but see Rieppel 2012). Lastly, the past two decades have seen considerable activity in terms of the discovery, interpretation, and reinterpretation of snake fossils; some of these debates involve the degree of macrostomy present in the fossils and the relationship(s) between these fossil forms and the three groups of extant snakes (e. g., Lee & Caldwell 1998; Lee 1999).

The second major difficulty that arises in attempting to link the evolution of the snake ear to macrostomy is the basic mechanics of the latter. The snake gape is achieved primarily through the actions of the quadrates and lower jaws (for a review, see Cundall & Greene 2000). The ventral surface of the braincase forms one of the checks or limits on the gape. With the exception of the Eustachian tube, the entire ear of a snake is dorsal to the ventral surface of the braincase, and, as such, modifications or reductions of the ear complex would not increase gape.

The third major difficulty in reconciling the structure of the snake ear with macrostomy is the performance of the existing snake ear. Wever (1978) found that the sensitivity of the snake ear was not influenced by the relative gape of the jaws, which he attributed to the mobility of the connections between the quadrate, columellar complex, and the oval window. If the vibration-conducting link between the quadrate and the oval window can accommodate the skeletal displacements associated with macrostomy, it is difficult to see why the soft-tissue structures of the ear could not. Put more succinctly, how would macrostomy render the presence of the round window disadvantageous?

The key to the structural features of the snake ear might lie not in macrostomy *per se*, but in the increased mobility of the lower jaw and in changes in the region of the quadrate-mandibular joint. Relative to most lizards, snakes exhibit (1) increased mobility of the quadrate in the transverse plane, in part through a looser connection between the distal end of the quadrate and the posterior end of the upper jaw (the pterygoid) and (2) increased mobility of the mandible about the quadrate, including angular displacement in both the parasagittal and frontal planes as well as rotation about the long axis of the mandible. This increased mandibular kinesis is facilitated by a reduction in the relative size of the retroarticular process in snakes; the smaller size of this process enables the mandible to rotate unimpeded about the pivot point on the quadrate.

The relative reduction of the retroarticular process in snakes would have had two impacts on the tympanic membrane (and adjacent tissues). In the typical lizard ear, the retroarticular process forms the ventral anchor for the tympanic membrane; reducing this process in snakes would have reduced the structural support for the tympanum. Perhaps more importantly, the retroarticular process is the insertion site for the depressor mandibulae, the primary abductor of the lower jaw. In lizards, this muscle generally inserts posterior to the tympanic membrane, but, in snakes, the depressor mandibulae covers nearly the entire retroarticular process and much of the posterior surface of the quadrate.

The relative expansion of the depressor mandibulae in snakes, coupled with the reduction of the retroarticular process, although critical for the enhanced mobility of the mandible, might be incompatible with a tympanic membrane. The expansion of the depressor mandibulae along with other muscles associated with increased jaw movement in snakes, such as the protractor quadratus, might have led to the functional reduction and obliteration of the middle-ear cavity. Baird (1970) has argued that snakes have retained a vestigial middle-ear cavity as a small space immediately adjacent to the columella. Most workers have not accepted this interpretation. If the middle-ear cavity of snakes was lost, the remaining structural “specialisations” of the snake ear would follow. A Eustachian tube has no obvious function once isolated from the middle-ear cavity. Similarly, without a middle-ear cavity, the round window would have, at best, reduced efficiency in vibrational-energy dissipation.

Any general treatment of the evolution of the jaw joint in snakes is complicated by the scolecophidians. As has been nicely demonstrated (e. g., Kley 2006), the jaw system of scolecophidians is structurally and functionally distinct from all other snakes: the mandibles are joined in the midline (see also Young 1998), the system incorporates a great deal of translational movement (Kley 2001), and there is distinct flexion at the intramandibular joint (Kley & Brainerd 1999). Whereas this mode of feeding is certainly distinct from that of macrostomatan snakes, both incorporate considerable displacement (in several planes) of the mandible about the distal end of the quadrate. As such, the scolecophidian feeding system (whether or not it represents a neomorphic derivative of macrostomy) could still be associated with an increase in musculature about the proximal end of the mandible and reduction in the middle-ear cavity.

Literature cited

Baird I.L. (1970). The anatomy of the reptilian ear. In: *The Biology of the Reptilia, Vol. 2, Morphology B*. (eds. Gans C & Parsons TS). Academic Press, London, 193–275.

Bellairs A.d'A. & Underwood G. (1951). The origin of snakes. *Biol. Rev.*, 26, 193–237.

Berman D. & Regal P. (1967). The loss of the ophidian middle ear. *Evolution*, 21, 641–643.

Christensen C.B., Christensen-Dalsgaard J., Brandt C. & Madsen P.T. (2012). Hearing with an atympanic ear: good vibration and poor sound-pressure detection in the royal python, *Python regius*. *J. Exp. Biol.*, 215, 331–342.

Christensen-Dalsgaard J. & Carr C.E. (2008). Evolution of a sensory novelty: tympanic ears and the associated neural processing. *Brain Res. Bull.*, 75, 365–370.

Cogger H.G. (1986). *Reptiles and Amphibians of Australia*. 3rd ed. Reed, Sydney.

Cundall D. & Greene H. (2000). Feeding in snakes. In: *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates* (ed. Schwenk K). Academic Press New York, 293–333.

de Beer G. (1937). *The Development of the Vertebrate Skull*. Clarendon Press, Oxford.

de Burlet H. (1934). Zur vergleichenden Anatomie und Physiologie des perilymphatischen Raumes. *Acta Oto-Laryng.*, 13, 153–187.

Defina A.V. & Kennedy M.C. (1983). The cochlear nuclei in colubrid and boid snakes: a qualitative and quantitative study. *J. Morphol.*, 178, 285–301.

Deufel A. & Bruce S.D. (2004). Burrowing with a kinetic snout in a snake (Elapidae: *Aspidelaps scutatus*). *Integr. Comp. Biol.,* 44, 545–545.

Ebert J. & Westhoff G. (2006). Behavioural examination of the infrared sensitivity of rattlesnakes (*Crotalus atrox*) *J. Comp. Physiol. A*, 192, 941–947.

Gans C. (1974). *Biomechanics: An Approach to Vertebrate Biology*. J.B. Lippincott, Philadelphia.

Greer A.E. (2002). The loss of the external ear opening in scincid lizards. *J. Herpetol.*, 36, 544–555.

Hartline P. (1971a). Physiological basis for detection of sound and vibration in snakes. *J. Exp. Biol.*, 54, 349–371.

Hartline P. (1971b). Midbrain responses to the auditory and somatic vibration system in snakes. *J. Exp. Biol.*, 54, 373–390.

Kamal A.M. & Hammouda H.G. (1965). On the laterosphenoid bone in Ophidia. *Anat. Anz.*, 116, 116–123.

Kley N. (2001). Prey transport mechanisms in blindsnakes and the evolution of unilateral feeding systems in snakes. *Am. Zool.*, 41, 1321–1337.

Kley N. (2006). Morphology of the lower jaw and suspensorium in the Texas blindsnake, *Leptotyphlops dulcis* (Scolecophidia: leptotyphlopidae). *J. Morphol.*, 267, 494–515.

Kley N. & Brainerd, E. (1999). Feeding by mandibular raking in a snake. *Nature*, 402, 369–370.

Lee M.S.Y. (1999). The origin of snake feeding. *Nature*, 400, 655–659.

Lee M.S.Y. & Caldwell, M.W. (1998). Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. *Philos. Trans. Roy. Soc. B*, 353, 1521–1552.

Lee M.S.Y., Hugall, A., Lawson, R. & Scanlon, J.D. (2007). Phylogeny of snakes (Serpentes): combining morphological and molecular data in likelihood, Bayesian and parsimony analyses. *Syst. Biodiv.*, 5, 371–389.

Lee M.S.Y. & Scanlon, J.D. (2002). Snake phylogeny based on osteology, soft anatomy and ecology. *Biol. Rev.*, 77, 333–401.

Ludicke M. (1978). Die Blutgefässe und Kapillarnetze der Columella, des Sinus pericapsularis und der Cisterna perilymphatica der Serpentes. *Zool. Jahrb. Abt. Anat. Ontog.*, 99, 437–459.

Manley G.A. (1972). Frequency response of the middle ear of geckos. *J. Comp. Physiol.*, 81, 251–258.

Manley G.A. (2000). Cochlear mechanisms from a phylogenetic viewpoint. *Proc. Natl. Acad. Sci. USA*, 97, 11736–11743.

Manley G.A. (2002). Evolution of structure and function of the hearing organ of lizards. *J. Neurobiol.*, 53, 202–211.

Miller, M.R. (1966). The cochlear duct of lizards and snakes. *Am. Zool.,* 6, 421–429.

Miller M.R. (1980). The cochlear nuclei of snakes. *J. Comp. Neur.,*192, 717–736.

Pyron R.A. & Burbrink, F.T. (2012). Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution*, 66, 163–178.

Rieppel O. (1980). The sound-transmitting apparatus in primitive snakes and its phylogenetic significance. *Zoomorphol.*, 96, 45–62.

Rieppel O. (1993). Patterns of diversity in the reptilian skull. In: *The Skull*, Vol. 2 (eds Hanken, J & Hall BK). University of Chicago Press Chicago, 344–390.

Rieppel O. (2012). "Regressed" macrostomatan snakes. *Fieldiana* (*Life Earth Sci.*), 5, 99–103.

Rieppel O. & Maisano J.A. (2007). The skull of the rare Malaysian snake *Anomochilus leonardi* Smith, based on high-resolution X-ray computed tomography. *Zool. J. Linn. Soc.*, 149, 671–685.

Ruggero M.A. & Temchin A.N. (2002). The roles of the external, middle, and inner ears in determining the bandwidth of hearing. *Proc. Natl. Acad. Sci. USA*, 99, 13206–13210.

Toerien M.J. (1963). The sound-conducting systems of lizards without tympanic membranes. *Evolution*, 17, 540–547.

Walls G.L. (1942). The vertebrate eye and its adaptive raqdiation. *Cranbrook Inst. Sci. Bull.*, 19, 1–785.

Werner Y.L. & Igic P.G. (2002). The middle ear of gekkonoid lizards: interspecific variation in structure in relation to body size and to auditory sensitivity. *Hear. Res.*, 167, 33–45.

Wever E. G. (1973a). Closure muscles of the external auditory meatus in Gekkonidae. *J. Herpetol.*, 7, 323–329.

Wever E. G. (1973b). The function of the middle ear in lizards: divergent types. *J. Exp. Zool.*, 184, 97–126.

Wever E. G. (1978). *The Reptile Ear: its Structure and Function*. Princeton University Press, Princeton, New Jersey.

Wever E. G. & Gans C. (1973). The ear in Amphisbaenia (Reptilia); further anatomical observations. *J. Zool., Lond.*, 171, 189–206.

Wever E. G. & Vernon J. (1960). The problem of hearing in snakes. *J. Aud. Res.,* 1, 77–83.

Wilcox T.P., Zwickl D., Heath T. & Hillis D. (2002). Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Mol. Phylogenet. Evol*., 25, 361–371.

Young B.A. (1998). The comparative morphology of the intramandibular connective tissue in snakes (Reptilia: Squamata). *Zool. Anz*., 237, 59–84.

Young B.A. (2003). Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. *Quart. Rev. Biol.,* 78, 303–325.

Young B.A. (2010). Vibration detection in snakes. In: *The Use of Vibrations in Communication: Properties, Mechanisms and Functions across Taxa*. (ed. O'Connell-Rodwell CE). Transworld Research, Trivandrum, 85–98.

Young B.A. & Aguiar, A. (2002). Response of western diamondback rattlesnakes *Crotalus atrox* to airborne sounds. *J. Exp. Biol.*, 205, 3087–3092.

Young B.A. & Harris J. (2006). Auditory response of the Northern Pacific rattlesnake (*Crotalus viridis oreganus*): does behavior match physiology? *Northwest Sci.,* 80, 218–233.

Young B.A. & Morain M. (2002). The use of ground-borne vibrations for prey-localization in the Saharan sand vipers (*Cerastes*). *J. Exp. Biol.*, 205, 661–665.

Merrythoughts of the past and present: revisiting the homology of the furcula

Brian K. Hall[1] *and Matthew K. Vickaryous*[2]

[1] Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada; E-mail: bkh@dal.ca

[2] Department of Biomedical Sciences, Ontario Veterinary College, University of Guelph, 50 Stone Road, Guelph, Ontario, N1G 2W1, Canada; E-mail: mvickary@uoguelph.ca

> *The longest recorded flight of a domestic chicken* (Gallus domesticus) *is 13 seconds during which a distance of 91.9 m was flown (Guinness World Records; www.guinnessworldrecords.com/).*

Abstract

The homology of the furcula (= merrythought; wishbone) is amongst the oldest documented questions in comparative anatomy, and has long been discussed with reference to the origin of birds. Whereas modern evidence clearly demonstrates that modern birds are the descendants of Mesozoic dinosaurs, and that the furcula is a feature shared by fossil theropods, the question of its homology remains unresolved. Here we summarise changing views of the furcula, focusing in part on the critical contributions of Anthony P. Russell to this debate.

Introduction

Assessment of homology is fundamental to any comparison between features of organisms and to any assessment of relationships based upon those features (Hall 2003). In 1555, the naturalist Pierre Belon (1517–1564) published

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a pair of woodcuts comparing the hanging skeletons of a human and a bird (Panchen 1994). These images, representing one of the earliest depictions of homology determination, reveal a host of similarities between the two species. One of the most significant differences is that birds have an unpaired 'V'-shaped element bracing the shoulder girdle with the sternum, whereas humans do not. Belon identifies this element as "*…la Lunette ou Fourchette…*" and notes that it not found in other animals (see Panchen 1994, figure 8). More recently, this element has been termed the merrythought, skipjack, wishbone and furcula: a short history of merrythoughts is provided in Box 1.

The merrythought, or to use its modern equivalent, furcula, is typically a slender curved rod of bone. Disproportionate with its modest appearance, the furcula has long played a pivotal role in one of the longest lasting and most acrimonious debates in evolutionary biology – the relationship between birds and dinosaurs (Benton 2004; Currie *et al.* 2004; Langer & Benton 2006; Chiappe 2007; Feduccia 2012). Underpinning these arguments (discussed below) is the widespread acceptance (exclusive of Belon (1555)) of the furcula as the homologue of the paired clavicles or of the clavicles fused with a third pectoral element (reportedly contributing the hypocleideum). Three main lines of evidence support this furcula-equals-clavicles hypothesis. Both the furcula and clavicles

1. occupy a similar, mid-ventral position in the pectoral apparatus;
2. fail to co-exist within the same individual (no vertebrate, fossil or living, has both clavicles and a furcula); and
3. develop via intramembranous ossification, a mode of skeletogenesis that is otherwise atypical for the postcranial skeleton.

Furthermore, both elements have long been recognised as the most idiosyncratic components of the pectoral apparatus, with each having been independently lost on several occasions. For example, in mammals clavicles are absent in ungulates and many carnivores, whereas the furcula has been lost in musophagiforms and some species of parrots (Flower 1876; Glenny 1954; Glenny & Friedmann 1954; Hall 1986).

Box 1. Merrythoughts

Sir Gavin de Beer, a highly successful if autocratic Director of the British Museum (Natural History) in London from 1950 to 1960, was a frequent ‘voice’ on the BBC as an expert called in to speak on matters both biological and evolutionary.

In a BBC Science Survey broadcast aired on Thursday January 13, 1955, de Beer discussed the well-known 150-million-year-old fossil bird *Archaeopteryx* (*Archaeopteryx lithographica* to give it its full scientific name). This, the ‘first wing drawn in stone’ was discovered first in 1860 as a single feather and then in 1861 as a wonderfully preserved fossil (minus the skull) we know as the Berlin specimen (Chambers 2002). Both these and later specimens were found in the fine-grained Jurassic Solnhofen Limestone of southern Germany, which had been quarried for floors and tiles by the Romans 2000 years ago. The timing of these discoveries is significant, coming as they did one and two years after the publication of *On the Origin of Species* by Charles Darwin. Darwin (1859) used missing links, atavisms and vestiges as important evidence for organismal relationships and for evolutionary transformation (see discussion in Hall and Hallgrímsson (2013)).

Given the security of our knowledge of bird skeletons, that *Archaeopteryx* is a bird, and that birds evolved from reptiles, we might expect to find features of the skeleton in *Archaeopteryx* that are not seen in reptiles on the one hand or that show clear affinities to reptiles on the other. de Beer drew attention to the former and to the latter in his BBC broadcast when he said: “In *Archaeopteryx* the two collarbones were jointed to make a merrythought, instead of remaining separate as in reptiles.” From the quotation you can see that de Beer understood that reptiles and birds both have clavicles (collarbones) and that these bones are separate in reptiles and jointed or fused in the midline in *Archaeopteryx* and other birds to form what was called a *merrythought*. Nowadays such a fused element is known as a furcula or wishbone. So, for the crossword clue “Ibsen who? (anagram) — merrythought (8)”, the answer is “ wishbone.”

The origin of the term merrythought is debatable. One version suggests that when this bone was pulled apart by two people, the one left with the longest piece of bone would marry first, which was regarded as a ‘merry

Box 1. Continued

thought’. Alternatively, an older derivation refers to the very superficial resemblance between a portion of the cooked and dissected chicken and the female pudenda, apparently also a merry thought. de Beer’s use of the term clearly shows that he regarded *Archaeopteryx* as a bird and its merrythought as fused clavicles.

Wishbones and dinosaurs

Up until the late 19th century, a veritable who’s who of academics and naturalists supported interpretation of birds as dinosaurs, including (but not limited to) such prominent European and American morphologists, anatomists and palaeontologists as Thomas Henry Huxley, Edward Drinker Cope, Othniel Charles Marsh, Karl Gegenbaur, Samuel Wendell Williston, William Kitchen and his son T. Jeffery Parker, Georg Baur (the latter, a neo-Lamarckian), and the prominent evolutionary biologists Charles Darwin and Ernst Haeckel. However, this view was dramatically altered in 1926 from an unexpected source: a Danish artist named Gerhard Heilmann. Born in 1859, Heilmann was an avid naturalist, knowledgeable of Darwin’s theory of evolution, and with a passionate interest in bird evolution. Heilmann was a successful painter at the Royal Porcelain Works in Copenhagen, a designer of Danish banknotes, an acknowledged book illustrator and the designer of the logo for the Danish Ornithological Society, of which he was an enthusiastic member. His first publications on the evolutionary origin of birds were in Danish and published by the journal of the Danish Ornithological Society; they attracted minimal attention. Heilmann later compiled his articles into the book *Vor Nuvaerende Viden om Fuglenes Afstamning* [Our Present Knowledge of the Origin of Birds] (Heilmann 1916), a volume that was also largely overlooked. After 10 years of searching, Heilmann finally secured the small London publisher H. F. and G. Witherby (which had begun to publish bird books early in the 20th century) to publish a revised and wonderfully illustrated version of his book under the title *The Origin of Birds* (Heilmann, 1926).

The Origin of Birds provided a unique synthesis of fossil and embryological evidence, more than any specialist had ever brought together. His central thesis was so thorough and compelling that the fourth and final section of the book ('The Proavian') became the final word on the evolution of birds for the next half century. Why? Because of the furcula.

Heilmann conducted a detailed re-examination of what were then the two most complete specimens of *Archaeopteryx*, namely the London and Berlin specimens. By comparing these skeletons with other known fossil reptiles including dinosaurs, Heilmann sought to identify likely ancestors for modern birds. Despite their name, ornithischians, such as the large-bodied and herbivorous sauropodomorphs (e. g., *Diplodocus*), ceratopsians (e. g., *Triceratops*) and thyreophorans (e. g., *Stegosaurus*), share few obvious similarities with birds. That left the ornithopods ('bird foot'), such as *Iguanodon*, and the theropods ('beast foot'), such as *Tyrannosaurus*. Heilmann's close point-by-point comparison revealed that theropod skeletons were the most similar to those of modern birds. Furthermore, from what was known of dinosaur ecology, theropods and birds appeared to have similar lifestyles, and perhaps even similar behaviours.

In spite of all the observed similarities, Heilmann also identified a single and yet unavoidable piece of evidence that argued *against* theropods as the ancestors of birds: theropods (and indeed all dinosaurs) appeared to lack a furcula as well as their widely assumed precursor, clavicles.

Heilmann was totally beholden to a law of evolution proposed by the Belgian palaeontologist Louis Dollo in 1893 (Dollo 1893; also see Gould 1970, Hall 2002). Dollo's law of irreversibility is simple: once a structure has been lost from a lineage it can never re-evolve. (It is worth noting however that Dollo actually said *never re-evolve in the same form*, an important detail that is usually omitted or not realised.) For Heilmann and his strict interpretation of irreversibility, one datum outweighed many, completely tipping the balance and changing the prevailing view of the origin of birds for more than 40 years. The fact that dinosaurs lacked a furcula/clavicles so convinced Heilmann that he disregarded all the other evidence and concluded that both birds and dinosaurs must have evolved from a more distant ancestor, one with clavicles. Clavicles were then retained (albeit in a fused form) by birds but lost in dinosaurs. Heilmann described a hypothetical ancestor, *Proavis*, and argued that *Archaeopteryx* was not a missing link between birds and reptiles but an early descendant of *Proavis* instead.

Heilmann's evidence, and more significantly, his interpretation of the evidence was greeted with acclaim, enthusiasm and barely a word of dissent, a finding second only to the discovery of *Archaeopteryx* itself. And so it remained for almost 50 years. Over time, new discoveries, such as the theropod *Deinonychus antirrhopus* with its distinctive wrist and claws (Ostrom 1969), and methods of investigating the interrelationships of species (e. g., Gauthier 1986) revised and refined our understanding of bird origins. Not long after describing the very bird-like *Deinonychus*, Ostrom began to re-evaluate bird origins (see Ostrom 1973, 1974, 1976, 1991). Ostrom was struck by many of the same compelling features bridging the gap between modern birds and fossil theropods that Huxley (1868, 1870) and others had accepted a century before. Furthermore, various furcula-bearing theropods had since been reported in the literature (e. g., *Segisaurus*; Camp 1936). Ostrom concluded that the issue of furcula homology was irrelevant to the question of bird evolution, stating that "…the putative absence of theropod clavicles has no bearing on the question of bird origins" (Ostrom 1976: 166).

In the years that followed, the furcula has since been identified among an ever increasing number of theropods dating back to the Late Triassic, including representative members of most major lineages (e. g., coelophysoids, coelurosaurs, oviraptorsaurs, therizinosauroids, allosauroids, tyrannosaurids, troodontids and dromaeosaurids; Barsbold 1983; Bryant & Russell 1993; Chure & Madsen 1996; Makovicky & Currie 1998; Norell *et al.* 1997; see also Nesbitt *et al.* 2009). Current evidence is unequivocal: (1) birds are dinosaurs, (2) theropod dinosaurs have a furcula, and (3) the evolution of the furcula predates the origin of flight. Although we might expect the story to end here, the question of homology remains. Does the furcula equal the fused clavicles?

