FIELDIANA

Life and Earth Sciences

NO. 5

Studies in Vertebrate Paleobiology—Essays in Honor of John R. Bolt

Editors,
R. Eric Lombard
Jason Anderson
Marcello Ruta
Stuart S. Sumida

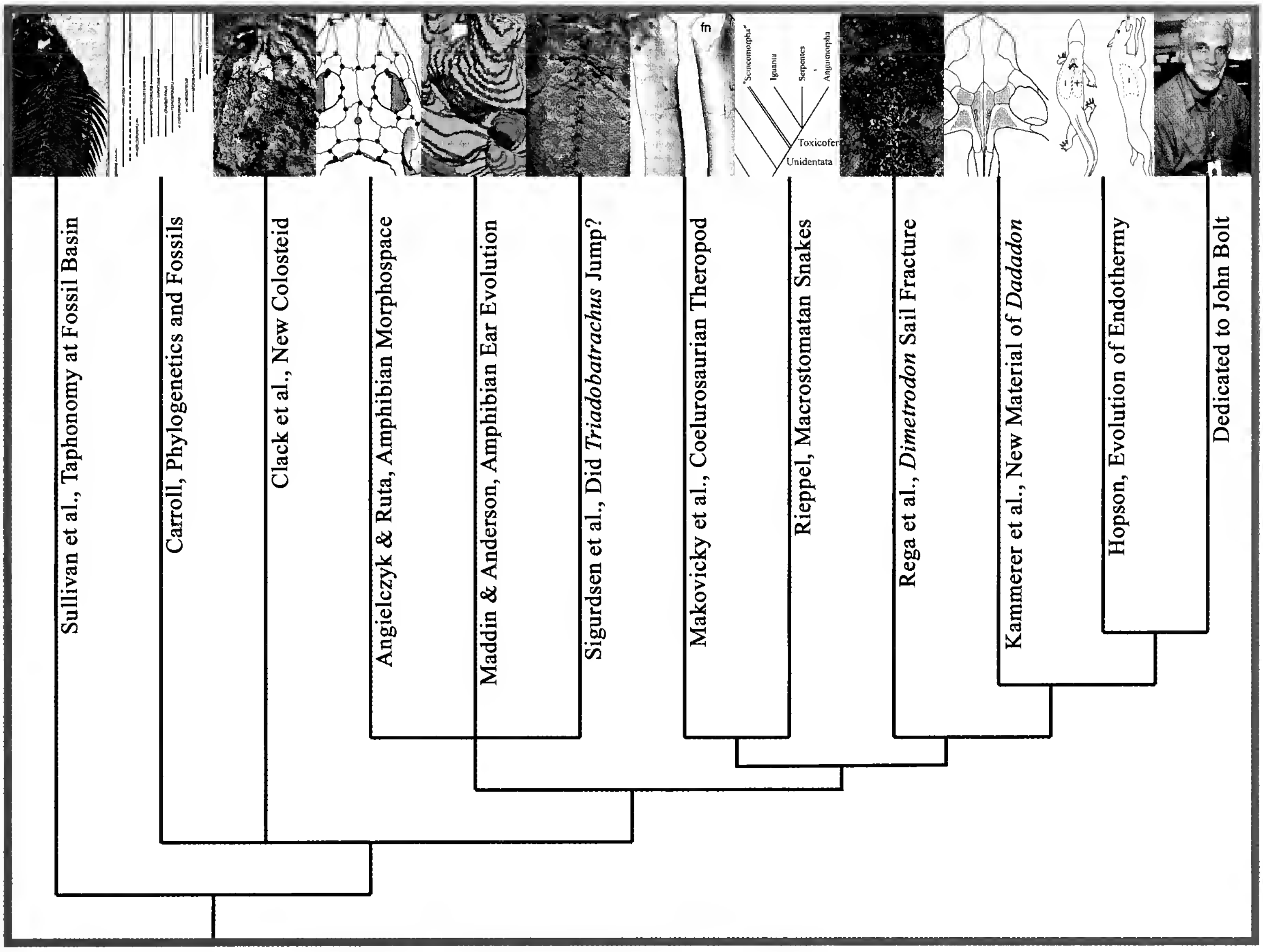

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Table of Contents

List of Figures

Dedication

Chapter 1.

Chapter 2.

Chapter 3.

CHAPTER 4.

CHAPTER 5.

CHAPTER 6.

CHAPTER 7.

CHAPTER 8

CHAPTER 9.

CHAPTER 10.

CHAPTER 11.

List of Tables

CHAPTER 1.

CHAPTER 4.

CHAPTER 5.

CHAPTER 6.

CHAPTER 9.