Questioning convention

As noted previously, the furcula-equals-clavicles hypothesis is supported by three main criteria. These two elements: (1) occupy a similar position in the body, (2) never co-exist in the same individual, and (3) share a common mode of development (intramembranous ossification). Whereas other elements of the pectoral apparatus, including the scapula, coracoid and sternum, arise as cartilage models later replaced by bone (Fell 1939; Klima 1962; also see the literature summarised in Vickaryous & Hall (2006, 2010)), the furcula and clavicles each form directly as bone without a transient cartilaginous phase. However, the intramembranous origin of the furcula has not gone unchallenged. In 1968, an investigation of furcula development in Japanese Quail (*Coturnix coturnix japonica*) concluded that this element did preform in cartilage (Lansdown 1968). As revealed by serial histology and a newly developed silver impregnation-toluidine blue histochemical protocol, the developing furcula demonstrates faint metachromatic staining, indicating the presence of glycosaminoglycans (a gel-like component of the extracellular matrix that is characteristic of, but not exclusive to, cartilage). Accordingly, it was reasoned that the furcula was similar to other elements of the pectoral apparatus in that it develops from a cartilaginous precursor (Lansdown 1968). It is here that Tony Russell enters our story.

In 1985, Russell and Joffe re-investigated Lansdown's conclusions by repeating his experiment, adding several other histochemical methods (Periodic acid-Schiff, Masson's trichrome, alizarin red and picro-ponceau), as well as looking at both quail and chicken (*Gallus gallus*) embryos (Russell & Joffe 1985). They observed that histogenesis of the furcula was identical to that observed in the palatine bone (an element widely recognised as undergoing intramembranous ossification) and quite unlike that of the coracoid (an element known to preform in cartilage). In particular, they found that whereas the coracoid is strongly metachromatic, similar staining was absent from the furcula and palatine. Furthermore, the matrix of the developing furcula and palatine were found to stain intensely with collagen stains whereas that of the coracoid did not. They concluded that the furcula did indeed undergo intramembranous ossification (Russell & Joffe 1985), a finding since confirmed by others (Hall 1986; Vickaryous & Hall 2010).

A second important contribution related to the furcula came from Russell's laboratory in 1993. Although the furcula remained widely recognised as the homologue of the fused clavicles (Hall 2005, in press), the test of congruence (*sensu* de Pinna 1991; Rieppel 1996)—as applied here: do the furcula and clavicles share a common ancestry?—had yet to be strictly applied. Bryant and Russell (1993; also see Box 2) reviewed the reported occurrence of the furcula and clavicles among dinosaurs and several closely related outgroups

Box 2. Homology, persistence and transformation (with thanks to Tony Russell).

A decade after the publication of the paper by Russell and Joffe (1985), one of us (BKH) received a letter from Tony (August 10, 1994) along with a copy of the Glenny and Friedman (1954) paper on the nature of the furculae in three species of birds from Madagascar that comprise the family Mesoenatidae: *Mesoenas variagata* (the White-Breasted Mesite), *Mesoenas unicolor* (the White-Breasted Roatelo) and *Mesoenas benschi* (the Roatelo). In the three species, the head of the clavicle (epicleidium) is reduced to a vestige. The place of the ramus of the clavicle is occupied by a strong ligament that is broad (*M. variagata*), "narrow and strong" (*M. unicolor*) or "thread-like or nearly absent" (*M. benschi*) (Glenny & Friedman 1954: 111). The authors' interpretation is that "the body of the clavicle… *remains as* a strong ligament in *Mesoenas*" (Glenny & Friedman 1954: 111; emphasis added), although they further note that identification of the ligament as "*ligamentum corpus clavicula*" (that is, as homologous with the clavicle) is a matter of interpretation (Glenny & Friedman 1954: 111).

Assessment of homology was Tony Russell's interest in the study: "I would be interested in…discussing with you the implications of clavicular non-ossification and persistence of a 'ligament'. There may be something very interesting here for the interpretation of homologies and the fluctuation of characters in phylogeny." (Letter dated August 10, 1994). In a follow-up letter dated September 27, 1994, BKH drew Tony's attention to a study just published in *Systematic Biology* in which McKitrick examined situations in birds in which individual muscles were present or absent, which looked to be a parallel situation in the role of ontogeny in homology assessment (McKitrick 1994).

BKH suggested surveying some museum collections, asking whether it was possible to find information from the literature on groups of birds with varying degrees of clavicle reduction. Tony's response (October 11, 1994) reveals his awareness of the thorniness of the issues: "I believe our problem is a rather thorny one in that it has a developmental transformational context. Is a clavicle a clavicle (or whatever) if it doesn't ossify? What is our nomenclatural basis for the recognition of structures? … Probably the best group of birds to look at developmental reduction in would be, from the viewpoint of accessibility, the parrots and their relatives." Glenny and Friedman (1954: 111) had noted that reduction of the clavicle to a ligament is "found in a great many of the Old World Parrots".

Box 2. Continued

BKH had published on secondary cartilage in the skull of a parrot, the Eastern Rosella (*Platycercus eximius*) (Hall 1967) and was organising a sabbatical in Western Australia. Over 300 parrots were housed in a collection in Canberra, ACT, but BKH never got around to examining them.

As it turned out, Tony had made a substantial start examining specimens at the British Museum (Natural History) avian repository in Tring in Hertfordshire, 48 km northwest of London. The birds examined included Glenny's specimens. Tony generously provided a copy of his notes, noting (October 31, 1994) "the potential for the occurrence of additional 'ossifications' within the field of the ligamentous sheet of the breast-shoulder apparatus, particularly between the coracoids and the sternum". The presence of such ossifications is likely one of the major confounding issues to assessing clavicle reduction and homology. Tony enclosed photographs of several specimens he had examined to show the extent of variation present. Were it not for having to keep this manuscript 'secret' from Tony, we would have asked for his permission to reproduce them here for these specimens show:

> "An extensive ligamentous sheet between the furcula and coracoids posteriorly, and the furcula and sternal keel ventrally" in the Little Corella (*Cacatua sanguinea*);
> "A very slight and reduced furcula and, behind it, two 'ossifications' extending from the sternum to the dorsal extremity of the coracoid" in the Ornate Lorikeet (*Trichoglossus ornatus*); and
> "Similar structures" in the Rainbow Lorikeet (*Trichoglossus haematodus*) (Letter from APR to BKH dated October 31, 1994).

Although a detailed comparative analysis of parrot clavicles/furculae and ligamentous ossifications remains for the future (post-retirement project?), Tony Russell continued his interest in furculae within the context of the presence of the paired clavicles in dinosaurs. The resulting paper (Bryant & Russell 1993), which is discussed in the text, raises fundamental issues concerning the homology of the furcula outlined in this chapter.

(e. g., the ornithodirans *Lagosuchus* and Pterosauria). Whereas they were able to confirm the presence of a furcula or paired clavicle-like elements among various fossil dinosaurs, the absence of these elements from immediate immediate outgroups was recognised as problematic. In particular, they noted that there were no stringent criteria for determining if the apparent non-appearance of the furcula (or clavicle-like elements) represented: (1) a true absence (i.e., they had been lost as is commonly accepted for fossil crocodylomorphs) or (2) that the element(s) were in fact present but not preserved/recovered or not ossified (as is commonly accepted for dinosaurian outgroups). As noted by Bryant and Russell (1993: 171) "…ancestral archosaurs [have] been protected from the test of congruence through *ad hoc* hypotheses of non-preservation". Since this publication first appeared, mounting evidence has clearly demonstrated that many fossil theropods had a furcula (see Nesbitt *et al.* 2009). However, whereas this provides important information on the presence of the furcula among theropods, it does not address the question of furcula homology (i.e., what is the homologue of the furcula among the immediate outgroups of Theropoda?). As first noted by Bryant and Russell (1993), the test of congruence (*sensu* de Pinna 1991; Rieppel 1996) has yet to be fully applied. How do we know if the furcula is the fused clavicles or something else?

An alternative proposal

To set out the problem, Bryant and Russell (1993) recognised three possibilities for the origin of the furcula:

1. a single element that arises by fusion of the paired clavicles and so is homologous with the clavicles;
2. a neomorphic skeletal element that occupies the same position as the clavicles in other groups, but that is unrelated to and therefore is not homologous with the clavicles; or
3. a single or fused element(s) homologous with another element of the ancestral pectoral girdle.

Ancestrally, all reptiles have a single midline bone that underpins the pectoral girdle. Among early fossil reptiles, modern lizards and crocodylians, this bone is known as the interclavicle. During the evolution of turtles, the interclavicle became integrated into the plastron (lower shell) and, given its distinct shape and position, received a new name, the entoplastron (Lee 1996).

Among archosaurs, the interclavicle is common to pseudosuchians (and remains well-developed in modern crocodylians), but is interpreted as having been lost among ornithodirans, the group including birds and fossil dinosaurs. Until recently, however, this *ad hoc* reasoning had yet to be challenged.

Similar to the furcula, the interclavicle occupies a mid-ventral position within the pectoral apparatus. Building on this observation, we (Vickaryous & Hall 2010) then compared the mode and pattern of skeletogenesis of each element. We determined that both the furcula and the interclavicle are unique among postcranial elements in that they each develop from a single pair of cell condensations that initiate intramembranous ossification before fusing into a single bone. Next we reviewed the fossil record. Although paired, clavicle-like elements have been reported for various non-theropod dinosaurs (e. g., basal ceratopsians, prosauropods; Chinnery & Weishampel 1998; Yates & Vasconcelos 2005) and the pectoral apparatus of basal ornithodirans (the immediate ancestors of dinosaurs) remains poorly understood. Therefore, it remains uncertain if the furcula of theropods represents the fusion of clavicles or if the paired elements of non-theropods represent the non-fusion of the interclavicular primordia. Accordingly, we advanced the alternative furcula-equals-interclavicle hypothesis (Vickaryous & Hall 2010). Similar to clavicles, both the furcula and interclavicle:

1. occupy a similar, mid-ventral position in the pectoral apparatus;
2. fail to co-exist within the same individual (no vertebrate, fossil or living, has both an interclavicle and a furcula); and
3. develop via intramembranous ossification, a mode of skeletogenesis that is otherwise atypical for the postcranial skeleton.

In support of these findings, mapping the occurrence of the dermal pectoral elements onto a phylogeny reveals that the interclavicle is more parsimoniously interpreted as the homologue of the furcula than are the fused clavicles (Maidment & Barrett 2011: their Figure 5; see also Vickaryous & Hall (2010: their Figure 4)). As demonstrated by Maidment & Barrett, the traditional furcula-equals-clavicle hypothesis requires clavicles to be lost three times (once in each of crocodylians, ornithischian dinosaurs and ratites birds such as ostriches, plus the loss of the interclavicle amongst ornithodirans), whereas the revised furcula-equals-interclavicle hypothesis requires the clavicles to be lost only twice (in each of ornithodirans and crocodylians). Although interclavicles have recently been identified in sauropods (Tschopp & Mateus 2012), suggesting that these elements were present in some non-avian dinosaurs, the issue of furcula homology is unlikely to be resolved until fossil material representing the complete transition between basal ornithodirans and dinosaurs is collected and the test of congruence reapplied.

We have come full circle. We know that birds arose from dinosaurs. We know that some non-avian dinosaurs possessed a furcula. But we still don't know whether the furcula represents the interclavicle, a neomorph or fused clavicles. Now that is a merry thought.

Acknowledgements

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Literature cited

Barsbold R. (1981). "Avian" features in the morphology of predatory dinosaurs. *Trans. Joint Soviet Mongo. Paleontol. Exp.,* 24, 96–103.

Belon P. (1555). *L'Histoire de la Nature des Oyseaux, avec leurs Descriptions, & Naifs Portraiêt Retirez du Naturel.* Guillaume Cavellat, Paris.

Benton M.J. (2004). Origin and relationships of Dinosauria. In: *The Dinosauria.* 2nd edition (eds. Weishampel DB, Dodson P & Osmolska H). University of California Press Berkeley, California, 7–19.

Bryant H.N. & Russell A.P. (1993). The occurrence of clavicles within Dinosauria: implications of homology of the avian furcula and the utility of negative evidence. *J. Vertebr. Paleontol.,* 13, 171–184.

Camp C.L. (1936). A new type of small bipedal dinosaur from the Navajo Sandstone of Arizona. *Univ. Calif. Publ., Bull. Dept. Geol. Sci.,* 24, 39–56.

Carrano M.T., Hutchinson J.R. & Sampson S.D. (2005). New information on *Segisaurus halli*, a small theropod dinosaur from the Early Jurassic of Arizona. *J. Vertebr. Paleontol.,* 25, 835–849.

Chambers P. (2002). *Bones of Contention: The Archaeopteryx Scandals*. John Murray, London.

Chiappe L.M. (2007). *Glorified Dinosaurs: The Origin and Early Evolution of Birds*. John Wiley and Sons, Hoboken, New Jersey.

Chure D.J. & Madsen J.H. (1996). On the presence of furculae in some non-maniraptoran theropods. *J. Vertebr. Paleontol.,*16, 573–577.

Chinnery B.J. & Weishampel D.B. (1998). *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsia) and relationships among basal Ceratopsians. *J. Vertebr. Paleontol*., 18, 569–585.

Currie P.J., Koppelhus E.B., Shugar M.A. & Wright, J.L. (2004). *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Indiana University Press, Bloomington, Indiana.

Darwin C. (1859). *On the Origin of Species by Means of Natural Selection.* John Murray, London.

de Pinna M. (1991). Concepts and tests of homology in the cladistic paradigm. *Cladistics,* 7, 367–394.

Dollo L. (1893). Les lois de l'évolution. *Bull. Belg. Soc. Geol. Palaeontol. Hydrol.,* 8, 164–166.

Flower W.H. (1876). *Osteology of the Mammalia.* 2nd edition. Macmillan and Co., London.

Feduccia A. (2012). *Riddle of the Feathered Dragons: Hidden Birds of China*. Yale University Press, New Haven, Connecticut.

Fell H.R. (1939). The origin and developmental mechanics of the avian sternum. *Philos. Trans. Roy. Soc. Lond. B,* 229, 407–463.

Gauthier J.A. (1986). Saurischian monophyly and the origin of birds. *Mem. Calif. Acad. Sci*., 8, 1–55.

Glenny F.H. & Friedmann H. (1954). Reduction of the clavicles in the Mesoenatidae, with some remarks concerning the relationship of the clavicle to flight-function in birds. *Ohio J. Sci.,* 54, 111–113.

Glenny F.H. (1954). The clavicles and dorsal carotid arteries as indices of phyletic relations and levels of avian evolution. *Anat. Anz*., 101, 95–100.

Gould S. J. (1970). Dollo on Dollo's Law: irreversibility and the status of evolutionary laws. *J. Hist. Biol.,* 3, 189–212.

Hall B.K. (1967). The distribution and fate of adventitious cartilage in the skull of the eastern rosella, *Platycercus eximius* (Aves: Psittaciformes). *Aust. J. Zool*., 15, 685–698

Hall B.K. (1986). The role of movement and tissue interactions in the development and growth of bone and secondary cartilage in the clavicle of the embryonic chick. *J. Embryol. Exp. Morphol.,* 93, 133–152.

Hall B.K. (2001). Development of the clavicles in birds and mammals. *J. Exp. Zool*., 289, 153–161.

Hall B.K. (2002). Dollo's Law. In *Encyclopedia of Evolution, Volume 1* (ed. Pagel M), Oxford University Press New York, 287–288.

Hall B.K. (2003). Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biol. Rev*., 78, 409–433.

Hall B.K. (2005). *Bones and Cartilage: Developmental and Evolutionary Skeletal Biology*. Elsevier Academic Press, New York.

Hall B.K. (In press). *Bones and Cartilage: Developmental and Evolutionary Skeletal Biology*. 2nd ed. Elsevier Academic Press, New York.

Hall B.K. & Hallgrímsson B. (2013). *Strickberger's Evolution*. 5th edition. Jones and Bartlett, Burlington, Massachusetts.

Heilmann G. (1916). *Vor Nuvaerende Viden om Fuglenes Afstamning*. Copenhagen.

Heilmann G. (1926). *The Origin of Birds*. Witherby, London.

Huxley T.H. (1868). On the animals which are most nearly intermediate between birds and reptiles. *Ann. Mag. Nat. Hist*., 2, 66–75.

Huxley T.H. (1870). Further evidence of the affinity between dinosaurian reptiles and birds. *Proc. Geol. Soc. Lond.,* 26, 12–31.

Klima M. (1962). The morphogenesis of the avian sternum. *Acta Acad. Sci. Cechslov.,* 34, 151–194.

Langer M.C. & Benton M.J. (2006). Early dinosaurs: a phylogenetic study. *J. Syst. Palaeontol.,* 4, 309–358.

Lansdown A.B.G. (1968). The origin and early development of the clavicle in the quail (*Coturnix c. japonica*). *J. Zool. Lond.,* 156, 307–312.

Lee M.S.Y. (1996). The homologies and early evolution of the shoulder girdle in turtles. *Proc. Roy. Soc. Lond. B,* 263, 111–117.

Maidment S.C.R. & Barrett P.M. (2011). The locomotor musculature of basal ornithischian dinosaurs. *J. Vertebr. Paleont.,* 31, 1265–1291.

Makovicky P. & Currie P.J. (1998). The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. *J. Vertebr. Paleontol.,* 18, 143–149.

McKitrick M. C. (1994). On homology and the ontological relationship of parts, *Syst. Biol.*, 43, 1–10.

Nesbitt S.J., Turner A.H., Spaulding M., Conrad J.L. & Norell M.A. (2009). The theropod furcula. *J. Morphol.*, 270, 856–879.

Norell M.A., Makovicky P. & Clark J. M. (1997). A *Velociraptor* wishbone. *Nature,* 389, 447.

Osborn H.F. (1924). Three new Theropoda, *Protoceratops* zone, Central Mongolia. *Am. Mus. Novit.*, 122, 1–12.

Ostrom J.H. (1969). Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.*, 30, 1–172.

Ostrom J.H. (1973). The ancestry of birds. *Nature,* 242, 136.

Ostrom J.H. (1974). *Archaeopteryx* and the origin of flight. *Quart. Rev. Biol.*, 49, 27–47.

Ostrom J.H. (1976). *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.*, 8, 91–182.

Ostrom J.H. (1991). The question of the origin of birds. In: *Origins of the Higher Groups of Tetrapods: Controversy and Consensus* (eds. Schultze, H-P & Trueb, L). Cornell University Press Ithaca, New York, 467–484.

Panchen A.L. (1994). Richard Owen and the concept of homology. In: *Homology: the Hierarchial Basis of Comparative Biology* (ed. Hall BK). Academic Press New York, 22–62.

Rieppel O. (1996). Testing the homology by congruence: the pectoral girdle of turtles. *Proc. Roy. Soc. Lond. Ser B. Biol. Sci.,* 263, 1395–1398.

Russell A.P. & Joffe D.J. (1985). The early development of the quail (*Coturnix c. japonica*) furcula reconsidered. *J. Zool.,* 206, 69–81.

Tschopp E. & Mateus O. (2013). Clavicles, interclavicles, gastralia, and sterna ribs in sauropod dinosaurs: new reports from Diplodocidae and their morphological, functional and evolutionary implications. *J. Anat.*, 222, 321–340.

Vickaryous, M.K. & Hall, B.K. (2006). Homology of the reptilian coracoid and a reappraisal of the evolution and development of the amniote pectoral apparatus. *J. Anat.,* 208, 263–285.

Vickaryous M.K. & Hall B.K. (2010). Comparative development of the crocodylian interclavicle and avian furcula, with comments on the homology of dermal elements in the pectoral apparatus. *J. Exp. Zool. (Mol. Dev. Evol.),* 314B, 196–207.

Yates A.M. & Vasconcelos C.C. (2005). Furcula-like clavicles in the prosauropod dinosaur *Massospondylus*. *J. Vertebr. Paleontol.,* 25, 466–468.

Habitat and microhabitat preferences in a Nova Scotian Carrion Beetle (Coleoptera: Silphidae) community

Amanda J. Lowe[1] *and Randolph F. Lauff*[2]

[1] Department of Biology, Saint Mary's University, 923 Robie Street, Halifax, Nova Scotia, B3H 3C3, Canada
[2] Department of Biology, St. Francis Xavier University, 2320 Notre Dame Avenue, Antigonish, Nova Scotia, B2G 2W5, Canada; E-mail: rlauff@stfx.ca

Abstract

The burying beetle community in Antigonish County, Nova Scotia, Canada, was surveyed in hemlock and mixed woods at two heights: canopy (10 m) and near-ground (1 m). Habitat preferences were found to exist in six of the nine silphid species captured. *Nicrophorus defodiens* and *Nicrophorus orbicollis* were caught at the mixed-wood site in significantly greater numbers than at the hemlock site, whereas *Nicrophorus sayi, Nicrophorus pustulatus, Necrophila americana,* and *Necrodes surinamensis* were caught in higher numbers at the hemlock site. Microhabitat preferences were found in all species, including three species never before noted in studies of height preference. *Nicrophorus tomentosus, N. pustulatus,* and *N. surinamensis* were captured in the canopy in higher numbers than in near-ground traps, whereas a higher number of *N. defodiens, N. sayi, N. orbicollis, N. americana, and Oiceoptoma noveboracense* were captured in near-ground traps than in canopy traps. It would appear that an understudied 3D component to the interactions exists among members of the burying beetle community.

Introduction

Carrion beetle preferences for habitats such as forests, marshes, open fields, and transition zones have been documented (Anderson 1982; Schubeck 1983;

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Beninger & Peck 1992). Sometimes, geographically-separated conspecifics have been shown to prefer two distinct habitat types. For example, the habitat preferences of nicrophorines in Kansas (Lingafelter 1995) were sometimes different from those of conspecifics that were previously recorded by Anderson (1982) in eastern Ontario and by Schubeck (1983) in New Jersey. The reason for such variation in habitat preference of a species remains unknown.

The appropriate substrate for burial is thought to be a determining factor in habitat use (Pukowski 1933; Scott 1998). Bishop *et al.* (2002) suggested that soil texture, including particle size and root proliferation, might influence species partitioning based on the ease of burial. Larger species, such as *Nicrophorus orbicollis,* can discriminate between soils to select those with more a fibrous nature (Muths 1991), whereas smaller species might not dig into substrate at all (Anderson & Peck 1985). This discriminatory behaviour is vital because the substrate will affect both the speed of burials and the exclusiveness of the resource (Muths 1991). A lack of favourable substrates for burial could result in beetles using less-preferred habitats within their geographical range.

Wilson *et al.* (1984: 216) suggested that the "competitive environment specific to a locality" might be the determining force affecting community structure. Congeners, along with a multitude of vertebrate and invertebrate scavengers as well as decomposers, create substantial competition pressure that a burying beetle must overcome to defend a carcass.

Walker (1957) attributed the differences in beetle abundance among similar habitats to the microclimates within them. Interspecific behavioural differences, like flight ability, are proposed mechanisms enabling species segregation into microhabitats. Shubeck (1970) noted that *Nicrophorus tomentosus* has the ability to fly directly to carrion whereas *N. orbicollis* flies to the general vicinity and then walks to the carrion. Thus, the two species can coexist in the same habitat by exploiting carrion of two different microhabitats. In addition, the temporal separation of adult activity likely also reduces much intrageneric competition.

Carrion beetles have been traditionally caught using ground-based methods, such as baited pitfall traps and ground-level carrion (Anderson 1982; Wilson & Fudge 1984; Lingafelter 1995). However, these sampling techniques might result in an incomplete survey of the *Nicrophorus* community. Wilson and Knollenberg (1984) found that recently eclosed beetles were more attracted to the pitfall traps than were reproductively-active adults. In addition, the baited pitfall traps used in most studies fail to catch beetles that do not routinely forage on the ground. Instead, studies over a vertical gradient reveal patterns of species' distributions that would otherwise go unnoticed (Su & Woods 2001; Wilhelm *et al.* 2001; Schroeder *et al.* 2009).

Shubeck (1970) was the first to compare the response of burying beetles between ground-level and suspended carrion (at 1.5 m above the ground). However, studies conducted at heights greater than a couple of metres have been investigated only recently (Su & Woods 2001; Ulyshen & Hanula 2007; Schroeder *et al.* 2009; Lowe & Lauff 2012). Using traps at several heights above the ground, Ulyshen *et al.* (2007) showed that the vertical distribution of beetles, even within a family, can be diverse.

The current study investigates the preference of carrion beetles (Coleoptera: Silphidae) between two forest types, mixed woods and hemlock, as well as between canopy and near-ground heights.

Materials and methods

Study sites and timing

This study ran for 14 weeks from May 20th to August 19th, 2008. Two study sites were used, both in the northeastern part of mainland Nova Scotia, Canada. The mixed-wood study site was located approximately 2 km north of the town of Antigonish on grounds owned by the Sisters of St. Martha, Bethany Convent (centred at N 45° 38' 47.3", W 61° 59' 11.6"; Fig. 1). This site was characterised by Red and Sugar Maples (*Acer rubrum* and *Acer saccharum*, respectively), Yellow and White Birch (*Betulla alleghaniensis* and *Betulla papyrifera*, respectively), Balsam Fir (*Abies balsamea*), White Spruce (*Picea glauca*), and White Ash (*Fraxinus americana*). There was abundant ground cover from young saplings and ferns, among others.

The hemlock stand was located approximately 5 km north of the mixed-wood site (centred at N 45° 42' 25.5", W 61° 56' 49.7"; Fig. 1). This site was located on a south-facing slope of a small valley. Other than the predominant Eastern Hemlocks (*Tsuga canadensis*), scattered Red Maple were also present. There were fewer understory saplings and less ground cover when compared with the mixed-wood site, which is characteristic of hemlock stands (Strickland 1987).

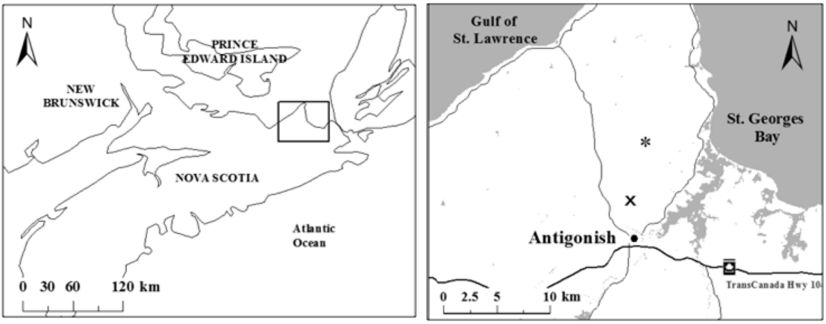

Figure 1:
The study site locations (✱ = hemlock habitat, **X** = mixed-wood habitat).

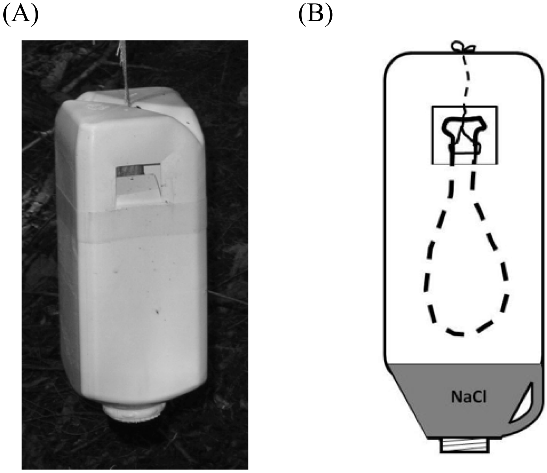

Figure 2:
(A) A trap head showing the entry hole for access to the bait. (B) Schematic drawing of the trap head showing the chicken leg bait and saturated salt solution in the bottom.

Trap design and placement

Each trap consisted of two trap heads made of upside-down, opaque 2 l plastic jugs (Fig. 2). Beetles gained access to the carrion by entering the trap through a 3 x 3 cm opening cut into one side of the jug, with the upper edge of the hole approximately 3 cm from the top of the trap head. Each trap head was baited with a single chicken leg hung by a string threaded through a hole in the upturned bottom of the jugs, (i.e. the top of the trap head). A pool of approximately 100 ml of a saturated salt solution at the bottom of the inverted jug was used to temporarily preserve the captured beetles. The bait was suspended above the surface of the solution and away from the sides of the jug to prevent beetles from climbing out of the trap.

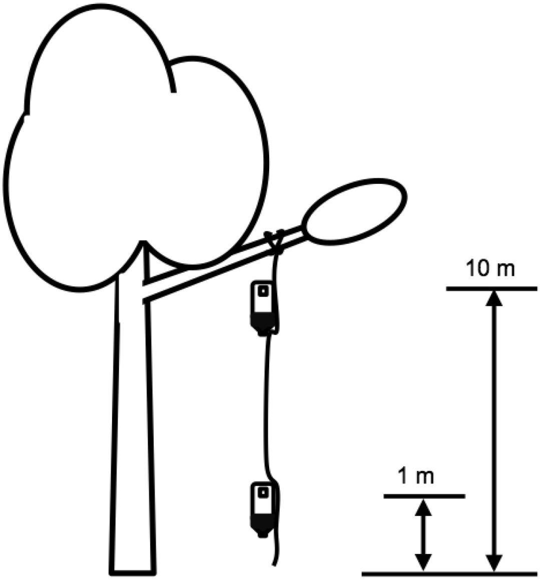

Figure 3:
Trap used to test the preference of *Nicrophorus* sp. between two microhabitats; trap head entrances were suspended at 1 m and 10 m from the ground. Not to scale.

At a given location, the two trap heads were attached 9 m apart one below the other along the same string (Fig. 3). The traps were strung in the trees such that the trap heads were 1 m and 10 m above the forest floor. Upper trap heads were kept a minimum of 1 m away from trunks and branches, where possible, to reduce access by vertebrate scavengers.

Six two-headed traps were hung at each site along a roughly linear transect. The first trap was hung in a suitable tree and using a spacing of at least 20 m along the transect, the next trap was hung in the nearest suitably tall tree. The six mixed-wood traps were spaced 28.4 ± 3.5 m apart (mean ± standard deviation); at the hemlock site, the six traps were spaced 36.9 ± 9.9 m apart. The spacing of the traps at the two sites was not significantly different from each other (Student's t-test, $p < 0.05$).

Collection and analysis

The two sites were visited weekly, at which time each trap head was emptied of beetles. The chicken and salt solution were replaced at least every other week or as needed if either the trap was damaged by scavengers or the chicken had decomposed.

All silphids were counted and identified to species according to Anderson and Peck (1985). The majority of the identified beetles were preserved in 70% isopropanol; representative specimens were pinned. The specimens have been deposited in the collection of the senior author at St. Francis Xavier University.

Statistical analysis

Preferences for habitat type and capture height for each species were tested using the Pearson's χ^2 test. An uncorrected p-value of less than 0.05 was considered significant.

Results

In total, 8108 carrion beetles were caught excluding six *Nicrophorus vespilloides,* an open-habitat specialist that will not be discussed further. Fifty-six percent of all specimens were *Nicrophorus* species, the remainder comprised other Silphidae. *Nicrophorus investigator* (Zetterstadt 1824) and *Thanatophilus lapponicus* (Herbst 1793) were the only local silphids not caught at all. The former is rare on mainland Nova Scotia; the latter is found locally, but only from beach dunes (pers. obs.). All species were present in both the mixed-wood and hemlock habitats and at both trap heights.

The number of individuals caught in each habitat differed significantly for all but two species: *N. tomentosus* ($\chi^2 = 0.5$; $p = 0.4884$) and *Oiceoptoma noveboracense* ($\chi^2 = 2.2$; $p = 0.145$; Fig. 4). Two species were caught in significantly greater numbers in the mixed wood habitat: *Nicrophorus defodiens* ($\chi^2 = 31.1$; $p < 0.0001$) and *N. orbicollis* ($\chi^2 = 27.3$; $p < 0.0001$). The remaining species, *Nicrophorus sayi* ($\chi^2 = 88.3$; $p < 0.0001$), *Nicrophorus pustulatus* ($\chi^2 = 20.3$; $p < 0.0001$), *Necrodes surinamensis* ($\chi^2 = 60.8$; $p < 0.0001$), and *Necrophila americana* ($\chi^2 = 7.8$; $p = 0.0053$), all showed a significant preference for the hemlock woods (Fig. 4).

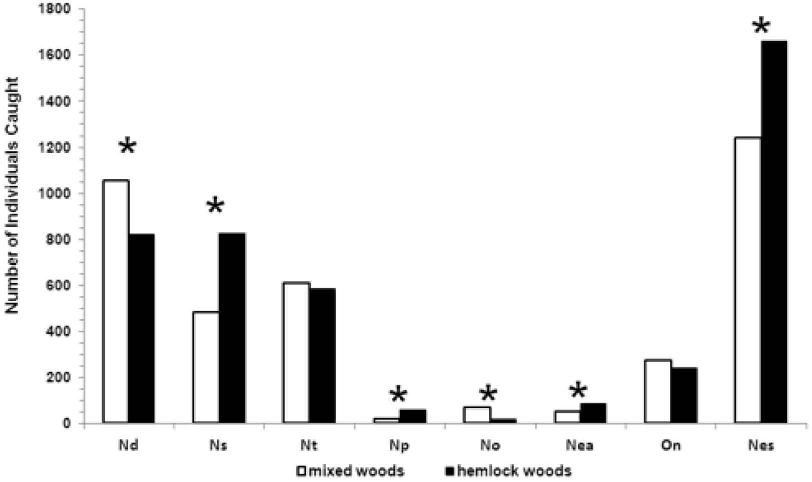

Figure 4:
A comparison of beetle captures at the mixed wood and hemlock sites. Significant differences (*df* = 1; $p < 0.0001$) are indicated using an asterisk. Nd, *Nicrophorus defodiens*; Ns, *Nicrophorus sayi*; Nt, *Nicrophorus tomentosus;* Np, *Nicrophorus pustulatus;* No, *Nicrophorus orbicollis*; Nea, *Necrophila americana*; On, *Oiceoptoma noveboracense;* Nes, *Necrodes surinamensis.*

All species displayed a height preference (Fig. 5). There was a significant preference for the canopy in three species: *N. tomentosus* ($\chi^2 = 50.9$; $p < 0.0001$), *N. pustulatus* ($\chi^2 = 19.3$; $p < 0.0001$), and *Necrodes surinamensis* ($\chi^2 = 8.3$; $p < 0.01$). By contrast, a significant preference for the near-ground trap heads was found among *N. defodiens* ($\chi^2 = 780.4$, $p < 0.0001$), *N. sayi* ($\chi^2 = 220.3$; $p < 0.0001$), *N. orbicollis* ($\chi^2 = 18.2$, $p < 0.0001$), *O. noveboracense* ($\chi^2 = 138.7$; $p < 0.0001$), and *N. americana* ($\chi^2 = 128.3$; $p < 0.0001$) (Fig. 5).

Discussion

Habitat preference

The results corroborate the diversity in forest use among carrion-beetle species previously found by other workers (e. g., Canaday 1987; Su & Woods 2001) and emphasises that such differences do indeed exist. The current study documents preferences between only two forest types, but further studies at this scale are needed to understand how these preferences might differ between other forest types and within the same forest types elsewhere; it should be emphasised that preferences found here might not be the same elsewhere. Additionally, it is unclear if there is a phylogenetic component; that is, if sister species have similar habitat affiliations than do more distantly related species.

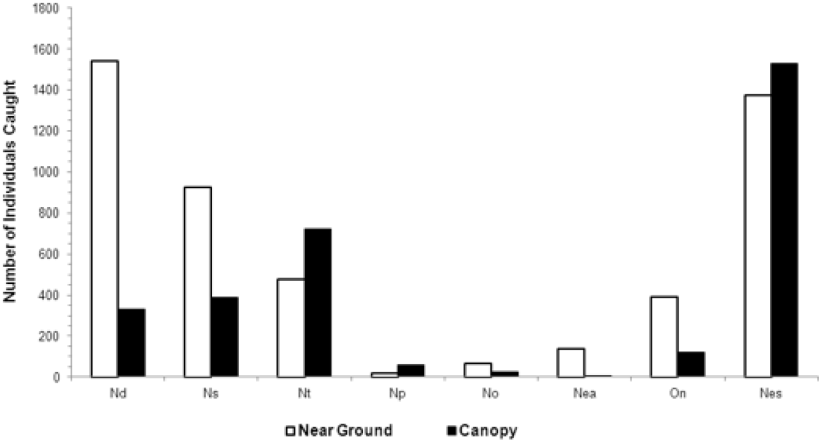

Figure 5:
A comparison of beetle captures in near-ground (1 m) and canopy (10 m) trap heads for each species. All differences were found to be significant ($df = 1$; $p < 0.05$). Abbreviations as in Fig. 4.

Nicrophorus sayi was found to have a preference for the hemlock forest. Although this species has previously been recorded to prefer forest over open habitats (Anderson 1982), the current study narrows the preference down to hemlock (among the two forest types tested); however, this does not mean that another forest type is even more preferred.

A lack of a forest type preference in *N. tomentosus* is in accordance with other literature suggesting that this species has the widest niche breadth of all burying beetles (Shubeck 1983; Lomolino & Creighton 1996; Bishop *et al.* 2002).

Nicrophorus defodiens was, along with *N. orbicollis*, found to prefer mixed woods. Previous studies have simply characterised *N. defodiens* as a forest-dwelling species (Anderson 1982; Trumbo & Bloch 2000). Normally, *N. defodiens* does not bury its brood-rearing carrion in the soil, but covers the carrion in place with leaves (Anderson & Peck 1985). Unlike hemlock woods, mixed woods provide suitable leaf litter for the carcass interments of this species. The preference for mixed woods by *N. orbicollis* could be due to the soil at the respective sites tested, with this species having demonstrated a preference for more fibrous soils in the laboratory (Muths 1991). Although not examined specifically here, the hemlock-forest soils would likely be the less fibrous of the two under study here because there would be less of a root network due to the scarcity of understory plants. Clearly, both species display some flexibility because neither was exclusively found in one forest type.

Similarly, the preference of *N. pustulatus* for the hemlock forest could be attributed to the soil found there. *Nicrophorus pustulatus* prefers habitats with alluvial soil (Bishop *et al.* 2002), which is similar to the moist, slightly sandy, well-drained soils in which eastern hemlock commonly grow (Strickland 1987).

Oiceoptoma noveboracense and *N. americana* are both commonly associated with open habitats (Anderson 1982; Shubeck 1983). The lack of preference for a forest type for *O. noveboracense* is perhaps then not surprising. Notwithstanding the previously recorded preferences for open areas, the small number of captured *N. americana* were found in slightly, but significantly, greater numbers in the hemlock forest in this study. However, it is unclear why this would be the case. That being said, there were pastures near both forest sites (distances and areas were not quantified) and it could simply be that there was a greater pool of *N. americana* near the hemlock site.

An association of *N. surinamensis* with hemlock forest was unexpected given that previous work found that this species preferred open habitats (Lingafelter 1995). Anderson (1982) and Shubeck (1983) each collected small numbers of individuals distributed almost equally between fields and forests; a significant preference for habitat could not be determined by either study. The results from the current study suggest that, like some other members of the Silphidae, *N. surinamensis* may have habitat preferences that differ across its range (Anderson 1982; Schubeck 1983; Lingafelter 1995).

Microhabitat preference

The canopy preferences seen in *N. pustulatus* and *N. tomentosus,* along with the near-ground preferences of *N. orbicollis, N. americana,* and *O. noveboracense* found in this study, agree with previous observations (Shubeck 1970; Ulyshen *et al.* 2007). The lower height preferences of *N. sayi* and *N. defodiens* and the higher height preferences of *N. surinamensis* have not been previously recorded. Despite a strong preference for the lower traps, *N. defodiens* has recently been documented to reproduce in the canopy (Lowe & Lauff 2012).

Previous studies of carrion-beetle distributions (e. g., Shubeck 1983; Wilson *et al.* 1984; Anderson & Peck 1985; Lingafelter 1995) might have inadvertently underrepresented the numbers of individuals of *N. tomentosus*, *N. pustulatus*, and *N. surinamensis* by only using ground-based trapping. The current findings reiterate the importance of sampling a vertical gradient when studying carrion-beetle distributions (Schroeder *et al.* 2009).

Carrion beetles might be present in the forest canopy for their own foraging or for breeding; both reasons would draw them to carrion-baited traps there. Although one expects more carrion on the forest floor, the canopy, as argued by Lowe and Lauff (2012), is likely not devoid of opportunities. For example, there are many cavity-nesting birds and mammals whose predation would leave altricial young in the cavity to starve. Carrion beetles might be among the scavengers to exploit these opportunistic resources.

Nicrophorus pustulatus—a special case

Due to the rare occurrence of *N. pustulatus* at baited pitfall traps, it was suggested that this species is not attracted to carrion (Robertson 1992) and might differ in its natural history from all other members of its genus (Anderson &

Peck 1985). *Nicrophorus pustulatus* has been found rearing its young on snake eggs (Blouin-Demers & Weatherhead 2000; Keller & Heske 2001); this might have inadvertently reinforced the design of subsequent studies to continue to focus on the forest floor. A reason for perplexity exists, however, because *N. pustulatus* can rear its young on the more typical small vertebrate carcasses in the lab (Smith *et al.* 2007), suggesting that it could do so in the wild as well. This inference together with the canopy preference found in the current study and combined with previous findings of this species in the nest cavities of a Northern Saw-Whet Owl (*Aegolius acadicus*) (Phillips *et al.* 1983), and an American Kestrel (*Falco sparverius*) (Lauff unpubl. data) provide compelling evidence that *N. pustulatus* might either reproduce on carcasses in the canopy or simply be preferentially foraging there. The significant habitat and microhabitat preferences of *N. pustulatus* documented here should result in future studies specifically targeting the canopy in hemlock. Although Lowe and Lauff (2012) found two *Nicrophorus* species breeding in the canopy, *N. pustulatus* was not one of them (although it was found to be associated with bird carrion there).

It is interesting to note that *N. pustulatus* and *N. orbicollis* showed opposing preferences for both habitat and microhabitat. Whereas *N. orbicollis* was found more often in lower traps of the mixed wood, *N. pustulatus* preferred upper traps in hemlock. Although of uncertain phylogenetic affinity to one another (Smith *et al.* 2007), both species are similar in size, have coinciding reproductive seasons, and similar geographic ranges (Anderson & Peck 1985; Bishop *et al.* 2002), thereby increasing the chance of their interaction and competition. Divergent height as well as habitat preferences could therefore be important for niche partitioning between these two species.

Conclusion

Species-specific habitat and height preferences found in this study contribute to a broader understanding of the ecology of local *Nicrophorus* beetles. It is suggested that arboreal traps be incorporated into any survey or other ecological study of carrion beetles.

Acknowledgements

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Literature cited

Anderson R.S. (1982). Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Can. J. Zool.,* 60, 1314–1325.

Anderson R.S. & Peck S.B. (1985). *The Insects and Arachnids of Canada Part 13. The Carrion Beetles of Canada and Alaska (Coleoptera: Silphidae and Agyrtidae).* Agriculture Canada Research Branch Publication 1778, Ottawa.

Beninger C.W. & Peck S.B. (1992). Temporal and spatial patterns of resource use among *Nicrophorus* carrion beetles (Coleoptera: Silphidae) in a Sphagnum bog and adjacent forest near Ottawa, Canada. *Can. Entomol.,* 124, 79–86.

Bishop A.A., Albrecht M., Hoback W.W. & Skinner K.M. (2002). A comparison of an ecological model and GIS spatial analysis to describe niche partitioning amongst carrion beetles in Nebraska. *Trans. GIS*, 6, 457–470.

Blouin-Demers G. & Weatherhead J. (2000). A novel association between a beetle and a snake: parasitism of *Elaphe obsoleta* by *Nicrophorus pustulatus*. *Ecoscience,* 7, 395–397.

Canaday C.L. (1987). Comparison of insect fauna captured in six different trap types in a Douglas-fir forest. *Can. Entomol.*, 119, 1101–1108.

Keller L.W. & Heske E.J. (2001). An observation of parasitism of black rat snakes (*Elaphe obsolete*) eggs by a beetle (*Nicrophorus pustulatus*) in Illinois. *Trans. Illinois State Acad. Sci.*, 94, 167–169.

Lingafelter S.W. 1995. Diversity, habitat preferences, and seasonality of Kansas carrion beetles (Coleoptera: Silphidae). *J. Kansas Entomol. Soc.*, 68, 214–223.

Lomolino M.V. & Creighton J.C. (1996). Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus. Biol. Cons.,* 77, 235–241.

Lowe A.J. & Lauff R.F. (2012). Arboreal burials in *Nicrophorus* spp. (Coleoptera: Silphidae). *Psyche,* 2012, 1–6.

Muths E.L. (1991). Substrate discrimination in burying beetles, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *J. Kansas Entomol. Soc.*, 64, 447–450.

Phillips J.R., Root M., & DeSimone P. (1983). Arthropods from a Saw-Whet Owl (*Aegolius acadicus*) nest in Connecticut. *Entomol. News,* 94, 60–64.