CHAPTER 11.

Dedication

This special issue celebrates the scientific and collegial activities of John Ryan Bolt, who retired at the end of December 2008 as a Curator of Fossil Amphibians and Reptiles in the Department of Geology at the Field Museum of Natural History. Over John's professional life, he has influenced, taught, and assisted colleagues and students, contributed to our understanding of the early evolution and diversification of tetrapods, and brought positive leadership to vertebrate paleontology and the Field Museum. His efforts have benefitted a great number of people, including this volume's editors. With abundant pleasure we have assembled a collection of eleven papers written with esteem and affection by some of John's colleagues, collaborators, and friends. John is a modest and private person. We hope that in highlighting his professional life and presenting him with this work, we make him only slightly uncomfortable and, that "*upon mature consideration*" in quiet moments he will sense the deserved high regard in which he is held by all of us.[1]

Young Scholar

> *In the course of a study of the structure of the teeth of amphibians we have become convinced that the three modern orders of Amphibia form a natural unit.* (Parsons & Williams, 1963)
>
> Doleserpeton *occurs in Lower Permian fissure fill deposits in southwestern Oklahoma. It is unique among nonlissamphibian tetrapods in that it possesses pedicellate, bicuspid teeth ….* (Bolt, 1969)

John was both born and grew up in Grand Rapids, Michigan, to which all his grandparents had immigrated from the Netherlands. In retrospect, he claims the public library to be that city's best feature. After high school, John became a geology major at Michigan State University, from which he received his BS in 1962. Two encounters occurred there that were significant events for John. As a freshman, he was placed in "Communications Skills," a magnet for students with advanced abilities in English. In that class he met Merry Joan Gowdy, who would in time become his wife and subsequently be known to us as Joanie. Later, John had the formative experience of extended field work in southwest Kansas with Claude W. Hibbard, a professor at the neighboring University of Michigan. Hibbard is notable in the history of vertebrate paleontology for introducing the technique of mass screen-washing, which especially revolutionized the collection of Mesozoic mammal teeth (Semken & Zakrzewski, 1975). John conveys a measure of fondness for this introduction to the rigors and excitement of discovery in the field, but it is also notable that he did not choose to screen for mammal teeth as his life's work.

John left Michigan State for the graduate program in Paleozoology at the University of Chicago, where he would complete his PhD in 1968. That interdisciplinary curriculum (now the Committee on Evolutionary Biology) then housed its students in the empty exhibit space of Walker Museum, the collections of which had been transferred to the Field Museum. In that haven of mischief and occasional science, John joined the flow of students attracted to the work of Everett C. Olson, one of the most productive and influential vertebrate paleontologists of the twentieth century (Bell, 1998). Two of Olson's students in particular were important for John. James A. Hopson (see Chapter 11) was in his last term and departing for Yale, and Robert DeMar maintained an office in Walker Museum for some time after he joined the faculty of what would become the University of Illinois at Chicago. Hopson would later return to the faculty at the University of Chicago and become an important friend and colleague. DeMar and John would establish a very fruitful collaboration focused primarily on tooth replacement patterns in Paleozoic tetrapods (Bolt & DeMar, 1975, 1978, 1983, 1986; DeMar & Bolt, 1981) but also including the surprising discovery of growth rings in the teeth of dinosaurs (Bolt & DeMar, 1980).

> *Returning from Yale to Chicago in 1967, my wife Sue and I developed a close friendship with John and Joanie that has lasted nearly 50 years. John's office at the Field Museum became something of a sanctuary for me, where he and I would discuss (never argue) politics over a cup of coffee. Although we never published together, we shared a common interest in tooth replacement phenomena and vertebrate ear function. I have always admired John for his insights into early tetrapod structure and evolution and, on more informal occasions, his insights into American politics. On both of these topics he always expresses himself in language noted for its directness, clarity, originality, and wit.* —James Hopson

As a student of Olson's, John was introduced to the collections of the Field Museum (Fig. 1), among which he would spend nearly all his professional life, and to the Permian of Texas and, especially, Oklahoma, which would provide both a beginning and continuing source for John's research interests. This was, and is, red rock, red dirt, and red pond country eroding into the Red River; all on a band of Lower Permian sedimentary rocks about 150 miles wide running north–south across present day Kansas and Oklahoma, and into Texas.

Olson and Alfred S. Romer, who had been Olson's thesis advisor, divided their north Texas Permian prospecting; Romer worked the older and much more fossiliferous Wichita Group beds and Olson took the younger Clear Fork Group beds. Olson, working up section found himself in Oklahoma

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[1] From a delightful passage to be found on page 294 in Huxley (1862) in which *Pholidogaster pisciformis* is described as a tetrapod and which is also the publication that we now recognize constitutes the earliest description of a stem tetrapod. John has always taken delight in it and we recommended the full text to you.