Pukowski E. (1933). Okologische untersuchungen an *Necrophorus* F. *Z. Morphol,* 27, 518–593.

Robertson I.C. (1992). Relative abundance of *Nicrophorus pustulatus* (Coleoptera: Silphidae) in a burying beetle community, with notes on its reproductive behaviour. *Psyche*, 99, 189–190.

Schroeder B., Buddle C.M. & Saint-Germain, M. (2009). Activity of flying beetles (Coleoptera) at two heights in canopy gaps and intact forests in a hardwood forest in Quebec. *Can. Entomol.*, 141, 515–520.

Scott M.P. (1998). The ecology and behaviour of burying beetles. *Ann. Rev. Entomol.,* 43, 595–618.

Shubeck P.P. (1970). Silphidae attraction to carrion-baited air cans versus carrion-based ground cans. *Coleop. Bull.,* 24, 66–70.

Shubeck P.P. (1983). Habitat preferences of carrion beetles in the Great Swamp National Wildlife Refuge, New Jersey (Coleoptera: Silphidae, Dermestidae, Nitidulidae, Histeridae, Scarabaeidae). *J. NY Entomol. Soc.,* 91, 333–341.

Smith G., Trumbo S.T., Sikes D.S., Scott M.P., & Smith R.L. (2007). Host shift by the burying beetles, *Nicrophorus pustulatus* a parasitoid of snake eggs. *J. Evol. Biol.,* 89, 1420–9101.

Strickland D. (1987). *Trees of Algonquin Provincial Park.* The Friends of Algonquin Park, Whitney, Ontario.

Su J.C. & Woods S.A. (2001). Importance of sampling along a vertical gradient to compare the insect fauna in managed forests. *Environ. Entomol.*, 30, 400–408.

Trumbo S.T. & Bloch P.L. (2000). Habitat fragmentation and burying beetle abundance and success. *J. Insec. Conserv.,* 4, 245–252.

Ulyshen M.D. & Hanula J.L. (2007). Comparison of the beetle (Coleoptera) fauna captured at two heights above the ground in a North American temperate deciduous forest. *Am. Midl. Nat.*, 158, 260–278.

Ulyshen M.D., Hanula J.L. & Horn S. (2007). Burying beetles (Coleoptera: Silphidae) in the forest canopy: the unusual case of *Nicrophorus pustulatus* Herschel. *Coleop. Bull.,* 61, 121–123.

Walker T.J. (1957). Ecological studies of the arthropods associated with certain decaying material in four habitats. *Ecology*, 38, 262–276.

Wilhelm S.I., Larson D.J. & Storey A.E. (2001). Habitat preference of two burying beetles (Coleoptera: Silphidae: *Nicrophorus*) living among seabirds. *Northeast. Nat.,* 8, 435–442.

Wilson D.S. & Fudge J. (1984). Burying beetles: intraspecific interactions and reproductive success in the field. *Ecol. Entomol.,* 9, 195–203.

Wilson D.S. & Knollenberg W.G. (1984). Food discrimination and ovarian development in burying beetles (Coleoptera: Silphidae: *Nicrophorus*). *Ann. Entomol. Soc. Am.,* 77, 165–170.

Wilson D.S., Knollenberg W.G. & Fudge J. (1984). Species packing and temperature dependent competitions among burying beetles (Silphidae, *Nicrophorus*). *Ecol. Entomol.*, 9, 205–216.

Amphibian fauna in Sri Lanka: status, threats and conservation

Senarathge R. Weerawardhena

Department of Zoology, University of Kelaniya, Kelaniya, 11600, Sri Lanka

Current Address: 106A–3615, 49th Street NW, Calgary, Alberta, T3A 2L8, Canada; E-mail: ranjithweerawardhena@yahoo.ca

Abstract

Amphibians display the highest degree of endemism among the Sri Lankan vertebrate fauna. The status of over 50% of Sri Lankan amphibian species are classified as threatened due to uncontrolled anthropogenic activities at a variety of levels. Thus, it is vital to understand the current status of Sri Lanka's amphibian species before they disappear from their vanishing habitats. In the present paper the current status of the Sri Lankan amphibian fauna is reviewed and possible conservation measures are discussed.

Introduction

Sri Lanka, a small island, is a detached part of the continental Deccan plateau of ancient crystalline rocks (Cooray 1984). The topography of the island is the result of millions of years of weathering activities by rain, wind, and sun. Many ancient travellers throughout history have described Sri Lanka (also known historically as Taprobane, Zerandib, or Ceylon, among others) as one of the most beautiful islands of the world because of its variety of features, such as coastal plains, lowland hills, central mountainous highlands, diverse natural flora and fauna. Today, Sri Lanka (together with the Western Ghats) is considered as one of the world's biodiversity hotspots because of its unique assemblages of plant and animal communities and for its amphibian fauna,

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which shows the highest degree of endemism within the Asian region, in particular (Meegaskumbura et al. 2002). In this review, current statuses of and threats towards the Sri Lankan amphibian fauna are discussed. Possible conservation awareness for this threatened and vulnerable group of vertebrates in Sri Lanka is also discussed.

Current status of Sri Lankan amphibian fauna

Kirtisinghe (1957) recognised 35 species amphibians from the island, with this figure increasing to 53 species by the end of the last century (Dutta & Manamendra-Arachchi 1996). From 1996 to 2011, more than 45 new amphibian species were added to this list by different authors (Manamendra-Arachchi & Pethiyagoda 2001a, 2001b, 2005; Meegaskumbura & Manamendra-Arachchi 2005; Fernando et al. 2007; Meegaskumbura *et al*. 2007, 2009, 2011). The island's inventory of amphibian species reached 107 with the description of *Polypedates ranwellai* from Gilimale forest reserve (Wickramasinghe *et al*. 2012a). With these new additions, over 84% of the species comprising the Sri Lankan amphibian fauna are endemic to the island. This is mainly due to the high endemism shown by the genus *Pseudophilautus*, where 46 of the 65 extant species are endemic to the country (Meegaskumbura *et al*. 2009). The Sri Lankan amphibian fauna is arrayed among six families: Bufonidae, Microhylidae, Nyctibatrachidae, Ranidae, Rhacophoridae, and Ichthyophiidae.

Regrettably, the Sri Lankan amphibian fauna also holds the highest rank in Asia with respect to the percentage of extinct amphibian species. According to the Global Amphibian Assessment (http://www.amphibians.org/redlist/), 21 of the 34 amphibian species confirmed to have gone extinct during the last 500 years were from Sri Lanka. (However, one of the Sri Lankan amphibian species that was presumed to be extinct has been rediscovered recently by Wickramasinghe *et al*. (2012b).) Apart from these extinct species, 53 Sri Lankan amphibian species are classified as at least being threatened according to the IUCN Red List of Threatened Species (http://www.iucnredlist.org), 11 as critically endangered, 36 as endangered and six as vulnerable (see Appendix).

Threats to Sri Lankan amphibian fauna

The main reason for the high percentage of threatened amphibian species in Sri Lanka is the ever-increasing human population density. For example, the Sri Lankan human population exceeded 20 million in 2012 despite a total land area of only 65 600 km^2. This rapidly growing human population together with current economic developmental pressure not only create conditions that endanger the existence of many vertebrate species, including amphibians, but also modify and destruct pristine natural ecosystems. These anthropogenic habitat alterations include deforestation, habitat fragmentation, modification, degradation and environmental pollution, overexploitation of natural resources, and global climate change. Habitat degradation, endangerment and extinction of species are not the aims of human societies, but are the unfortunate by-products of anthropogenic activities (Groom *et al*. 2006).

Deforestation

Deforestation, where virgin forests are cut down for agricultural purposes, has been drastic in Sri Lanka (Pethiyagoda & Manamendra-Arachchi 1998; Manamendra-Arachchi & Pethiyagoda 1999; Pethiyagoda 2005; Meegaskumbura et al. 2007). The process was initiated on a large scale in the 18th century and has continued to the present (Weerawardhena 2010). The wet mountainous areas (700 m and 1300 m above from the sea level) of Sri Lanka were originally exploited for the cultivation of coffee (*Coffea arabica*). Later, these areas were further cleared for tea (*Camellia sinensis*) and cardamom (*Elettaria cardamomum*) plantations (Forrest 1967; Marby 1972). In 1867, seven ha were planted with tea. By 1967, 24 038 ha were devoted to tea plantations (Forrest 1967; Jayaraman 1975), including 2796 ha in the Kelebokka area of the Knuckles, which was first planted with tea between 1874 and 1875 (Forrest 1967). Later, tea was planted in wet mountainous areas resulting in the clearing of 404 685 ha of virgin rain forest (Manamendra-Arachchi & Pethiyagoda 1999). Up-country wet montane forest habitats (2000 m above from the sea level) were cleared for potato (*Solanum tuberosum*) plantations and areas in the intermediate zone were cleared for rubber (*Hevea brasiliensis*) plantations. To plant sugar cane (*Saccharum afficinarum*) and maize (*Zea mays*), vast areas in the dry zone have also been cleared. Thus, much of the undisturbed virgin forest habitats have been cleared in the island for the cultivation of agricultural cash crops (Fig. 1).

This on-going rapid deforestation reduces the quantity and quality of wildlife habitat harbouring rich biological diversity. The process therefore affects survival of fauna as well as flora, possibly leading to local extinction of amphibian species.

Habitat fragmentation, modification and degradation

Habitat fragmentation, modification and degradation also represent major threats to amphibians on the island. Habitat fragmentation is caused primarily by villagers and farmers when the native vegetation is cleared for the purpose of agriculture in the Knuckles as well as in other virgin forest areas of the island. Here, areas in which habitats were once continuous become divided into separate small fragments and isolated from each other by agricultural fields, forest patches, roads, or similar features. Furthermore, illegal slash-and-burn agricultural practices by neighbouring villagers also modified the pristine habitat fragments of the Knuckles. However, after years of cultivation, these agricultural lands, including the slash-and-burn agricultural plots, were abandoned because these were no longer as productive as at the beginning of the period of agricultural exploitation (Weerawardhena & Russell 2010). As a consequence of all these anthropogenic activities, pristine habitats in the forest areas are degraded. The majority of Sri Lankan amphibian species, particularly the endemics, are confined to the virgin forest habitats of the island (Pethiyagoda & Manamendra-Arachchi 1998), most of which are fragmented. Instead, only approximately 750 km^2 of undisturbed virgin forest habitat remains in Sri Lanka.

The main impact of habitat fragmentation is that it affects biological diversity by reducing the amount of suitable habitat for all organisms in the forest ecosystem, including amphibians. It invariably involves some amount of habitat destruction as well, largely through the clearing of habitats for agriculture. Together, habitat destruction and modification represent processes in which natural pristine habitats are rendered functionally unable to support the species present. Thus, the organisms that previously used the habitat are displaced or killed during these processes and biological diversity is ultimately reduced.

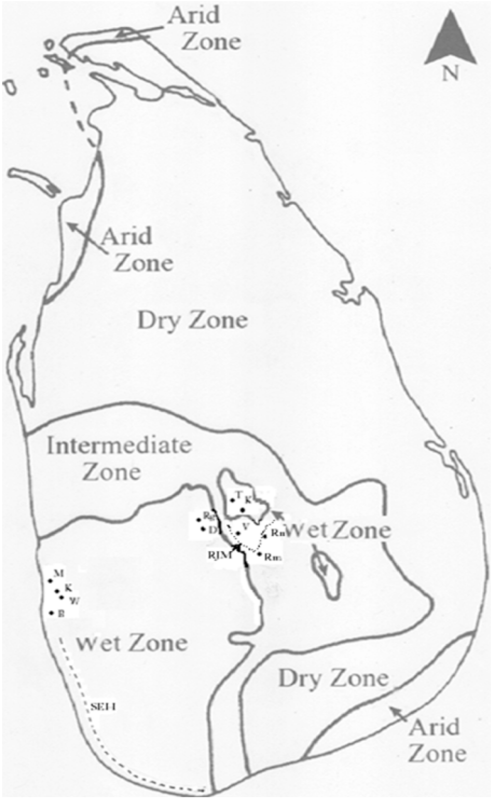

Figure 1:
Map of Sri Lanka showing its main geographical zones and **B**=Bellanwila-Attidiya, **D**=Digana, **Ke**=Kelaniya, **Kn=**Knuckles, **M**=Muthurajawella, **Rg**=Rajawella Golf Course, **RJM**=Raja Mawatha, **Rm**=Rantambe**, Rn**=Randenigala, **SEH**=Southern Express Highway, **T**=Theldeniya, **V**=Victoria, and **W**=Wedamulla.

Most Sri Lankan amphibians are found in small and localised populations. This is particularly so for the endemic species and is frequently taken to represent point endemism for these species: endemic species confined to less than 0.5 km^2 (Pethiyagoda & Manamendra-Arachchi 1998; Manamendra-Arachchi & Pethiyagoda 1999; Manamendra-Arachchi & Pethiyagoda, 2006; Meegaskumbura *et al.* 2007, 2009). The predominant reason for such range restrictions is not known but it may derive from combinations of habitat fragmentation resulting from anthropogenic activities such as deforestation and man-made forest fires, and from natural catastrophic events such as severe droughts, natural forest fire, soil erosion, earth slides and floods. These patterns of disturbances are prevalent in the wet zone of Sri Lanka, where habitat degradation has been severe due to the vast scale of legal and illegal agricultural practices (Pethiyagoda & Manamendra-Arachchi 1998; Manamendra-Arachchi & Pethiyagoda 1999; Meegaskumbura *et al.* 2007). In addition, legal and illegal gem mining in terrestrial and aquatic habitats (e. g., along streams and in wetlands) and quarrying have also contributed to the degradation of pristine ecosystems.

In addition to habitat fragmentation and degradation, habitat modification also exerts a negative influence on amphibian species. Due to rapid economic growth, most pristine habitats are used to develop infrastructure such as housing developments in rural areas; roads (e. g., Raja Mawatha), including highways (e. g., Southern Express Highway); golf courses (e. g., Rajawella Golf Course) and irrigation systems; hydroelectric power plants, including dams (e. g., Victoria, Randenigala and Rantambe reservoirs); and suburban developments (e. g., Digana, Theldeniya new town). Due to these activities, many natural habitats are shrinking or disappearing at alarming rates. Even though the development of infrastructure is necessary for growing human communities, such activities unfortunately lead to diminishment or disappearance of pristine natural ecosystems, including the wildlife they support.

Furthermore, the filling of wetland habitats (e. g., Bellanwila-Attidiya, Muthurajawela, and Wedamulla near Kelaniya) to convert natural ecosystems into human-suitable habitation destroys breeding habitats of aquatic breeding amphibians. For example, *Euphlyctis hexadactylus* and *Euphlyctis cyanophlyictis* depend on aquatic water bodies for their reproduction and also aquatic vegetation as the feeding grounds for adult *E. hexadactylus* (Weerawardhena 2003). However, the populations of both of these aquatic species are decreasing due to the shrinking and modification of their habitats (pers. obs. since 1998 at Wedamulla near Kelaniya).

Environmental pollution

The widespread and uncontrolled application of agrochemicals to agricultural fields, particularly in the case of tea plantations and rice fields, has resulted in the direct mortality of non-targeted organisms including terrestrial amphibians. This chemical contamination indirectly reduces the availability of insect prey to post-metamorphic amphibians, which also impacts adversely on the survival of the amphibian populations (Pethiyagoda *et al.* 2006). In addition, the author has also observed several malformed aquatic adult anurans. The exact cause of such malformations is unknown—the morphology of a malformation does not define its cause (Meteyer 2000)—but these malformations might be due to chemical pollution of the aquatic habitat in which their bearers developed or live.

Nitrogen-phosphorus-potassium fertilisers are used in tea plantations in large quantities and this has led to lowered soil fertility over a period of 33 years (Mohammed 1996). Continuous application of artificial fertilisers to tea-plantation soil leads to a gradual increase in soil acidity, correlated with decreases in the abundances of soil fauna, especially earthworms (Weerawardhena 1993). Due to this loss in soil fertility, some tea plantations have been abandoned. For example, the Duckwari Group in the Knuckles had 655 ha of land in 1898 and most of the area was planted in tea before this. In 1967, however, only 481 ha of tea planted areas remained; 48 ha were under cardamom plantation, one ha was cultivated with paddy, and 125 ha had been abandoned (Marby 1972). Of the latter lands, some have been replanted with crops, whereas others have remained abandoned and are undergoing natural ecological succession.

Finally, acid rain and mist have been implicated in the dieback of montane forests comprising key amphibian habitats, including the Knuckles and Horton Plains National Park (Bambaradeniya & Ekanayake 2003). Nevertheless, there are no reports concerning the adverse impacts of acid rain and mist on amphibians in Sri Lanka. These events might represent potential problems for survival of amphibian species because the pristine habitats in the Knuckles and Horton Plains National Park were degraded due to acid rain and mist.

Overexploitation of natural resources

The villagers in and around primary and secondary forest habitats in Sri Lanka use such areas as sources of fuel wood, timber (Weerawardhena & Russell 2012a), common and rare medicinal plants, and indigenous vertebrates, in particular indigenous freshwater fishes (Gunasekara 2011). For example, 80 villages are currently immediately outside of and encircle the Knuckles (Nanayakkara *et al.* 2009). Many of the villagers who live in these villages carry out unlimited and uncontrolled extractions of natural resources from the pristine habitats, thereby slowly converting such habitats into degraded ecosystems. Furthermore, over-collection of amphibians as specimens for scientific studies and for research activities also poses a serious threat, especially to the populations of endemic and threatened species (Weerawardhena & Russell 2012c).

Global climate change

Global climate change and severe weather conditions such as prolonged droughts, temperature fluctuations, and flooding have further added to the decline of amphibian populations in restricted natural ecosystems (Pethiyagoda & Manamendra-Arachchi 1998). These events might be especially harmful to species with low population densities and restricted geographical distribution patterns (Pethiyagoda & Manamendra-Arachchi 1998). However, it is very difficult to evaluate the effects of global climate change on Sri Lankan amphibians because studies directed at this phenomenon are, at this point in time, not abundant.

Conservation of the Sri Lankan amphibian fauna

More than 84% of Sri Lankan amphibian species are endemic to the island, where many of them show restricted patterns of geographical distribution. Apart from their endemicity and restricted distributions, most of these species are also sensitive to anthropogenic habitat modifications and some of them are at the edge of extinction. To improve the current status of Sri Lankan amphibian fauna, the following steps—some of which are already being taken by the appropriate authorities—should be taken or promoted further.

Enforcement of conservation legislation

Illegal practices such as deforestation, habitat degradation, modification, fragmentation, and overexploitation of natural resources have been reduced considerably in Sri Lanka, mainly due to enforcement of existing conservation legislation by the state. Nearly all the nature reserves that exist presently are state-owned and under the purview of three institutions, namely the Divisional Secretaries, the Department of Wildlife Conservation, and the Forest Department. Current legislation for protected areas, including the fines and penalties for illegal activities in them, is mainly set out in the Fauna and

Flora Protection Ordinance-1937 (Sri Barathi 1979), with an amended version of this Ordinance having been approved by the Cabinet of Ministers on March 12th, 2008. Additional policies relating to protected areas are also set out in the Management and Wildlife Conservation National Policy. General enforcement of these policies has been stepped up since this legislation was passed.

Establishment of protected areas

The identification of the most important geographic areas to amphibian conservation must be prioritised because some parts of the island, such as montane forest habitats, have greater significance in terms of biological diversity than other areas. These important areas are identified as Protected Areas (*Dudley 2008*), which have already been set up to cover nearly 20% of the total land area, thereby affording protection to many critical amphibian habitats. The area above 1500 m in the Knuckles Range was declared as a Climatic Reserve in 1873 (Sri Barathi 1979). Furthermore, “Dotalugala”, a prominent peak in the Knuckles, was given the status of “Man and the Biosphere Reserve” in April 2000 under the remit of the Forest Department. In May 2000, this area was subsequently included in the 17 500 ha of the Knuckles by the Gazette Notification. According to this declaration, areas in the Knuckles above an altitude of 1067 m are protected as the “Knuckles Conservation Area” within which anthropogenic activities including the establishment of tea and cardamom plantations are banned. Furthermore, the World Heritage Committee UNESCO proclaimed the Knuckles as a “World Heritage Site” in its 34th session in Brasilia, Brazil on July 30th 2010. Altogether, these efforts recognise the Knuckles as an important locality in Sri Lanka in terms of its biological diversity and endemicity and one that is vulnerable to uncontrolled human influences.

Apart from the above localities, many other natural habitats are also declared as strict nature reserves (SNRs; IUCN category Ia), which is the highest category of protected area recognised by the World Commission on Protected Areas (WCPA) of the IUCN. The SNRs are generally established exclusively for scientific fieldwork (e. g., Hakkgala, Ritigala, and a section of Yala in Sri Lanka), with most housing endemic as well as endangered vertebrate species, including amphibians.

Research activities

Since the 1990s, there is growing interest on the part of many local and foreign scientists in studying the Sri Lankan amphibian fauna. Most have focussed their efforts on descriptions of new species or the taxonomy of Sri Lankan amphibians (Manamendra-Arachchi & Pethiyagoda 2001a, 2001b, 2005; Meegaskumbura & Manamendra-Arachchi 2005; Fernando *et al.* 2007; Meegaskumbura *et al.* 2007, 2009, 2011; Wickramasinghe *et al.* 2012a), which, in one case, has resulted in the rediscovery of a species presumed to be extinct (Wickramasinghe *et al.* 2012b). Additional research has also focussed on ecological and biological studies of Sri Lankan amphibians (e. g., Bahir *et al.* 2005; Wickramasinghe *et al.* 2004, 2005; Weerawardhena and Russell 2012a, 2012b, 2012c). Herpetological research into demographic trends in populations of Sri Lankan amphibian species, and upon the impact of environmental pollution on these species, would be of particular value because no such data are available in the current literature.

Ex-situ conservation programmes

Ex-situ conservation programs have been conducted for several species of threatened Sri Lankan amphibian species by different organisations (e. g., the Amphibian and Reptile Research Organization in Sri Lanka, the Wildlife Heritage Trust, among others). A cogent example is the Amphibian Conservation and Breeding Assessment workshop that was held in Kandy, Sri Lanka on November 2009 and was organised by the Durrell Wildlife Conservation Trust's International Training Centre and Ark Organization. During this workshop, ten frog species were evaluated as being close to extinction and the need for *ex-situ* rescue programs was pointed out. Thirty-three species that would benefit from different research activities, such as the preparation and implementation of recovery programs, captive breeding and artificial propagation, were also identified during the workshop.

Monitoring the application of agrochemicals

Nitrogen-phosphorus-potassium fertilisers have been used on Sri Lankan rice fields, rubber, coconut, and tea plantations in large quantities, which has led to lowered soil fertility over the years (Mohammed 1996) and the abandonment of some tea plantations in the Knuckles in turn (Weerawardhena & Russell 2012b). Some farmers mix several agrochemicals in different quantities arbitrarily and apply these mixtures to their fields. Because these types of activities can destroy useful as well as non-target organisms, such devastating activities should be banned. However, the use of agrochemical such as fungicides, herbicides, and weedicides in Sri Lanka is still largely unregulated. The Pesticide Control Act (Anon. 1980) addresses only threats to human health and not any potential impact on non-target organisms (e. g., amphibians and insects). Therefore, monitoring the application of agrochemicals is necessary if Sri Lankan biodiversity is to be conserved. In particular, it is advisable to promote and encourage farmers to use organic farming methods and to implement biological control methods for pest control.

Conclusions

The total number of species (107) and the high degree of endemism displayed by the Sri Lankan amphibian fauna are remarkable. More than 84% of the Sri Lankan amphibian species are endemic to the island and 53 of these endemics are under threat. However, no island-wide conservation program has yet been undertaken to conserve these threatened taxa with the exception of a few species. The main factors negatively affecting the amphibian fauna in Sri Lanka are deforestation; habitat fragmentation, modification and degradation; environmental pollution; overexploitation of natural resources; and global climate change.

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Literature cited

Anon. (1980). *Control of Pesticides Act.* Government Publications Bureau, Colombo, Sri Lanka.

Bahir M.M., Meegaskumbura M. Manamendra-Arachchi K. Schneider C.J. & Pethiyagoda R. (2005). Reproduction and terrestrial direct development in Sri Lankan shrub frogs (Ranidae: Rhacoporinae: *Philautus*). *Raffles Bull. Zoology Suppl.*, 12, 339–350.

Bambaradeniya C.N.B. & Ekanayake S.P. (2003). *A Guide to the Biodiversity of Knuckles Forest Region*. IUCN Country Office, Colombo, Sri Lanka

Cooray P.G. (1984). *An Introduction to the Geology of Sri Lanka*. Department of Geology, Government Printing Press, Colombo, Sri Lanka.

Dudley N. (20*08*). *Guidelines for Applying Protected Area Management Categories*. *IUCN,* Gland, *Switzerland*.

Dutta S.K. & Manamendra-Arachchi K. (1996). *The Amphibian Fauna of Sri Lanka*. Wildlife Heritage Trust, Colombo, Sri Lanka.

Fernando S., Wickramasingha M.L.J., & Rodirigo R.K. (2007). A new species of endemic frog belonging to genus *Nannophrys* Günther, 1869 (Anura: Dicroglossinae) from Sri Lanka. *Zootaxa,* 1403, 55–68.

Forrest D.M. (1967). *A Hundred years of Ceylon Tea: 1867–1967*. Chatto and Windus, London.

Groom M.J., Meffe G.K. & Carroll C.R. (2006). *Principles of Conservation Biology*, 3rd Edition. Sinauer Associates, Inc, Sunderland, Massachusetts.

Gunasekara S. (2011). *Export Trade of Indigenous Fresh Water Fishes of Sri Lanka*. Author publication.

Jayaraman R. (1975). *Caste Continuities in Ceylon: A study of the Social Structure of Three Tea Plantations*. Popular Prakashan, Bombay, India.

Kirtisinghe P. (1957). *The Amphibian Fauna of Ceylon*. Author publication, London.

Manamendra-Arachchi K. & Pethiyagoda R. (1999). Sri Lanka: the global amphibian hotspot. *Sri Lanka Nature,* 3, 51–54.

Manamendra-Arachchi K. & Pethiyagoda R. (2001a). *Polypedates fastigo*, a new tree frog (Ranidae: Rhacophoridae) from Sri Lanka. *J. S. Asian Nat. Hist.,* 5, 191–199.

Manamendra-Arachchi K. & Pethiyagoda R. (2001b). *Ramanella nagaoi*, a new tree-hole frog (Microhylidae) from southern Sri Lanka. *J. S. Asian Nat. Hist.*, 5, 121–133.

Manamendra-Arachchi K. & Pethiyagoda R. (2005). The Sri Lankan shrub-frogs of the genus *Philautus* Gistel, 1848 (Ranidae: Rhacophorinae), with description of 27 new species. *Raffles Bull. Zool. Suppl.*, 12, 163–303.

Marby H. (1972). *Tea in Ceylon: An Attempt at a Regional and Temporal Differentiation of the Tea Growing Areas in Ceylon*. Franz Steiner Verlag GmbH, Wiesbaden, Germany.

Meegaskumbura M., Bossuyt F., Pethiyagoda R., Manamendra-Arachchi K., Bahir M.M., Milinkovitch M.C. & Schneider C.J. (2002). Sri Lanka: an amphibian hot spot. *Science,* 238, 379.

Meegaskumbura M. & Manamendra-Arachchi K. (2005). Description of eight new species of shrub frogs (Ranidae: Rhacophorinae: *Philautus*) from Sri Lanka. *Raffles Bull. Zool. Suppl.*, 12: 305–338.

Meegaskumbura M., Manamendra-Arachchi K., Schneider C.J., and Pethiyagoda R. (2007). New species amongst Sri Lanka's extinct shrub frogs (Amphibia: Rhacophoridae: *Philautus*). *Zootaxa,* 1397, 1–15.

Meegaskumbura M., Manamendra-Arachchi K. & Pethiyagoda R. (2009). Two new species of shrub frogs (Rhacophoridae: *Philautus*) from the lowlands of Sri Lanka. *Zootaxa,* 2122, 51–68.

Meegaskumbura M. & Manamendra-Arachchi K. (2011). Two new species of shrub frogs (Rhacophoridae: *Pseudophilautus*) from Sri Lanka. *Zootaxa,* 2747, 1–18.

Meteyer C.U. (2000). Field guide to malformations of frogs and toads with radiographic interpretations. *Biol. Sci. Rep.* USGS/BRD/BSR-2000-0005.

Mohammed M. (1996). Tea and environmental pollution. *J. Tea Coffee Trade*, 2, 2–3.

Nanayakkara A.,Herath H.M.D.R., and Wickremasinghe K. (2009). *Forest Governance Project, Strengthening Voices for Better Choices: Sri Lanka Country Report*. IUCN Country Office, Colombo, Sri Lanka.

Pethiyagoda R. (2005). The amphibian diversity in the Knuckles massif with special reference to the relict species. *Lyriocephalus,* 6, 9–12.

Pethiyagoda R. (1994). Threats to indigenous freshwater fishes of Sri Lanka and remarks on their conservation. *Hydrobiologia,* 285, 189–201.

Pethiyagoda R. & Manamendra-Arachchi K. (1998). Evaluating Sri Lanka's amphibian diversity. *Occas. Pap. Wildl. Heritage Trust,* 2, 1–12.

Pethiyagoda P., Manamendra-Arachchi K., Bahir M.M. & Meegaskumbura M. (2006). Sri Lankan amphibians: diversity, uniqueness and conservation. In: *The Fauna of Sri Lanka*: *Status of Taxonomy, Research and Conservation* (ed. Bambaradeniya CNB). IUCN – The World Conservation Union, Sri Lanka. 125–133.

Pethiyagoda R. & Manamendra-Arachchi K. (1998). Evaluating Sri Lanka's amphibian diversity. *Occas. Pap. Wildl. Heritage Trust,* 2, 1–12.

Sri Barathi K.P. (1979). Man and biosphere reserves in Sri Lanka. *Sri Lanka Forester*, 14, 37–40.

Weerawardhena S.R. (1993). Some aspects of the population ecology of earthworms in the Central Region of Sri Lanka. *Proc. Sri Lanka Assoc. Adv. Sci.,* 49, 153–154.

Weerawardhena S.R. (2003). *Spatial Variation in Morphometric and Food Habits of Green Frog* Euphlyctis hexadactylus *(Lesson, 1843) in Sri Lanka*. M.Phil. thesis. University of Kelaniya, Sri Lanka.

Weerawardhena S.R. (2010). *Patterns of Recolonization by Tropical Anurans Following Forest Habitat Alteration*. M.Sc. thesis. University of Calgary, Canada.

Weerawardhena S.R. & Russell A.P. (2012a). Historical land-use patterns in relation to conservation strategies for the Riverstone area, the Knuckles massif, Sri Lanka: insights gained from the recovery of anuran communities. *Taprobanica,* 4, 92–102.

Weerawardhena S.R. & Russell A.P. (2012b). Cover-dependency of anurans in the Riverstone, Knuckles mountain forest range, Sri Lanka. *Taprobanica,* 4, 12–19.

Weerawardhena S.R. & Russell A.P. (2013). Forest secondary succession and anuran amphibian recolonization of abandoned tea plantations in Sri Lanka. *Hamdryard,* 36, 108–129.

Wickramasinghe D.D., Kotagama S.W. & Wassersug R.J. (2004). The terrestrial breeding biology of the ranid rock frog *Nannophrys ceylonensis*. *Behaviour,* 141, 899–913.

Wickramasinghe D.D., Kotagama S.W. & Wassersug R.J. (2005). Raising semi-terrestrial tadpoles of *Nannophrys ceylonensis* (Anura, Ranidae) in the laboratory. *Herpetol. Rev.*, 36, 23–26.

Wickramasinghe L.J.M., Munindradasa D.A.I. & Fernando P. (2012). A new species of *Polypedates tschudi* (Amphibia, Anura, Rhacophoridae) from Sri Lanka. *Zootaxa,* 3498, 63–80.

Wickramasinghe L.J.M., Vidanapathirana D.R. & Wickramasinghe N. (2012). Back from the dead: the world's rarest toad *Adenomus kandianus* rediscovered in Sri Lanka. *Zootaxa,* 3347, 63–68.

Appendix

Threatened amphibian species in Sri Lanka based on the Global Amphibian Assessment (http://www.amphibians.org/redlist/).

Status	Family	Species
Critically endangered	Bufonidae	Das's Dwarf Toad (*Adenomus dasi*) (Manamendra-Arachchi & Pethiyagoda 1998)
	Microhylidae	Karunaratne's Narrow-Mouth Frog (*Microhyla karunaratnei*) (Fernando & Siriwardhane 1996)
	Ranidae	Marbled Rock-Frog (*Nannophrys marmorata*) (Kirtisinghe 1946) Sri Lanka Tribal Rock-Frog (*Nannophrys naeyakai*) (Fernando, Wickramasinghe & Rodrigo 2007)
		Haycock Shrub-Frog (*Pseudophilautus limbus*) (Manamendra-Arachchi & Pethiyagoda, 2005)
		Handapanella Shrub-Frog (*Pseudophilautus lunatus*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Bigfoot Shrub-Frog (*Pseudophilautus macropus*) (Günther 1869)
		Whistling Shrub-Frog (*Pseudophilautus nemus*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Papilated Shrub-Frog (*Pseudophilautus papillosus*) (Manamendra-Arachchi & Pethiyagoda 2005)
Critically endangered	Ranidae	Cheeky Shrub-Frog (*Pseudophilautus procax*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Sinharaja Shrub-Frog (*Pseudophilautus simba*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Morningside Tree-Frog (*Polypedates fastigo*) (Manamendra-Arachchi & Pethiyagoda 2001)
Endangered	Bufonidae	Kotagama's Dwarf Toad (*Bufo kotagamai*) (Fernando & Dayawansa 1994)
		Noellert's Toad (*Bufo noellerti*) (Manamendra-Arachchi & Pethiyagoda 1998)
	Microhylidae	Sri Lanka Narrow-Mouth Frog (*Microhyla zeylanica*) (Parker & Hill 1949)
		Half-Webbed Pug-Snout Frog (*Ramanella palmate*) (Parker 1934)
		Sri Lanka Paddy-Field Frog (*Fejervarya greenii*) (Boulenger 1904)

Status	Family	Species
		Horton Plains Shrub-Frog (*Pseudophilautus alto*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Asanka's Shrub-Frog (*Pseudophilautus asankai*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Golden Shrub-Frog (*Pseudophilautus auratus*) (Manamendra-Arachchi & Pethiyagoda 2005)
Endangered	Microhylidae	Blue-Thigh Shrub-Frog (*Pseudophilautus caeruleus*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Sharp-Snout Shrub-Frog (*Pseudophilautus cuspis*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Hollow-Snout Shrub-Frog (*Pseudophilautus cavirostris*) (Günther 1869)
		Elegant Shrub-Frog (*Pseudophilautus decoris*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Round-Snout Pygmy Shrub-Frog (*Pseudophilautus femoralis*) (Günther 1864)
		Leaf-Dwelling Shrub-Frog (*Pseudophilautus folicola*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Frankenberg's Shrub-Frog (*Pseudophilautus frankenbergi*) (Megaskumbura & Manamendra-Arachchi 2005)
		Knuckles Shrub-Frog (*Pseudophilautus fulvus*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Hoffmann's Shrub-Frog (*Pseudophilautus hoffmanni*) (Megaskumbura & Manamendra-Arachchi 2005)
		Small-Eared Shrub-Frog (*Pseudophilautus microtympanum*) (Günther 1859)
Endangered	Microhylidae	Mittermeier's Shrub-Frog (*Pseudophilautus mittermeieri*) (Megaskumbura & Manamendra-Arachchi 2005)
		Moore's Shrub-Frog (*Pseudophilautus mooreorum*) (Megaskumbura & Manamendra-Arachchi 2005)
		Golden-Eyed Shrub-Frog (*Pseudophilautus ocularis*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Side-Striped Shrub-Frog (*Pseudophilautus pleurotaenia*) (Boulenger 1904)
		Poppy's Shrub-Frog (*Pseudophilautus poppiae*) (Megaskumbura & Manamendra-Arachchi 2005)
		Reticulated-Thigh Shrub-Frog (*Pseudophilautus reticulatus*) (Günther 1864)
		Schmarda's Shrub-Frog (*Pseudophilautus schmarda*) (Kelaart 1854)

Status	Family	Species
		Pug-Nosed Shrub-Frog (*Pseudophilautus silus*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Forest Shrub-Frog (*Pseudophilautus silvaticus*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Steiner's Shrub-Frog (*Pseudophilautus steineri*) (Megaskumbura & Manamendra-Arachchi 2005)
Endangered	Microhylidae	Stuart's Shrub-Frog (*Pseudophilautus stuarti*) (Megaskumbura & Manamendra-Arachchi 2005)
		Dull Green Shrub-Frog (*Pseudophilautus viridis*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Gannoruwa Shrub-Frog (*Pseudophilautus zorro*) (Manamendra-Arachchi & Pethiyagoda 2005)
		Mountain Hourglass Tree Frog (*Polypedates eques*) (Günther 1858)
		Long-Snout Tree-Frog (*Polypedates longinasus*) (Ahl 1931)
		Muller's Shrub-Frog (*Pseudophilautus sarasinorum*) (Müller 1887)
Vulnerable	Microhylidae	Nagao's Ramanella (*Ramanella nagaoi*) (Manamendra-Arachchi & Pethiyagoda 2001)
	Ranidae	Sri Lanka Rock-Frog (*Nannophrys ceylonensis*) (Günther 1868)
		Small Wood-Frog (*Rana aurantiaca*) (Boulenger 1904)
		Halliday's Shrub-Frog (*Pseudophilautus hallidayi*) (Megaskumbura & Manamendra-Arachchi 2005)
	Ichthyophiidae	Pattipola Caecilian (*Ichthyophis orthoplicatus*) (Taylor 1965)
		Lesser Yellow-Banded Caecilian (*Ichthyophis pseudangularis*) (Taylor 1965)

IV. Appendix

Publications of Anthony P. Russell to 2013

Russell A.P. (1972). The last of the ruling reptiles, alligators, crocodiles and their kin (Review). *J. Nat. Hist.*, 6, 243–244.

Romoli Sassi A., Russell A.P. & Lanza B. (1972). On a previously unrecorded gekkonid lizard from Somalia: *Hemidactylus mercatorius* Gray 1842. *Monit. Zool. Ital. N.S.*, Suppl. IV, 14, 317–326.

Russell A.P. (1973). The functional morphology of the tokay foot (*Gekko gecko*). *Am. Zool.*, 13, 522.

Russell A.P. (1975). A contribution to the functional analysis of the foot of the Tokay, *Gekko gecko* (Reptilia: Gekkonidae). *J. Zool.*, 176, 437–476.

Russell A.P. (1975). A guide to Alberta vertebrate fossils from the age of dinosaurs (Review). *Alberta Nat.*, 5, 49–51.

Russell A.P. (1976). Some comments concerning interrelationships amongst gekkonine geckos. In: *Morphology and Biology of Reptiles* (eds. Bellairs A & Cox CB). Academic Press London, 217–244.

Russell A.P. (1977). Comments concerning postcloacal bones in geckoes (Reptilia: Gekkonidae). *Can. J. Zool.*, 55, 1201–1205.

Russell A.P. (1977). The genera *Rhoptropus* and *Phelsuma* (Reptilia: Gekkonidae) in southern Africa: a case of convergence and a reconsideration of the biogeography of *Phelsuma*. *Zool. Afr.*, 12, 393–408.

Russell A.P. (1977). The phalangeal formula of *Hemidactylus* Oken, 1817 (Reptilia: Gekkonidae): a correction and a functional explanation. *Zbl. Vet. Med. C. Anat. Histol. Embryol.*, 6, 332–338.

Rosenberg H.I. & Russell A.P. (1978). Morphology of a unique caudal gland in some diplodactyline geckos. *Am. Zool.*, 18, 601.

Russell A.P. (1978). Modeling without models: permanent anatomical preparations from once-living systems. *Q. Can. Mus. Assoc.*, 11, 5–7.

Russell A.P. (1978). The status of the lizard genera *Blaesodactylus* Boettger and *Homopholis* Boulenger (Reptilia: Gekkonidae). *Copeia*, 1978, 25–29.

Russell A.P. (1979). A new species of *Luperosaurus* (Gekkonidae) with comments on the genus. *Herpetologica*, 35, 282–288.

Russell A.P. (1979). Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia*, 1979, 1–21.

Russell A.P. (1979). The origin of parachuting locomotion in gekkonid lizards (Reptilia: Gekkonidae). *Zool. J. Linn. Soc.*, 65, 233–249.

Russell A.P. & Rewcastle S.C. (1979). Digital reduction in *Sitana* (Reptilia: Agamidae) and the dual roles of the fifth metatarsal in lizards. *Can. J. Zool.*, 57, 1129–1135.

Rosenberg H.I. & Russell A.P. (1980). Structural and functional aspects of tail squirting: a unique defense mechanism of *Diplodactylus* (Reptilia: Gekkonidae). *Can. J. Zool.*, 58, 865–881.

Russell A.P. (1980). *Underwoodisaurus* Wermuth 1965, a junior synonym of *Phyllurus* Schinz 1822. *J. Herpetol.*, 14, 415–416.

Nicholls E.L. & Russell A.P. (1981). A new specimen of *Struthiomimus altus* from Alberta, with comments on the classificatory characters of Upper Cretaceous ornithomimids. *Can. J. Earth Sci.*, 18, 518–526.

Russell A.P. (1981). Arteries of the antebrachium and manus of the tokay (*Gekko gecko*) (Reptilia: Gekkonidae). *Can. J. Zool.*, 59, 573–582.

Russell A.P. (1981). Descriptive and functional anatomy of the digital vascular system of the Tokay, *Gekko gecko*. *J. Morphol.*, 169, 293–323.

Russell A.P. (1981). Lizard. In: *McGraw-Hill Yearbook of Science and Technology* (ed. Parker SB). McGraw-Hill New York, 228–231.

Russell A.P. & Rosenberg H.I. (1981). Self-grooming in *Diplodactylus spinigerus* (Reptilia: Gekkonidae), with a brief review of such behaviour in reptiles. *Can. J. Zool.*, 59, 564–566.

Russell A.P. & Rosenberg H.I. (1981). Subgeneric classification in the gekkonid genus *Diplodactylus*. *Herpetologica*, 37, 86–92.

Russell A.P. (1983). Winter: a test of survival. *Dinny's Digest*, Autumn 1983, 3–9.

Powell G.L. & Russell A.P. (1984). The diet of the eastern short-horned lizard (*Phrynosoma douglassi brevirostre*) in Alberta and its relationship to sexual size dimorphism. *Can. J. Zool.*, 62, 428–440.

Rosenberg H.I., Russell A.P. & Kapoor M. (1984). Preliminary characterization of the defensive secretion of *Diplodactylus* (Reptilia: Gekkonidae). *Copeia*, 1984, 1025–1028.

Nicholls E.L. & Russell A.P. (1985). Structural and functional aspects of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). *Palaeontol.,* 28, 675–709.

Powell G.L. & Russell A.P. (1985). Field thermal ecology of the eastern short-horned lizard (*Phrynosoma douglassi brevirostre*) in southern Alberta. *Can. J. Zool.*, 63, 228–238.

Powell G.L. & Russell A.P. (1985). Growth and sexual size dimorphism in Alberta populations of the eastern short-horned lizard, *Phrynosoma douglassi brevirostre*. *Can. J. Zool.*, 63, 139–154.

Russell A.P. (1985). The polar wanderer (a glimpse at the life of the polar bear). *Dinny's Digest*, Spring 1985, 3–9.

Russell A.P. & Joffe D.J. (1985). The early development of the quail (*Coturnix c. japonica*) furcula reconsidered. *J. Zool.*, 206, 69–81.

Russell A.P. & Thomason J.J. (1985). Mechanical aspects of the evolution of the mammalian secondary palate. *Am. Zool.*, 25, 145A.

Bauer A.M. & Russell A.P. (1986). *Hoplodactylus delcourti* n. sp. (Reptilia: Gekkonidae), the largest known gecko. *N.Z. J. Zool.*, 13, 141–148.

Russell A.P. (1986). The morphological basis of weight-bearing in the scansors of the tokay gecko (Reptilia: Sauria). *Can. J. Zool.*, 64, 948–955.

Russell A.P. (1986). The other mammals. *Dinny's Digest*, Summer 1986, 3–11.

Russell A.P. (1986). The reptiles of western North America: past glory, present challenge. In: *Scientific proceedings of the 40th Annual Conference of the International Union of Directors of Zoological Gardens*, Royal Zoological Society of Scotland Edinburgh, 23–40.

Russell A.P. (1986). The Structure, Development and Evolution of Reptiles, edited by M.W.J. Ferguson (Review). *Copeia*, 1986, 841–844.

Russell A.P. & Bauer A.M. (1986). Le gecko géant *Hoplodactylus delcourti* et ses relations avec le gigantisme et l'endemisme insulaire chez les Gekkonidae. *Mésogée*, 46, 25–28.

Russell A.P. & Curtis B.D. (1986). Preparation, from dissection discards, of skeletal material for teaching and display. *Coll. Forum,* 2, 8–9.

Thomason J.J. & Russell A.P. (1986). A general purpose plastic cage for experiments with the opossum (*Didelphis virginiana*). *Lab. Anim. Sci*., 1986, 547–549.