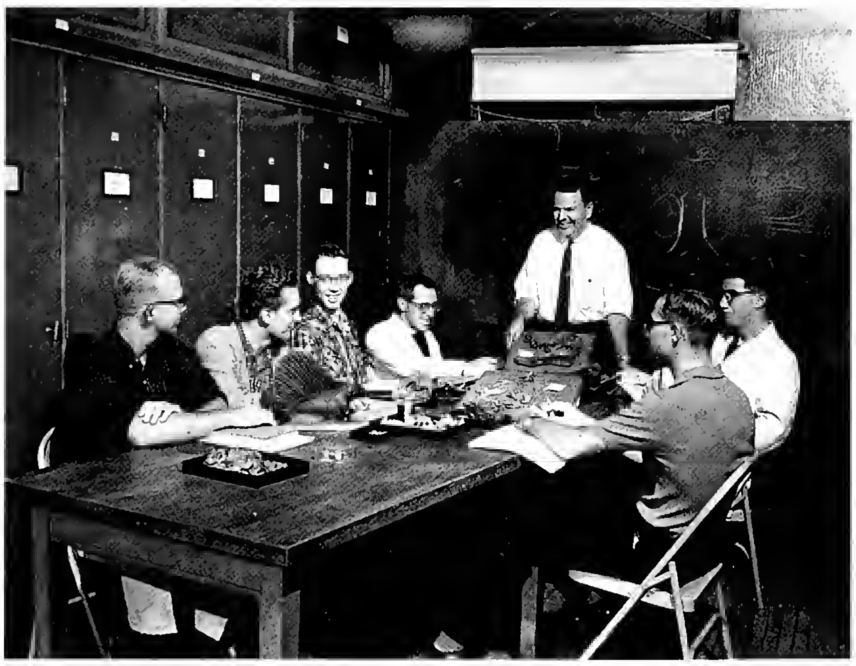

FIG. 1. John Bolt in his first term as a graduate student in Everett C. Olson's vertebrate paleontology class at the Field Museum of Natural History, November 1963. John, from the safety of *Dimetrodon's* sail, has just answered a question posed by Olson in a way that brings delight to everyone. Left to right: Keith "Joe" Carson, John Ryan Bolt, Wentworth "Pete" Chapham, Father Yvon Pageau, Everett Claire Olson, Robert Maclellan West, and Ted Cavender. © The Field Museum, GEO82834, photographer unknown.

and was able to make successful collections over a nearly continuous sequence of summer fieldwork expeditions. In this progression, John was exposed to the hard scratching and meager Oklahoma prizes at Pond Creek, Roman Nose, Waurika, and Grandview, among other dusty red places. Notable among the Permian localities that provided John with important fossil material was one near Fort Sill, Oklahoma. Camp Wichita, the "Soldier House at Medicine Bluffs," Indian Territory, was staked out on 8 January 1869, by Major General Philip H. Sheridan, who was sent, as was the custom then, to suppress raids into Kansas and Texas by Native Americans. In time, Camp Wichita became Fort Sill, and the surrounding part of Indian Territory became Oklahoma. Just north of Fort Sill, and originally in service to railroad-building, lies the Dolese Brothers limestone quarry at Richards Spur (a railroad track, not a boot attachment). The Dolese quarry, "Older Than Oklahoma" (Dolese, 2012), supplies Ordovician limestone in which fissures are filled with soft Lower Permian sediment. These fissure-fill sediments, discarded in "mud piles," have over time proven a bountiful source of exquisitely preserved terrestrial vertebrate fossils: well over two dozen taxa have been described (Fröbisch & Reisz, 2008).