Thomason J.J. & Russell A.P. (1986). Mechanical factors in the evolution of the mammalian secondary palate: a theoretical analysis. *J. Morphol*., 189, 199–213.

Bauer A.M. & Russell A.P. (1987). *Hoplodactylus delcourti* (Reptilia: Gekkonidae) and the kawekaweau of Maori folklore. *J. Ethnobiol.*, 7, 83–91.

Bauer A.M. & Russell A.P. (1987). Supraocular bones in geckos. *Am. Zool.*, 27, 126A.

Russell A.P. (1987). Alberch, P. 1985. Museum collections and evolutionary study of growth and development, chapter 4, 29–41. In Miller, E.H. (ed.), Museum Collections: their Roles and Future in Biological Research. Occasional Papers 25. British Columbia Provincial Museum, Victoria BC (Review). *Coll. Forum*, 3, 36.

Russell A.P. (1987). Getting to grips with the world: those astounding geckos. *Rotunda*, 20, 7–8.

Russell A.P. (1987). Some like it hot (and dry). Deserts and the life they support. *Dinny's Digest*, 1987.

Russell A.P. & Bauer A.M. (1987). Caudal morphology of the knob-tailed geckos, genus *Nephrurus* (Reptilia: Gekkonidae), with special reference to the tail tip. *Aust. J. Zool*., 35, 541–551.

Russell A.P. & Bauer A.M. (1987). Morphology of the tail tip of the gekkonid genus *Nephrurus*. *Am. Zool*., 27, 64A.

Russell A.P. & Bauer A.M. (1987). Rediscovery of *Uroplatus guentheri* Mocquard (Reptilia: Gekkonidae). *Bull. Mus. Natl. Hist. Nat. Paris* 4^e *Ser. 9 Sect. A*, 4, 961–966.

Russell A.P., Bauer A.M. & Walker R.L. (1987). Microfil injections of small vertebrates: an adjunct to clearing and staining. *Coll. Forum*, 3, 3–5.

Thomason J.J. & Russell A.P. (1987). The mechanical effects of the in vitro removal of the hard palate in a long-faced mammal. *J. Am. Osteopathol. Assoc.*, 87, 781.

Bauer A.M. & Russell A.P. (1988). Osteological evidence for the prior occurrence of a giant gecko in Otago, New Zealand. *Cryptozool.*, 7, 22–37.

Bauer A.M. & Russell A.P. (1988). The morphology of gekkonid cutaneous sensilla, with comments on function and phylogeny in the Carphodactylini. *Can. J. Zool.*, 66, 1583–1588.

Bauer A.M., Russell A.P. & Shadwick R.E. (1988). Morphological and mechanical aspects of integumentary autotomy in the gecko *Ailuronyx*. *Am. Zool.*, 28, 194A.

Russell A.P. (1988). Limb muscles in relation to lizard systematics: a reappraisal. In *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp* (eds. Estes R & Pregill G). Stanford University Press, Stanford, 493–568.

Russell A.P. & Bauer A.M. (1988). Alternative designs of and potential constraints on the morphology of digit I in geckos. *Am. Zool.*, 28, 38A.

Russell A.P. & Bauer A.M. (1988). An early description of a member of the genus *Phelsuma* (Reptilia: Gekkonidae), with comments on names erroneously applied to *Uroplatus fimbriatus*. *Amphib.-Reptilia*, 9, 107–116.

Russell A.P. & Bauer A.M. (1988). Paraphalangeal elements of gekkonid lizards: a comparative survey. *J. Morphol.*, 197, 221–240.

Russell A.P., Walker R.L. & Bauer A.M. (1988). A technique for visualization of the circulatory system in small lizards. *Copeia*, 1988, 797–800.

Bauer A.M. & Russell A.P. (1988). Evidence for the Tzuchinoko equivocal. *Cryptozool.*, 7, 110–113.

Bauer A.M. & Russell A.P. (1989). A systematic review of the genus *Uroplatus* (Reptilia: Gekkonidae), with comments on its biology. *J. Nat. Hist.*, 23, 169–203.

Bauer A.M. & Russell A.P. (1989). Supraorbital ossifications in geckos. *Can. J. Zool.*, 67, 678–684.

Bauer A.M., Russell A.P. & Edgar B.D. (1989). Utilization of termites by gekkonid lizards near Keetmanshoop, South West Africa. *S. Afr. J. Zool*, 24, 239–243.

Bauer A.M., Russell A.P. & Rosenberg H.I. (1989). Formal taxa, species groups and the perception of the genus *Diplodactylus* (Reptilia: Gekkonidae). *Z. Syst. Evolutionsforsch.*, 27, 44–48.

Bauer A.M., Russell A.P. & Shadwick R.E. (1989). Mechanical properties and morphological correlates of fragile skin in gekkonid lizards. *J. Exp. Biol.*, 145, 79–102.

Perry S.F., Bauer A.M., Russell A.P., Alston J.T. & Maloney J. (1989). Lungs of the gecko *Rhacodactylus leachianus* (Reptilia: Gekkonidae): a correlative gross anatomical and light and electron microscopic study. *J. Morphol.*, 199, 23–40.

Rosenberg H.I., Bauer A.M. & Russell A.P. (1989). Surface morphology of the developing hemipenes of the dwarf chameleon, *Bradypodion pumilum* (Reptilia: Chamaeleonidae). *Can. J. Zool.*, 67, 884–890.

Russell A.P. & Bauer A.M. (1989). Hypertrophied phalangeal epiphyses in the gekkonid lizard genus *Phelsuma*: a unique aid to adhesion. *Ann. Soc. R. Zool. Belg.*, 119 (Suppl. 1), 72.

Russell A.P. & Bauer A.M. (1989). The morphology of the digits of the golden gecko, *Calodactylodes aureus* (Reptilia: Gekkonidae) and its implications for the occupation of rupicolous habitats. *Amphib.-Reptilia*, 10, 125–140.

Russell A.P. & Bauer A.M. (1989). Ungual asymmetry in the context of pedal symmetry in *Ailuronyx* (Reptilia: Gekkonidae) modification for an opposable grip. *J. Zool.*, 218, 1–11.

Bauer A.M. & Russell A.P. (1990). Alternative digital scansor design in the New Caledonian gekkonid genera *Bavayia* and *Eurydactylodes*. *Mem. Qld. Mus.*, 29, 299–310.

Bauer A.M. & Russell A.P. (1990). Dentitional diversity in the genus *Rhacodactylus* (Reptilia: Gekkonidae). *Mem. Qld. Mus.*, 29, 311–322.

Bauer A.M. & Russell A.P. (1990). Recent advances in the search for the living giant gecko of New Zealand. *Cryptozool.*, 9, 66–73.

Bauer A.M., Russell A.P. & Dollahon N.R. (1990). Skin folds in the gekkonid lizard genus *Rhacodactylus*: a natural test of the damage limitation hypothesis of mite pocket function. *Can. J. Zool.*, 68, 1196–1201.

Bauer A.M., Russell A.P. & Shadwick R.E. (1990). Skin mechanics and morphology of the gecko *Sphaerodactylus roosevelti*. *Am. Zool.*, 30, 101A.

Nicholls E.L. & Russell A.P. (1990). Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. *Paleogeogr., Paleoclimatol., Paleoecol.*, 79, 149–169.

Russell A.P. (1990). Letter: Reply to Green. *Int. Soc. Cryptozool. Newsl.*, 9, 10–11.

Russell A.P. & Bauer A.M. (1990). Digit I in pad-bearing gekkonine geckos: alternate designs and the potential constraints of phalangeal number. *Mem. Qld. Mus.*, 29, 453–472.

Russell A.P. & Bauer A.M. (1990). Hypertrophied phalangeal chondroepiphyses in the gekkonid lizard genus *Phelsuma*: their structure and relation to the adhesive mechanism. *J. Zool.*, 221, 205–217.

Russell A.P. & Bauer A.M. (1990). *Oedura* and *Afroedura* (Reptilia: Gekkonidae) revisited: similarities of digital design, and constraints on the development of multiscansorial subdigital pads. *Mem. Qld. Mus.*, 29, 473–486.

Russell A.P. & Bauer A.M. (1990). Structure of the vocal apparatus of the tokay (*Gekko gecko*). *Am. Zool.*, 30, 78A.

Russell A.P. & Bauer A.M. (1990). Substrate excavation in the Namibian web-footed gecko, *Palmatogecko rangei*, and its ecological significance. *Trop. Zool.*, 3, 197–207.

Thomason J.J., Russell A.P. & Morgeli M. (1990). Forces of biting, body size, and masticatory muscle tension in the opossum *Didelphis virginiana*. *Can. J. Zool.*, 68, 318–324.

Bauer A.M. & Russell A.P. (1991). Pedal specializations in dune dwelling geckos. *J. Arid Environ.*, 20, 43–62.

Bauer A.M. & Russell A.P. (1991). The maximum size of giant geckos: a cautionary tale. *Bull. Chicago Herpetol. Soc.*, 26, 25–26.

Bryant H.N. & Russell A.P. (1991). A research program for the reconstruction of unpreserved attributes in fossil vertebrates. *J. Vertebr. Paleontol.*, 11 Suppl., 18A.

Bryant H.N. & Russell A.P. (1991). Homologs vs. neomorphs: the role of systematics in morphological interpretation of the avian furcula). *Am. Zool.*, 31, 62A.

Moore B.A., Russell A.P. & Bauer A.M. (1991). The structure of the larynx of the Tokay gecko (*Gekko gecko*) with particular reference to the vocal cords and glottal lips. *J. Morphol.*, 210, 227–238.

Nicholls E.L. & Russell A.P. (1991). The plesiosaur pectoral girdle: the case for a sternum. *N. Jahrb. Geol. Palaeontol.*, 182, 161–185.

Powell G.L. & Russell A.P. (1991). Distribution of the eastern short-horned lizard (*Phrynosoma douglassii brevirostre*) in Alberta. *Northwest. Nat.*, 72, 21–26.

Powell G.L. & Russell A.P. (1991). Parturition and clutch characteristics of short-horned lizards (*Phrynosoma douglassi brevirostre*) from Alberta. *Can. J. Zool.*, 69, 2759–2764.

Powell G.L. & Russell A.P. (1991). Report on the 1991 search for the pygmy short-horned lizard (*Phrynosoma douglassii douglassii*) in the region of Osoyoos, British Columbia. Report submitted to the Wildlife Branch, British Columbia Environment.

Russell A.P. (1991). Desert geckos—moving in the dunes. *J. Alberta Amphib. Reptil. Soc.*, 25, 1–11.

Russell A.P. (1991). Preparing for Winter: Migration? Resistance? Hibernation? *Dinny's Digest*, Autumn 1991, 3–9.

Russell A.P. & Bryant H.N. (1991). The homology of the maniraptoran furcula: the phylogenetic evidence. *J. Vertebr. Paleontol.*, 11 Suppl., 53A.

Russell A.P. & Bauer A.M. (1991). Amphibians and reptiles of the Calgary area. *Alberta Nat.*, 21, 123–128.

Russell A.P. & Bauer A.M. (1991). Amphibians and reptiles of the Calgary area. *J. Alberta Amphib. Reptil. Soc.*, 26, 12–23.

Russell A.P. & Bauer A.M. (1991). Amphibians and reptiles of the Calgary area. *Pica*, 11, 3–15.

Russell A.P. & Bauer A.M. (1991). *Anolis garmani*. *Cat. Am. Amphib. Reptil.,* 513, 1–3.

Russell A.P. & Bauer A.M. (1991). *Anolis grahami*. *Cat. Am. Amphib. Reptil.,* 514, 1–4.

Russell A.P. & Bauer A.M. (1991). *Anolis opalinus*. *Cat. Am. Amphib. Reptil.,* 515, 1–2.

Russell A.P. & Bauer A.M. (1991). The giant gecko *Hoplodactylus delcourti* and its relations to gigantism and insular endemism in the Gekkonidae. (translated by P. Gritis). *Bull. Chicago Herpetol. Soc.*, 26, 26–30.

Shadwick R.E., Russell A.P. & Lauff R.F. (1991). Structure and mechanical design of White Rhinoceros dermal armor. *Am. Zool.*, 31, 54A.

Bauer A.M., Doherty J. & Russell A.P. (1992). Vocalizations of the New Caledonian giant gecko, *Rhacodactylus leachianus*. *Amphib.-Reptilia*, 13, 412–417.

Bauer A.M. & Russell A.P. (1992). Caudal morphology and caudal autotomy in prehensile-tailed carphodactyline geckos. *Am. Zool.*, 32, 138A.

Bauer A.M. & Russell A.P. (1992). Regional integumentary loss as an escape strategy in island gekkonid lizards. In: *Proceedings of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica* (eds. Korsós Z & Kiss I). Hungarian Natural History Museum Budapest, 69–71.

Bauer A.M. & Russell A.P. (1992). The evolutionary significance of regional integumentary loss in island geckos: a complement to caudal autotomy. *Ethol. Ecol. Evol.*, 4, 343–358.

Bauer A.M., Russell A.P. & Shadwick R.E. (1992). Skin mechanics and morphology in *Sphaerodactylus roosevelti* (Reptilia: Gekkonidae). *Herpetologica*, 48, 124–133.

Bininda-Emonds O.R.P. & Russell A.P. (1992). Effects of preservation on the morphometry of bat wings: recommendations to minimize potential problems. *Coll. Forum*, 8, 9–14.

Bryant H.N. & Russell A.P. (1992). Jaw mechanics and carnassial wear in the nimravid cats *Dinictis* and *Hoplophoneus*. *J. Vertebr. Paleontol.*, 12 Suppl., 19A–20A.

Bryant H.N. & Russell A.P. (1992). The position of the carnassials in saber-toothed carnivorans: a test of Greaves's model. *Am. Zool.*, 32, 140A.

Bryant H.N. & Russell A.P. (1992). The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Phil. Trans. R. Soc.*, 337B, 405–418.

Powell G.L. & Russell A.P. (1992). A preliminary survey of the distribution and abundance of the Eastern Short-Horned Lizard (*Phrynosoma douglassii brevirostre*) in Alberta. Report submitted to the Recreation, Parks and Wildlife Foundation, Edmonton, Alberta.

Powell G.L. & Russell A.P. (1992). Locomotor correlates of ecomorph designation in *Anolis*: an examination of three sympatric species from Jamaica. *Can. J. Zool.*, 70, 725–739.

Rosenberg H.I., Russell A.P. & Cavey M.J. (1992). Development of the subdigital adhesive pads of *Ptyodactylus guttatus* (Reptilia: Gekkonidae). *J. Morphol.*, 211, 245–258.

Russell A.P. & Bauer A.M. (1992). The m. caudifemoralis longus and its relationship to caudal autotomy and locomotion in lizards. *J. Zool.*, 227, 127–143.

Russell A.P., Bauer A.M. & Laroiya R. (1992). Morphological correlates of the secondarily symmetrical pes of the Tokay gecko (Reptilia: Gekkonidae). *Am. Zool.*, 32, 150A.

Shadwick R.E., Russell A.P. & Lauff R.F. (1992). The structure and mechanical design of rhinoceros dermal armour. *Phil. Trans. R. Soc.*, 337B, 419–428.

Bauer A.M. & Russell A.P. (1993). *Aristelliger barbouri*. *Cat. Am. Amphib. Reptil.*, 566, 1.

Bauer A.M. & Russell A.P. (1993). *Aristelliger* – generic account. *Cat. Am. Amphib. Reptil.*, 565, 1–4.

Bauer A.M. & Russell A.P. (1993). *Aristelliger georgeensis*. *Cat. Am. Amphib. Reptil.*, 568, 1–2.

Bauer A.M. & Russell A.P. (1993). *Aristelliger hechti*. *Cat. Am. Amphib. Reptil.*, 569, 1–2.

Bauer A.M. & Russell A.P. (1993). *Aristelliger lar*. *Cat. Am. Amphib. Reptil.*, 570, 1–3.

Bauer A.M. & Russell A.P. (1993). *Aristelliger praesignis*. *Cat. Am. Amphib. Reptil.*, 571, 1–4.

Bauer A.M. & Russell A.P. (1993). Functional, ontogenetic and phylogenetic constraints in the digital morphology of gekkonid lizards. *Second World Congr. Herpetol. Abstr.*, 16.

Bauer A.M. & Russell A.P. (1993). Regional integumentary loss as an antipredator strategy in lizards. *Second World Congr. Herpetol. Abstr.*, 16–17.

Bauer A.M., Russell A.P. & Dollahon N.R. (1993). Function of the mite pockets of lizards: a reply to E.N. Arnold. *Can. J. Zool.*, 71, 865–868.

Bauer A.M., Russell A.P. & Shadwick R.E. (1993). Skin mechanics and morphology of the gecko *Teratoscincus scincus*. *Amphibia-Reptilia*, 14, 321–331.

Bauer A.M., Russell A.P. & Shadwick R.E. (1993). Skin mechanics and morphology of two species of *Pachydactylus* (Reptilia: Gekkonidae). *S. Afr. J. Zool.*, 28, 192–197.

Bininda-Emonds O.R.P. & Russell A.P. (1993). Effects of preservation on wing morphometry of the little brown bat (*Myotis lucifugus*). *J. Zool.*, 230, 141–158.

Bryant H.N. & Russell A.P. (1993). The occurrence of clavicles within Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. *J. Vertebr. Paleontol.*, 13, 171–184.

Bryant H.N., Russell A.P. & Fitch W.D. (1993). Phylogenetic relationships within the Mustelidae (carnivora): appraisal of the cladistic status of the Simpsonian subfamilies. *Zool. J. Linn. Soc.*, 108, 301–334.

Lauff R.F., Russell A.P. & Bauer A.M. (1993). Topography of the digital cutaneous sensilla of the Tokay, *Gekko gecko* (Reptilia, Gekkonidae) and their potential role in locomotion. *Can. J. Zool.*, 71, 2462–2472.

Powell G.L., Nelson S.J. & Russell A.P. (1993). The Bow Valley long-toed salamander population study: a preliminary report on the 1992 field season. Report submitted to Alberta Forestry, Lands and Wildlife, Fish and Wildlife Division, Calgary, Alberta.

Powell G.L. & Russell A.P. (1993). A radiotelemetric study of movement and thermal ecology in an Alberta population of the eastern short-horned lizard (*Phrynosoma douglassii brevirostre*). Report submitted to Alberta Forestry, Lands and Wildlife, Fish and Wildlife Division, Edmonton, Alberta.

Powell G.L. & Russell A.P. (1993). Monitoring amphibian populations in Alberta: are they declining? In: *Proceedings of the Third Prairie Conservation and Endangered Species Workshop* (eds. Holroyd GL, Dickson HL, Regnier M & Smith HC). *Prov. Mus. Alberta Nat. Hist. Occas. Pap.*, 19, 276–277.

Powell G.L. & Russell A.P. (1993). The range and status of the eastern short-horned lizard in the Canadian Prairies. In: *Proceedings of the Third Prairie Conservation and Endangered Species Workshop* (eds. Holroyd GL, Dickson HL, Regnier M & Smith HC). *Prov. Mus. Alberta Nat. Hist. Occas. Pap.*, 19, 278–290.

Russell A.P. (1993). The aponeuroses of the lacertilian ankle. *J. Morphol.*, 218, 65–84.

Russell A.P. (1993). The aponeuroses of the lacertilian ankle and their relation to sprawling locomotion. *Second World Congr. Herpetol. Abstr.*, 227–228.

Russell A.P. & Bauer A.M. (1993). *The Amphibians and Reptiles of Alberta: a Field Guide and Primer of Boreal Herpetology*. University of Calgary Press, Calgary.

Russell A.P. & Thomason J.J. (1993). Mechanical analysis of the mammalian head skeleton. In: *The Skull, Volume 3, Functional and Evolutionary Mechanisms* (eds. Hanken J & Hall BK). University of Chicago Press Chicago, 345–383.

Wu X.-C., Brinkman D.B., Russell A.P., Dong Z.-M., Currie P.J., Hou L.-H. & Cui G.-H. (1993). The oldest known amphisbaenian from the Upper Cretaceous of Chinese Inner Mongolia. *Nature*, 366, 57–59.

Bauer A.M. & Russell A.P. (1994). Is autotomy frequency reduced in geckos with “actively functional” tails? *Herpetol. Nat. Hist.*, 2, 1–15.

Bininda-Emonds O.R.P. & Russell A.P. (1994). Flight style in bats as predicted from wing morphometry: the effects of specimen preservation. *J. Zool.*, 234, 275–289.

Bryant H.N. & Russell A.P. (1994). Claw retraction in felids—the significance of skeletal microvariation. *J. Morphol.*, 220, 329–330.

Gardner J.D. & Russell A.P. (1994). Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. *N. Jahrb. Paläont.*, 193, 209–244.

Powell G.L. & Russell A.P. (1994). A radiotelemetric study of movement, thermal ecology and hibernation site selection in an Alberta population of the estern short-horned lizard (*Phrynosoma douglasii brevirostre*). Report submitted to Alberta Environmental Protection, Fish and Wildlife Division, Lethbridge, Alberta.

Russell A.P. (1994). The mammalian masticatory apparatus: an introductory comparative exercise. *J. Morphol.*, 220, 390.

Bauer A.M. & Russell A.P. (1995). The systematic relationships of *Dravidogecko anamallensis* (Günther 1875). *Asiat. Herpetol. Res.*, 6, 30–35.

Bryant H.N. & Russell A.P. (1995). Carnassial functioning in nimravid and felid sabertooths: theoretical basis and robustness of inferences. In: *Functional Morphology in Vertebrate Paleontology* (ed. Thomason JJ). Cambridge University Press Cambridge, 116–135.

Gardner J.G., Russell A.P. & Brinkman D.B. (1995). Taxonomy and systematics of soft-shelled turtles (Family Trionychidae) from the Judith River Group (Upper Campanian) of North America. *Can. J. Earth Sci.*, 32, 631–643.

McAllister C.T., Bauer A.M. & Russell A.P. (1995). Nonproliferous tetrathyridia of *Mesocestoides* sp. (Eucestoda: Mesocestoididea) in *Ptenopus garrulus maculatus* (Sauria: Gekkonidae) from Namibia, South West Africa, with a summary of the genus from Old World lizards. *J. Helminthol. Soc. Wash.*, 62, 94–98.

Nelson S.J., Powell G.L. & Russell A.P. (1995). Population survey of the long-toed salamander (*Ambystoma macrodactylum*) in southwestern Alberta. Report submitted to Fish and Wildlife, Environmental Protection, Edmonton, Alberta.

Oseen K.L., Powell G.L. & Russell A.P. (1995). The distribution of the long-toed salamander (*Ambystoma macrodactylum*) in southwestern Alberta. Report submitted to Fish and Wildlife, Environmental Protection, Edmonton, Alberta.

Oseen K.L., Powell G.L. & Russell A.P. (1995). The distribution of the long-toed salamander (*Ambystoma macrodactylum*) in northwestern Alberta. Report submitted to Fish and Wildlife, Environmental Protection, Edmonton, Alberta.

Peng J., Brinkman D.B. & Russell A.P. (1995). A paleoecologic study of vertebrate microfossil assemblages from the lower Judith River Group (Campanian) of southeastern Alberta, Canada. In: *Proceedings of the*

Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota (eds. Sun AL & Wang YQ). China Ocean Press, Beijing, 185–187.

Powell G.L. & Russell A.P. (1995). Status report on the short-horned lizard, *Phrynosoma douglassii* in Canada. Report submitted to Committee on the Status of Endangered Wildlife in Canada.

Russell A.P., Bryant H.N., Powell G.L. & Laroiya R. (1995). Scaling relationships within the maxillary tooth row of the Felidae, and the absence of the second upper premolar in *Lynx*. *J. Zool.*, 236, 161–182.

Bauer A.M., Russell A.P. & Powell G.L. (1996). The evolution of locomotor morphology in *Rhoptropus* (Squamata: Gekkonidae): functional and phylogenetic considerations. *Afr. J. Herpetol.*, 45, 8–30.

Bininda-Emonds O.R.P. & Russell A.P. (1996). A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). *Bonn. Zool. Monogr.*, 41, 1–256.

Bryant H.N., Russell A.P., Laroiya R. & Powell G.L. (1996). Claw retraction and protraction in the Carnivora: skeletal microvariation in the phalanges of the Felidae. *J. Morphol.*, 229, 289–308.

Dollahon N.R. Bauer A.M. & Russell A.P. (1996). Hoemoparasitic protozoans (Plasmodiidae and Haemogregarinidae) from a New Caledonian gekkonid lizard *Rhacodactylus leachianus*. *Can. J. Zool.*, 74, 2104–2108.

Hamilton I.M., Graham K.L., Powell G.L. & Russell A.P. (1996). Population survey of the long-toed salamander (*Ambystoma macrodactylum*) in west-central and northwestern Alberta. Report submitted to Fish and Wildlife, Environmental Protection. Edmonton, Alberta.

Hamilton I.M., Russell A.P. & Powell G.L. (1996). Distribution and abundance of the Canadian toad (*Bufo hemiophrys*) in Alberta. Report submitted to Alberta Environmental Protection, Natural Resources Services, Edmonton, Alberta.

Powell G.L., Oseen K.L. & Russell A.P. (1996). Volunteer amphibian monitoring in Alberta 1992–1994: the results of the pilot project. Report submitted to Alberta Environmental Protection, Fish and Wildlife Division.

Powell G.L. & Russell A.P. (1996). Alberta's amphibians and reptiles: current research and conservation issues. In: *Proceedings of the Fourth Prairie Conservation and Endangered Species Workshop* (eds. Willms

WD & Dormaar JF). *Prov. Mus. Alberta Nat. Hist. Occas. Pap.*, 23, 253–256.

Powell G.L. & Russell A.P. (1996). A preliminary study of the eastern short-horned lizard (*Phrynosoma douglassii brevirostre*) in Grasslands National Park. *Grasslands Natl. Park Ann. Rep.*, 1, 35–43.

Powell G.L. & Russell A.P. (1996). Movement, thermal ecology, seasonal activity, and overwintering behaviour in an Alberta population of the eastern short-horned lizard (*Phrynosoma douglassi brevirostre*). The 1994 Study. Report submitted to Alberta Environmental Protection, Fish and Wildlife Division.

Powell G.L. & Russell A.P. (1996). Short-horned lizards (*Phrynosoma douglassi brevirostre*) in Grasslands National Park. A report on the 1995 field season. Report submitted to Grasslands National Park, Parks Canada, Val Marie, Saskatchewan.

Powell G.L. & Russell A.P. (1996). Short-horned lizards (*Phrynosoma douglassi brevirostre*) in the East Block of Grasslands National Park. Report submitted to Parks Canada.

Powell G.L. & Russell A.P. (1996). The long-toed salamander in the Bow Corridor: a preliminary report. Report submitted to Alberta Environmental Protection, Fish and Wildlife Division.

Rittenhouse D., Russell A.P. & Richards D. (1996). Morphological modeling via isosurfacing: the laryngeal skeleton of gekkonid lizards as a test case. *Acta Anat.*, 155, 282–290.

Russell A.P., Powell G.L. & Hall D.R. (1996). Growth and age in Alberta long-toed salamanders (*Ambystoma macrodactylum krausei*): a comparison of two methods of estimation. *Can. J. Zool.*, 74, 397–412.

Wu X.-C., Brinkman D.B. & Russell A.P. (1996). A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians. *Palaeontol.*, 39, 351–375.

Wu X.-C., Brinkman D.B. & Russell A.P. (1996). A new crocodyliform (*Sunosuchus junggarensis*) from the Upper Jurassic of Xinjiang, northwest China, with comments on the ontogenetic variation of its skull. *Can. J. Earth Sci.*, 33, 606–630.

Wu X.-C., Brinkman D.B. & Russell A.P. (1996). *Sineoamphisbaena hexatabularis*, an amphisbaenian (Diapsida: Squamata) from the Upper

Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China) and comments on the phylogenetic relationships of the Amphisbaenia. *Can. J. Earth Sci.*, 33, 541–577.

Bauer A.M. & Russell A.P. (1997). A living plesiosaur? A critical assessment of the description of *Cadborosaurus willsi*. *Cryptozool.*, 12, 1–18.

Bourne G.B. & Russell A.P. (1997). Biological Sciences 2000: revising a curriculum to face a future of reduced funding and demands of flexibility. In: *Science and Technology Education for Responsible Citizenship and Economic Development International Organization for Science and Technology Education. 8th Symposium Proceedings* (eds. Calhoun K, Panwar R & Shrum S). University of Alberta Edmonton, Alberta, pg. 218.

James J.D., Russell A.P. & Powell G.L. (1997). Status of the eastern short-horned lizard (*Phrynosoma douglassii brevirostre*) in Alberta. *Alberta Wildl. Status Rep.* No. 5: vi + 1–20.

Powell G.L., Brisson R. & Russell A.P. (1997). A preliminary survey of the amphibian and turtle species of Grasslands National Park. Report submitted to Parks Canada, Grasslands National Park, Val Marie, Saskatchewan.

Powell G.L., Russell A.P., James J.D., Nelson S.J. & Watson S.M. (1997). Population biology of the long-toed salamander, *Ambystoma macrodactylum*, in the Front Range of Alberta. In: *Amphibians in decline: Canadian studies of a global problem* (ed. Green DM). *Herpetol. Conserv.*, 1, 37–44.

Rittenhouse D.R., Russell A.P. & Bauer A.M. (1997). Laryngotracheal morphology of the *Uroplatus fimbriatus* complex (Reptilia: Gekkonidae): yet another autapomorphic organ system in a group of highly aberrant geckos. *Afr. J. Herpetol.*, 46, 36–48.

Russell A.P., Bauer A.M. & Deufel A. (1997). *Comparative Osteological Examinations of Geckonids, Eublepharids and Uroplatids*, With a Foreword. (Translation) Herpbooks, Logan, Utah.

Russell A.P., Bauer A.M. & Laroiya R. (1997). Morphological correlates of the secondarily symmetrical pes of gekkotan lizards. *J. Zool.*, 241, 767–790.

Russell A.P. & Bryant H.N. (1997). Claw retraction in felids: how the cheetah cheats. *J. Morphol.*, 232, 318.

Russell A.P. & Hall D.R. (1997). Coracoclavicular membranes of birds: their morphology, histology and biomechanics in relation to flight. *J. Morphol.*, 232, 318.

Russell A.P., Rittenhouse D.R. & Bauer A.M. (1997). The larynx and trachea of the barking gecko *Ptenopus garrulus maculatus* in relation to vocalization. In: *Herpetology 97: Abstracts of the Third World Congress of Herpetology* (eds. Rocek Z & Hart S). Ministry of Environment Prague, pg. 179.

Russell A.P. & Wu X.-C. (1997). The Crocodylomorpha at and between geological boundaries: the Baden-Powell approach to change. *J. Morphol.*, 232, 318.

Russell A.P. & Wu X.-C. (1997). The Crocodylomorpha at and between geological boundaries: the Baden-Powell approach to change. *Zoology*, 100, 164–182.

Ryan M.J. & Russell A.P. (1997). Color. In: *Encyclopedia of Dinosaurs* (eds. Currie PJ & Padian K). Academic Press Toronto, 134–135.

Watson S.M. & Russell A.P. (1997). Status of the prairie rattlesnake (*Crotalus viridis viridis*) in Alberta. *Alberta Wildl. Status Rep.* No. 6: vii + 1–27.

Wu X.-C. & Russell A.P. (1997). Functional morphology. In: *Encyclopedia of Dinosaurs* (eds. Currie PJ & Padian K). Academic Press Toronto, 258–268.

Wu X.-C. & Russell A.P. (1997). Systematics. In: *Encyclopedia of Dinosaurs* (eds. Currie PJ & Padian K). Academic Press Toronto, 704–712.

Wu X.-C., Russell A.P. & Brinkman D.B. (1997). Phylogenetic relationships of *Sineoamphisbaena hexatabularis*: further considerations. *Can. J. Earth Sci.*, 34, 883–885.

Bininda-Emonds O.R.P., Bryant H.N. & Russell A.P. (1998). Supraspecific taxa as terminals in cladistic analysis: implicit assumptions of monophyly and errors in phylogenetic inference. *Biol. J. Linn. Soc.*, 64, 101–133.

Powell G.L. & Russell A.P. (1998). The status of the short-horned lizards, *Phrynosoma douglassii*, and *P. hernandezi* in Canada. *Can. Field Nat.*, 112, 1–16.

Powell G.L., Russell A.P. & Fargey P.J. (1998). The distribution of the eastern short-horned lizard (*Phrynosoma hernandezi*) in Saskatchewan, Canada. *Northwest. Nat.*, 79, 19–26.

Powell G.L., Russell A.P., Hill M.M.A., O'Brien N.E. & Skilnick J. (1998). A preliminary investigation of movements, habitat use, and population trends in the prairie rattlesnake (*Crotalus viridis*) in a multiple-use rural landscape in southeastern Alberta. The 1997 Field Season. Report submitted to the Alberta Conservation Association.

Rittenhouse D.R., Russell A.P. & Bauer A.M. (1998). The larynx and trachea of the barking gecko, *Ptenopus garrulus maculatus* (Reptilia: Gekkonidae) and their relation to vocalization. *S. Afr. J. Zool.*, 33, 23–30.

Rosenberg H.I. & Russell A.P. (1998). Review of textbooks of comparative vertebrate anatomy. *Am. Zool.*, 38, 406–409.

Russell A.P. (1998). Osteology of the Reptiles. Alfred Sherwood Romer. Krieger Publishing Company (Review). *Am. Zool.*, 38, 795–796.

Russell A.P. (1998). The mammalian masticatory apparatus: an introductory comparative exercise. In: *Tested Studies for Laboratory Teaching, Vol. 19. Proceedings of the 19th Workshop/Conference of the Association for Biology Laboratory Education (ABLE)* (ed. Karcher SJ). Purdue University Lafayette, Indiana, 271–286.

Ryan M.J., Eberth D.A., Brinkman D.B. & Russell A.P. (1998). A sub-adult *Styracosaurus* (Ornithischia) from the Dinosaur Park Formation (Late Campanian), Alberta, Canada. *J. Vertebr. Paleontol.*, 18, 73A.

Vickaryous M.K., Russell A.P., Currie P.J., Carpenter K. & Kirkland J.I. (1998). The cranial sculpturing of ankylosaurs (Dinosauria: Ornithischia): reappraisal of developmental hypotheses. *J. Vertebr. Paleontol.,* 18, 83A.

Beavan N.R. & Russell A.P. (1999). A marine vertebrate microfossil assemblage from the Lethbridge Coal Zone (Dinosaur Park Formation: Campanian), Alberta, Canada. *J. Paleontol.*, 73, 494–503.

Powell G.L. & Russell A.P. (1999). Amphibians and reptiles on the Alberta prairies—current issues. In: *Proceedings of the Fifth Prairie Conservation and Endangered Species Conference* (eds. Thorpe J, Steeves TA & Gollop M). *Prov. Mus. Alberta Nat. Hist. Occas. Pap.*, 24, 331–334.

Russell A.P. (1999). Past glory and present challenge: the amphibians and reptiles of Alberta. In: *Proceedings of the 1st, 2nd, and 3rd Canadian Herpetological Symposia*. Drumheller, Alberta, 52–60.

Russell A.P., Vickaryous M.K. & Snively E. (1999). Palaeontological impact assessment of two Red Deer river crossings. Report submitted to Golder Associates Ltd. for AMOCO Canada.

Russell A.P. (2000). Mary Needler Arai. A family tree of sea scholars. *Can. Soc. Zool. Bull.*, 31, 17–20.

Russell A.P. & Bauer A.M. (2000). *The Amphibians and Reptiles of Alberta: a Field Guide and primer of Boreal Herpetology*. 2nd edition. University of Calgary Press, Calgary, Alberta.

Russell A.P. & Bels V. (2000). Biomechanics of locomotion in lizards: phylogenetic and functional constraints. *Comp. Biochem. Physiol. A*, 126 Suppl. 1, S130.

Russell A.P., Rittenhouse D.R. & Bauer A.M. (2000). Laryngotracheal morphology of Afro-Madagascan geckos: a comparative survey. *J. Morphol.*, 245, 241–268.

Tarsitano S.F., Russell A.P., Horne F., Plummer C. & Millerchip K. (2000). On the evolution of feathers from an aerodynamic and constructional viewpoint. *Am. Zool.*, 40, 676–686.

Tarsitano S.F., Russell A.P., Rodriguez D., Sandoval D. & Stegall L. (2000). Aerodynamic evidence for the evolution of protofeathers and avian sister group relationships. *Q. J. Dinosaur Soc.*, 4, 24–25.

Watson S. & Russell A.P. (2000). A posthatching developmental staging table for the long-toed salamander, *Ambystoma macrodactylum krausei*. *Amphib.-Reptilia*, 21, 143–154.

Bauer A.M. & Russell A.P. (2001). The first record of reptiles in Alberta: Aemilius Simpson's journal of 1826. *Herpetol. Rev.*, 32, 174–176.

Bergmann P.J. & Russell A.P. (2001). Growth of the original tail in *Anolis grahami*: isometry of the whole is a product of regional differences. *J. Herpetol.*, 35, 232–238.

Bergmann P.J. & Russell A.P. (2001). Patterns of hindlimb segment growth in various lizards and their relation to lizard ecology. *Am. Zool.*, 41, 1390–1391.

Hill M.M.A., Powell G.L. & Russell A.P. (2001). Diet of the prairie rattlesnake, C*rotalus viridis viridis*, in southeastern Alberta. *Can. Field Nat.*, 115, 241–246.

Peng J., Russell A.P. & Brinkman D.B. (2001). Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Campanian) of southeastern Alberta, Canada: an illustrated guide. *Prov. Mus. Alberta Nat. Hist. Occas. Pap.*, 25, ii + 1–54.

Russell A.P. (2001). Amphibians and Reptiles of Madagascar and the Mascarene, Seychelles and Comoro Islands. F.W. Henkel and W. Schmidt (Review). *Q. Rev. Biol.*, 76, 507.

Russell A.P. (2001). Fidelity of convergence in saurian digital adhesive systems: gekkotans and anolines. *J. Morphol.*, 248, 278.

Russell A.P. (2001). Scaling the spandrels of San Marco: integrative functional morphology of the gekkotan adhesive system. *Am. Zool.*, 41, 1573–1574.

Russell A.P. & Bels V. (2001). Biomechanics and kinematics of locomotion in lizards: review, synthesis and prospectus. *Comp. Biochem. Physiol. A*, 131, 89–112.

Russell A.P. & Bels V. (2001). Digital hyperextension in *Anolis sagrei*. *Herpetologica*, 57, 58–65.

Russell A.P. & Bels V. (2001). Introduction to the Symposium—"Learning about the comparative biomechanics of locomotion and feeding". *Comp. Biochem. Physiol. A*, 131, 1–5.

Russell A.P., Bergmann P. & Barbadillo L.J. (2001). Maximal caudal autotomy in *Podarcis hispanica* (Lacertidae): the caudifemoralis muscle is not sundered. *Copeia*, 2001, 154–163.

Russell A.P. & Bryant H.N. (2001). Claw retraction and protraction in the Carnivora: the cheetah as an atypical felid. *J. Zool.*, 254, 67–76.

Russell A.P. & Dijkstra L.D. (2001). Patagial morphology of *Draco volans* (Reptilia: Agamidae) and the origin of glissant locomotion in flying dragons. *J. Zool.*, 253, 457–471.

Russell A.P., Dijkstra L.D. & Powell G.L. (2001). Structural characteristics of the patagium of *Ptychozoon kuhli* (Reptilia: Gekkonidae) in relation to parachuting locomotion. *J. Morphol.*, 247, 252–263.

Russell A.P., Pereschitz R.M. & Powell G.L. (2001). The cranial osteology of Richardson's ground squirrel (*Spermophilus richardsonii*). *Ann. Zool.*, 51, 117–131.

Ryan M.J., Currie P.J. & Russell A.P. (2001). New material of *Avimimus portentosus* (Theropoda) from the Iren Dabasu formation (Upper Cretaceous) of the Erenhot region of Inner Mongolia. *J. Vertebr. Paleontol.*, 21(3) Suppl., 95.

Ryan M.J. & Russell A.P. (2001). Dinosaurs of Alberta (exclusive of Aves). In: *Mesozoic Vertebrate Life: New Research Inspired by the Palaeontology of Philip J. Currie* (eds. Tanke DH & Carpenter K). NRC Research Press / Indiana University Press Bloomington, Indiana, 279–297.

Ryan M., Russell A.P., Currie P.J. & Eberth D.A. (2001). Taphonomy of a *Centrosaurus* (Dinosauria: Ornithischia) bone bed from the Dinosaur Park Formation (Campanian) of Alberta, Canada. *Palaios*, 16, 482–506.

Snively E. & Russell A.P. (2001). Distal unification hypothesis of tyrannosaurid arctometatarsus function. *J. Vertebr. Paleontol.*, 21(3), Suppl., 102.

Snively E. & Russell A.P. (2001). Integrated bone and ligament function of the metatarsus of tyrannosaurid dinosaurs. *J. Morphol.*, 248, 286.

Vickaryous M.K., Russell A.P. & Currie P.J. (2001). Cranial ornamentation of ankylosaurs (Ornithischia: Thyreophora): re-appraisal of developmental hypotheses. In *The Armored Dinosaurs* (ed. Carpenter K). Indiana University Press Bloomington, Indiana, 318–340.

Vickaryous M.K., Russell A.P., Currie P.J. & Zhao X.-J. (2001). A new ankylosaurid (Dinosauria: Ankylosauria) from the Late Cretaceous of China, with comments on ankylosaurian relationships and osteological terminology. *Can. J. Earth Sci.*, 38, 1767–1780.

Vickaryous M.K. & Russell A.P. (2001). New information on the skull of the ankylosaurian dinosaur *Euoplocephalus tutus* Lambe (1902) and a review of ankylosaurian cranial osteology. *J. Vertebr. Paleontol.*, 21(3), Suppl., 110.

Vikaryous M.K. & Russell A.P. (2001). The osseous secondary palate of ankylosaurs: variation in configuration of the nasal pathways. *J. Morphol.*, 248, 295.

Wu X.-C., Cheng Z. & Russell A.P. (2001). Cranial anatomy of a new crocodyliform (Archosauria: Crocodylomorpha) from the Lower Cretaceous of Song-Liao Plain, Northeastern China. *Can. J. Earth Sci.*, 38, 1653–1663.

Wu X.-C. & Russell A.P. (2001). Redescription of *Turfanosuchus dabanensis* (Archosauriformes) and new information on its phylogenetic relationships. *J. Vertebr. Paleontol.*, 21, 40–50.

Wu X-C., Russell A.P. & Brinkman D.B. (2001). A review of *Leidyosuchus canadensis* Lambe, 1907 (Archosauria: Crocodylia) and an assessment of cranial variation based upon new material. *Can. J. Earth Sci.*, 38, 1665–1687.

Wu X.-C., Russell A.P. & Cumbaa S.L. (2001). *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *J. Vertebr. Paleontol.*, 21, 492–514.

Bergmann P.J. & Russell A.P. (2002). Phylogenetic and ecological aspects of hindlimb segment growth patterns in various lizards. *Bull. Can. Soc. Zool.*, 33, 7.

Kundrát M., Seichert V., Russell A.P. & Smetana K. Jr. (2002). Pentadactyl pattern of the avian wing autopodium and pyramid reduction hypothesis. *J. Exp. Zool. (Mol. Dev. Evol.)*, 294, 152–159.

Powell G.L., Russell A.P. & Ryan M.J. (2002). Ontogenetic scaling of the cephalic armature of the horned lizard *Phrynosoma orbiculare* (Squamata: Phrynosomatidae). *J. Herpetol.*, 36, 578–589.

Russell A.P. & Bauer A.M. (2002). *Thecadactylus*. *Cat. Am. Amphib. Reptil.*, 735, 1–16.

Russell A.P. & Bauer A.M. (2002). Underwood's classification of the geckos: a 21st century appreciation. *Bull. Nat. Hist. Mus. Zool.*, 68, 113–121.

Snively E. & Russell A.P. (2002). The tyrannosaurid metatarsus: bone strain and inferred ligament function. *Senckenb. Lethaea*, 82, 35–42.

Vickaryous M.K. & Russell A.P. (2002). A redescription of the skull of *Euoplocephalus tutus* (Archosauria: Ornithischia): a foundation for comparative and systematic studies of ankylosaurian dinosaurs. *Zool. J. Linn. Soc.*, 137, 157–186.

Bauer A.M. & Russell A.P. (2003). *Phyllodactylus wirshingi*. *Cat. Am. Amphib. Reptil.*, 770, 1–4.

Bergmann P.J., Lessard S. & Russell A.P. (2003). Tail growth in *Chamaeleo dilepis* (Sauria: Chamaeleonidae): functional implications of segmental patterns. *J. Zool.*, 261, 417–425.

Bergmann P.J. & Russell A.P. (2003). Lamella and scansor numbers in *Thecadactylus rapicauda* (Gettonidae): patterns revealed through correlational analysis and implications for systematic and functional studies. *Amphib.-Reptilia*, 24, 379–385.

Druckenmiller P. & Russell A.P. (2003). A preliminary report on a diverse assemblage of Early Cretaceous plesiosaurs and ichthyosaurs from the Clearwater Formation, Northern Alberta, Canada. *J. Vertebr. Paleontol.*, 23(3) Suppl., 46A.

Jamniczky H.A., Brinkman D.B. & Russell A.P. (2003). Vertebrate microsite sampling: how much his enough? *J. Vertebr. Paleontol.*, 23, 725–734.

Jasinoski S., Russell A.P. & Currie P.J. (2003). The evolution of the theropod shoulder apparatus up to birds: an integrated approach. *J. Vertebr. Paleontol.*, 23(3) Suppl., 66A.

Russell A.P. (2003). Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integr. Comp. Biol.*, 42, 1154–1163.

Ryan M.J. & Russell A.P. (2003). New centrosaurine ceratopsids from the late Campanian of Alberta and Montana, and a review of contemporaneous and regional patterns of centrosaurine evolution. *J. Vertebr. Paleontol.*, 23(3) Suppl., 91A.

Snively E.S. & Russell A.P. (2003). Kinematic model of tyrranosaurid (Dinosauria: Theropoda) arctometatarsus function. *J. Morphol.*, 255, 215–227.

Weerawardhena S.R., Russell A.P. & Ratnayaka R.M.C.S. (2003). A molar tooth of the extinct hippopotamus *Hexaprotodon sivalensis* (Hippopotamidae) from upper Pleistocene deposits of the Central Province of Sri Lanka. *Ceylon J. Sci. (Biol. Sci.)*, 31, 69–73.

Bergmann P.J., Hobbs A.M., Kavalench M. & Russell A.P. (2004). Modulated but conserved segmental growth of the original tail in *Callisaurus draconoides* (Phrynosomatidae) and *Calotes versicolor* (Agamidae). *Herpetologica*, 60, 62–74.

Bergmann P.J. & Russell A.P. (2004). Patterns of variation in relation to tail morphology, vertebral number and tail length in lizards. *Integr. Comp. Biol.*, 44, 524.

Bergmann P.J. & Russell A.P. (2004). Use of principal component analysis in modelling growth of segmental structures. *J. Morphol.* 260, 278.

Brinkman D., Russell A.P., Eberth D.A. & Peng J. (2004). Vertebrate palaeocommunities of the Lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, 213, 295–313.

Delannoy S.M., Gutierrez A.M. & Russell A.P. (2004). Do mustelid carnivores have semi-retractile claws? A comparative morphometric assessment. *Bull. Can. Soc. Zool.*, 35, 69.

Delannoy, S.M., Gutierrez A.M. & Russell A.P. (2004). Do mustelid carnivores have semi-retractile claws? A comparative morphometric assessment. *J. Morphol.*, 260, 286.

Jamniczky H. & Russell A.P. (2004). A geometric morphometric assessment of the “batagurine process” of testudinoid turtles. *Amphib.-Reptilia*, 25, 369–379.

Jamniczky H.A. & A.P. Russell A.P. (2004). Cranial arterial foramen diameter in turtles: a quantitative assessment of size-independent phylogenetic signal. *Anim. Biol.*, 54, 417–436.

Jamniczky H.A. & Russell A.P. (2004). In the eye of the beholder: a geometric morphometric assessment of the batagurine process of testudinoid turtles. *J. Morphol.*, 260, 302.

Jamniczky H.A. & Russell A.P. (2004). You can’t believe your eyes: a geometric morphometric assessment of the batagurine process of testudinoid turtles. *Bull. Can. Soc. Zool.*, 35, 96.

Peattie A.M., Delannoy S.M., Russell A.P. & Full R.J. (2004). Deformation of isolated gecko setal arrays: bending or buckling? I. Kinematics. *Integr. Comp. Biol.*, 44, 619.

Russell A.P. (2004). Who goes there? Amphibians and reptiles in the vicinity of Edmonton. In: *Program of the 9th Annual Meeting of the Canadian Amphibian and Reptile Conservation Society*. Edmonton, 4–5.

Russell A.P., Bergmann P.J. & Melin A. (2004). Segmental and regional growth of the rat vertebral column. *Bull. Can. Soc. Zool.*, 35, 146.

Russell A.P., Bergmann P.J. & Melin A. (2004). Segmental and regional growth in the rat vertebral column. *J. Morphol.*, 260, 324.

Snively, E., A.P. Russell and G.L. Powell. (2004). Evolutionary morphology of the coelurosaurian arctometatarsus: descriptive, morphometric, and phylogenetic approaches. *Zool. J. Linn. Soc.*, 142, 525–553.

Brinkman D.B., Russell A.P. & Peng J.H. (2005). Vertebrate microfossil sites and their contribution to studies of paleoecology. In: *Dinosaur Provincial Park: a Spectacular Ancient Ecosystem Revealed* (eds. Currie PJ & Koppelhus, EB). University of Indiana Press Bloomington, Indiana, 88–98.

Jamniczky H.A., Brinkman D.B. & Russell A.P. (2005). Character analysis and the turtle carotid circulation. In: *Dinosaur Park Symposium* (eds. Braman D, Therrien F, Koppelhus EB & Taylor W). Royal Tyrrell Museum Drumheller, Alberta, pp. 49–51.

Johnson M.K., Russell A.P. & Bauer A.M. (2005). Locomotor morphometry of the *Pachydactylus* radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Can J. Zool.*, 83, 1511–1524.

Kronauer D.J.C., Bergmann P.J., Mercer J.M. & Russell A.P. (2005). A phylogeographically deep and distinct divergence in the widespread of the neotropical turnip-tailed gecko, *Thecadactylus rapicauda*. *Mol. Phylogenet. Evol.*, 34, 431–437.

Melin A.D., Bergmann P.J. & Russell A.P. (2005). Mammalian postnatal growth estimates: the influence of weaning on the choice of a comparative metric. *J. Mammal.*, 86, 1042–1049.

Russell A.P. (2005). Amphibians and Reptiles of Montana. J. Kirwin Werner et al. (Review). *Gt. Plains Res.*, 15, 342–344.

Russell A.P. & Bauer A.M. (2005). Variation in structure and its relationship to function: correlation, explanation and extrapolation. In: *Variation:*

a Central Concept in Biology (eds. Hallgrímsson B & Hall BK). Academic Press New York, 399–434.

Russell A.P., Bauer A.M. & Johnson M.K. (2005). Migration in amphibians and reptiles: an overview of patterns, and orientation mechanisms. In: *Migration of Organisms: Climate, Geography, Ecology* (ed. Elewa AMT). Springer-Verlag Heidelberg, Germany, 151–203.

Russell A.P., Bourne G.B., Barclay R.M.R. & Yeung E.C. (2005). Undergraduate zoologists in the grade 1–6 classroom: content specialists and curriculum enhancement. *Bull. Can. Soc. Zool.*, 36, 13–16.

Ryan M.J. & Russell A.P. (2005). A new centrosaurine ceratopsid from the Oldman Formation of Alberta and its implications for centrosaurine taxonomy and systematics. *Can. J. Earth Sci.*, 42, 1369–1387.

Thompson M.D. & Russell A.P. (2005). Glacial retreat and its influence on migration of mitochondrial genes in the long-toed salamander (*Ambystoma macrodactylum*) in Western North America. In: *Migration of Organisms: Climate, Geography, Ecology* (ed. Elewa AMT). Springer-Verlag Heidelberg, Germany, 205–246.

Bergmann P.J., Melin A.D. & Russell A.P. (2006). Differential segmental growth of the vertebral column of the rat (*Rattus norvegicus*). *Zoology*, 109, 54–65.

Delannoy S.M. & Russell A.P. (2006). Complexity of the gecko adhesive: setal stalk, tip and density dimensions across the subdigital pads of *Gekko gecko*. *Bull. Can. Soc. Zool.*, 37, 38.

Druckenmiller P.S. & Russell A.P. (2006). A new elasmosaurid plesiosaur (Reptilia: Sauropterygia) from the Lower Cretaceous Clearwater Formation, northeastern Alberta, Canada. *Paludicola,* 5, 184–199.

Jamniczky H.A., Brinkman D.B. & Russell A.P. (2006). Phylogenetic implications of turtle cranial circulation: a review. *Fossil Turtle Res.*, 1, 84–92.

Jasinoski S.C., Russell A.P. & Currie P.J. (2006). An integrated phylogenetic and extrapolatory approach to the reconstruction of dromaeosaur (Theropoda: Eumaniraptora) shoulder musculature. *Zool. J. Linn. Soc.*, 146, 301–344.

Johnson M.K. & Russell A.P. (2006). The relationship between locomotor surface structure and the subdigital adhesive system of geckos: insight from natural substrata. *Bull. Can. Soc. Zool.*, 37, 37–38.

Russell A.P. & Delannoy S.M. (2006). Subdigital fields of the tokay gecko—patterns of variation and evolutionary implications. *Bull. Can. Soc. Zool.*, 37, 36–37.

Ryan M. & Russell A.P. (2006). The status of the problematic taxon *Monoclonius* (Ornithischia: Ceratopsidae) and the recognition of adult-sized dinosaur taxa. *Abstr. Geol. Soc. Am., April 20–21, Akron, Ohio. North Central Sect.*, 78, 62.

Bels V., Baussart S., Delheusy V., Russell A.P., Jamniczky H.A. & Kardong K.V. (2007). The mechanism of drinking in lizards. *J. Morphol.*, 268, 1048.

Bergmann P.J. & Russell A.P. (2007). Systematics and biogeography of the widespread Neotropical gekkonid genus *Thecadactylus* (Squamata), with the description of a new cryptic species. *Zool. J. Linn. Soc.*, 149, 339–370.

Jamniczky H.A., Brinkman D.B. & Russell A.P. (2007). A repeatable and efficient sampling protocol for vertebrate microsites. In: *Vertebrate Microfossil Assemblages: their Role in Paleoecology and Paleobiogeography* (eds. Sankey JT & Baszio S). Indiana University Press Bloomington, Indiana, 9–16.

Jamniczky H.A. & Russell A.P. (2007). Reappraisal of patterns of nonmarine cryptodiran turtle carotid circulation: evidence from osteological correlates and soft tissues. *J. Morphol.,* 268, 571–587.

Jamniczky H.A., Russell A.P. & Fitch W.D. (2007). Asking why: inquiry-based learning in the comparative vertebrate anatomy laboratory. *J. Morphol.*, 268, 1089.

Johnson M.K. & Russell A.P. (2007). Variation on a theme: characteristics of setal fields and associated locomotor substratum in the gecko genus *Rhoptropus*. *J. Morphol.*, 268, 1090.

Knoll H.M. & Russell A.P. (2007). The avian furcula in its anatomical context: seeking explanation for patterns of reduction and loss of the wishbone. *J. Morphol.,* 268, 1094.

Powell G.L. & Russell A.P. (2007). Life history implications for conservation and monitoring of lizards in Canada. In: *Ecology, Conservation, and Status of Reptiles in Canada* (eds. Seburn CNL & Bishop CA).

Herpetological Conservation Number 2. Society for the Study of Amphibians and Reptiles Salt Lake City, Utah, 23–40.

Russell A.P. (2007). The way of a gecko on a rock: why the animal's real environment matters. *The Boreal Dip Net*, 11, 9–10.

Russell A.P. (2007). The zoology undergraduate curriculum—where to from here? *Bull. Can. Soc. Zool.*, 38, 12–17.

Russell A.P. & Johnson M.K. (2007). Natural substratum topography and its relation to the prolific adhesive capacity of geckos. In: *Proceedings of the 30th Annual Meeting of the Adhesion Society* (ed. Jagota, A). Adhesion Society, 61–63.

Russell A.P. & Johnson M.K. (2007). Real-world challenges to, and capabilities of, the gekkotan adhesive system: contrasting the rough and the smooth. *Can. J. Zool.,* 85, 1228–1238.

Russell A.P. & Johnson M.K. (2007). Scales across scales: the adhesive capacity of geckos in its environmental context. *J. Morphol.*, 268, 1126.

Russell A.P., Johnson M.K. & Delannoy S.M. (2007). Insights from studies of gecko-inspired adhesion and their impact on our understanding of the evolution of the gekkotan adhesive system. *J. Adhes. Sci. Technol.*, 21, 1119–1143.

Ryan M.J., Holmes R. & Russell A.P. (2007). A revision of the late Campanian controsaurine ceratopsid genus *Styracosaurus* from the western interior of North America. *J. Vertebr. Paleontol.*, 27, 944–962.

Snively E.S & Russell A.P. (2007). Craniocervical feeding dynamics of *Tyrannosaurus rex*. *Paleobiology*, 33, 610–638.

Snively E.S. & Russell A.P. (2007). Functional morphology of neck musculature in the Tyrannosauridae (Dinosauria, Theropoda) as determined via a hierarchical inferential approach. *Zool. J. Linn. Soc.*, 151, 759–808.

Snively E.S. & Russell A.P. (2007). Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. *Anat. Rec. Part A,* 290, 934–957.

Wise P.A.D. & Russell A.P. (2007). Skeletal development of the embryonic leopard gecko (*Eublepharis macularius*): a real-time study of the genesis of gross pattern and its correlation with developmental stages. *J. Morphol.*, 268, 1150.

Druckenmiller P.S. & Russell A.P. (2008). A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews 1922. *Zootaxa*, 1863, 1–120.

Druckenmiller P.S. & Russell A.P. (2008). Skeletal anatomy of an exceptionally complete specimen of a new genus of plesiosaur from Early Cretaceous (Early Albian) of northeastern Alberta, Canada. *Palaeontogr. Abt. A*, 283, 1–33.

Jamniczky H.A. & Russell A.P. (2008). Carotid circulatory development in turtles: using existing materials to seek critical developmental stages that localize establishment of clade-specific patterns. *Amphib.-Reptilia*, 29, 270–277.

Russell A.P. (2008). Reptiles and Amphibians of Canada. C. Fisher, A. Joynt and R. Brooks. 2007 (Review). *Can. Assoc. Herpetol. Bull.*, 15, 8–11.

Russell A.P. & Bauer A.M. (2008). The appendicular locomotor apparatus of, and locomotion in lizards and *Sphenodon*. In: *Biology of the Reptilia*, vol. 21 (eds. Gans C, Gaunt A & Adler KK), Society for the Study of Amphibians and Reptiles Ithaca, New York, 1–466.

Wise P.A.D. & Russell A.P. (2008). *Chamaeleo rudis*—reproduction. *Herpetol. Rev.*, 39, 87–88.

Brown C., Russell A.P. & Ryan M.J. (2009). Pattern and transition of surficial bone texture of the centrosaurine frill and their ontogenetic and taxonomic implications. *J. Vertebr. Paleontol.* 29, 132–141.

Druckenmiller P.S. & Russell A.P. (2009). Earliest North American occurrence of Polycotylidae (Sauropterygia: Plesiosauria) from the Lower Cretaceous (Albian) Clearwater Formation, Alberta, Canada. *J. Paleontol.*, 83, 981–989.

Druckenmiller P.S. & Russell A.P. (2009). The new plesiosauran genus *Nichollssaura* from Alberta, Canada: a replacement for the preoccupied genus *Nichollsia*. *J. Vertebr. Paleontol.*, 29, 276.

Jamniczky H.A., Russell A.P., Johnson M.K., Montuelle S. & Bels V. (2009). Morphology and histology of the tongue and oral chamber of *Eublepharis macularius* (Squamata: Gekkonidae), with special reference to the foretongue and its role in fluid uptake and transport. *Evol. Biol.*, 36, 397–406.

Johnson M.K. & Russell A.P. (2009). Configuration of the setal fields of *Rhoptropus* (Gekkota: Gekkonidae): functional, evolutionary, ecological and phylogenetic implications of observed pattern. *J. Anat.*, 214, 937–955.

Johnson M.K., A.P. Russell and S.M. Delannoy. (2009). Surface characteristics of locomotor substrata and their relationship to gekkonid adhesion: a case study of *Rhoptropus* cf. *biporosus*. In: *Functional Surfaces in Biology. Volume 2. Adhesion Related Phenomena* (ed. Gorb SN). Springer Dordrecht, 123–154.

Kundrát M., Janácek J. & Russell A.P. (2009). Developmental patterns of the crocodilian and avian columella auris: reappraisal of interpretations of the derivation of the dorsal hyoid arch in archosaurian tetrapods. *Zool. J. Linn. Soc.*, 156, 384–410.

Maddin H.C., Eckhardt L., Jaeger K., Russell A.P. & Ghannadan M. (2009). The anatomy and development of the claws of *Xenopus laevis* (Lissamphibia: Anura) reveal alternate pathways of structural evolution in the integument of tetrapods. *J. Anat.*, 214, 607–619.

Russell, A.P. (2009). Situating and teaching 21st century zoology: revealing pattern in the form and function of animals. *Integr. Zool.*, 4, 309–315.

Russell A.P. & Higham T.E. (2009). A new angle on clinging in geckos: incline, not substrate, triggers the deployment of the adhesive system. *Proc. R. Soc. B, Biol. Sci.*, 276, 3705–3709.

Webster N.D., Johnson M.K. & Russell A.P. (2009). Ontogenetic scaling of scansorial surface area and setal dimensions of *Chondrodactylus bibronii* (Gekkota: Gekkonidae): testing predictions derived from cross-species comparisons of gekkotans. *Acta Zool. (Stockholm)*, 90, 18–29.

Wise P.A.D., Vickaryous M.K. & Russell A.P. (2009). An embryonic staging table for *in ovo* development of *Eublepharis macularius*, the leopard gecko. *Anat. Rec. Part A*, 292, 1198–1212.

Higham T.E. & Russell A.P. (2010). Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko. *Biol. J. Linn. Soc.*, 101, 860–869.

Higham T.E. & Russell A.P. (2010). Flip, flop and fly: modulated motor control and highly variable movement patterns of autotomized gecko tails. *Biol. Lett.*, 6, 70–73.

Higham T.E. & Russell A.P. (2010). Gecko tails flip out: modulated motor control and variable movement following autotomy. *Integr. Comp. Biol.*, 50, E74.

Russell A.P. & Higham T.E. (2010). Modulation and modularity: behavioral insights into secondary reduction and loss of the gekkotan adhesive system. *Integr. Comp. Biol.*, 50, E154.

Wise P.A.D. & Russell A.P. (2010). Development of the dorsal circumorbital bones in the Leopard gecko (*Eublepharis macularius*) and its bearing on the homology of these elements in the Gekkota. *Anat. Rec. Part A*, 293, 2001–2006.

Brown C.M., Boyd C.A. & Russell A.P. (2011) A new basal ornithopod dinosaur (Frenchman Formation, Saskatchewan, Canada), and implications for late Maastrichtian ornithischian diversity in North America. *Zool. J. Linn. Soc.*, 163, 1157–1198.

Russell A.P., Maddin H.C. & Chrbet T. (2011). Restorative regeneration of digital tips in the African clawed frog (*Xenopus laevis* Daudin). *Anat. Rec. Part A*, 294, 253–262.

Brown C.M. & Russell A.P. (2012). Homology and architecture of the caudal basket of Pachycephalosauria (Dinosauria: Ornithischia): The first occurrence of myorhabdoi in Tetrapoda. *PLoS ONE*, 7, e30212.

Gamble T., Greenbaum E., Jackman T.R., Russell A.P. & Bauer A.M. (2012). Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, 7, e39429.

Higham T.E. & Russell A.P. (2012). Dancing with the tails: comparative dynamics of caudal autotomy in geckos. *Integr. Comp. Biol.*, 52, E78.

Higham T.E. & Russell A.P. (2012). Time-varying motor control of autotomized Leopard gecko tails: multiple inputs and behavioral modulation. *J. Exp. Biol.*, 215, 435–441.

Jonasson K.A., Russell A.P. & Vickaryous M.K. (2012) Histology and histochemistry of the gekkotan notochord and their bearing on the development of notochordal cartilage. *J. Morphol.*, 273, 596–603.

Longrich N.R., Vinther J., Meng Q.J., Li Q.G. & Russell A.P. (2012). Primitive wing feather arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Curr. Biol.*, 22, 2262–2267.

Maddin H.C., Russell A.P. & Anderson J.S. (2012). Phylogenetic implications of the morphology of the braincase of caecilian amphibians (Gymnophiona). *Integr. Comp. Biol.*, 52, E111.

Maddin H.C., Russell A.P. & Anderson J.S. (2012). Phylogenetic implications of the morphology of the braincase of caecilian amphibians (Gymnophiona). *Zool. J. Linn. Soc.*, 166, 160–201.

Weerawardhena S.R. & Russell A.P. (2012). Historical land-use patterns in relation to conservation strategies for the Riverstone area, the Knuckles massif, Sri Lanka: insights gained from the recovery of anuran communities. *Taprobanica,* 4, 92–102.

Weerawardhena S.R. & Russell A.P. (2012). Cover-dependency of anurans in the Riverstone, Knuckles mountain forest range, Sri Lanka. *Taprobanica,* 4, 12–19.

Brown C.M., Evans D.C., Ryan M.J. & Russell A.P. (2013). New data on the diversity and abundance of small-bodied ornithopods (Dinosauria, Ornithischia) from the Belly River Group (Campanian) of Alberta. *J. Vertebr. Paleontol.*, 33, 495–520.

Cuthbertson R.S., Russell A.P. & Anderson J.S. (2013). Cranial morphology and relationships of a new Grippidian (Ichthyopterygia) from the Vega-Phroso Siltstone Member (Lower Triassic) of British Columbia, Canada. *J. Vertebr. Paleontol.*, 33, 831–847.

Cuthbertson R.S., Russell A.P. & Anderson J.S. (2013). Reinterpretation of the cranial morphology of *Utatsusaurus hataii* (Ichthyopterygia) (Osawa Formation, Lower Triassic, Miyagi, Japan) and its systematic implications. *J. Vertebr. Paleontol.*, 33, 817–830.

Higham T.E., Lipsett K.R., Syme D.A. &. Russell A.P. (2013). Controlled chaos: three-dimensional kinematics, fiber histochemistry, and muscle contractile dynamics of autotomized lizard tails. *Physiol. Biochem. Zool.*, 86, 611–630.

Higham T.E., Russell A.P. & Zani P.A. (2013). Integrative biology of tail autotomy in lizards. *Physiol. Biochem. Zool.*, 86, 603–610.

Lynn S.E., Borkovic B.P. & Russell A.P. (2013). Relative apportioning of resources to the body and regenerating tail in juvenile Leopard geckos (*Eublepharis macularius*) maintained on different dietary rations. *Physiol. Biochem. Zool.*, 86, 659–668.

Moore A.L., Budny J.E., Russell A.P. & Butcher M.T. (2013). Architectural specialization of the intrinsic thoracic limb musculature of the American badger (*Taxidea taxus*). *J. Morphol.*, 274, 35–48.

Weerawardhena S.R. & Russell A.P. (2013). Forest secondary succession and anuran amphibian recolonization of abandoned tea plantations in Sri Lanka. *Hamdryard,* 36, 108–129.