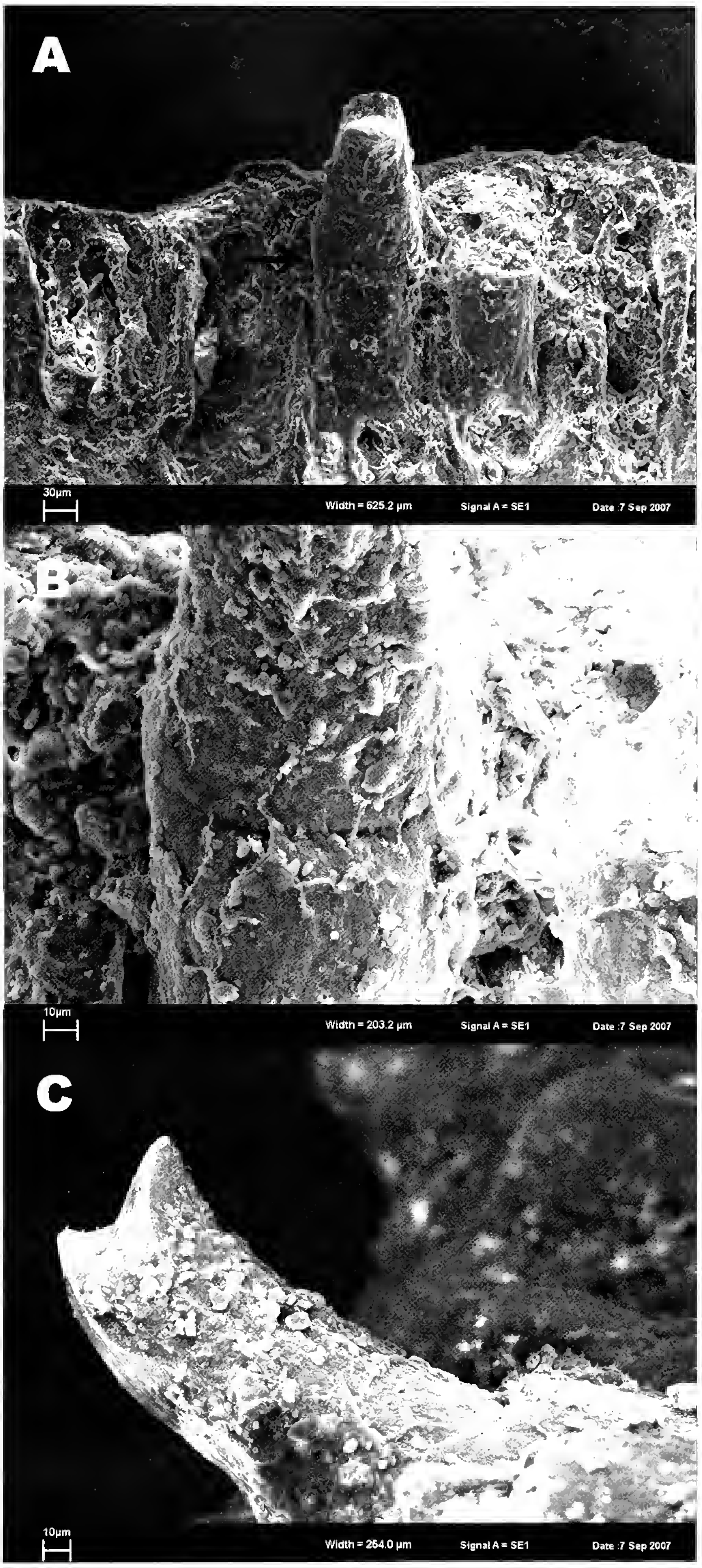

FIG. 2. Bicuspid, pedicellate teeth of *Doleserpeton annectens*. (**A**) Partial lower jaw in lingual view. One tooth preserves an attached crown; to its right the tooth preserves only the pedicel. The **arrow** indicates the joint between the crown and pedicel. Scale bar is 30 µm. © The Field Museum, GEO86661d_06, photographer John Bolt. (**B**) Close-up of a tooth shaft showing the indentation between the pedicel and crown (**arrow**). Scale bar is 10 µm. © The Field Museum, GEO86661d_08, photographer John Bolt. (**C**) The bicuspid crown. Scale bar is 10 µm. © The Field Museum, GEO86661d_11, photographer John Bolt.

John's thesis topic arrived by chance in a shipment of Dolese quarry specimens sent to Olson for identification. The taxa from this locality are usually small organisms—disarticulated, very often preserved in three dimensions, an attractive blue-black, and encased in buff-colored sediment. Preparation requires patient work under a microscope. All this was true for the specimens entrusted to John and out of which came the new taxon *Doleserpeton annectens,* the substance of his PhD thesis (Bolt, 1968). New taxa are the ordinary stuff of thesis work, but new taxa with an important role to play in larger stories are rare. *Doleserpeton* proved to be such a special creature: John discovered that the (tiny) teeth of *Doleserpeton* were both bicuspid and pedicellate (Fig. 2). This was, and remains, highly significant because bicuspid pedicellate teeth are the one unique skeletal feature that may be used to link living amphibians together as a natural group, the Lissamphibia (Parsons & Williams, 1963). Until *Doleserpeton*, no fossil taxon had been discovered with this type of tooth. Exactly 100 years after Sheridan got off his horse at Fort Sill, the structure and significance of *Doleserpeton*'s teeth were announced in *Science* (Bolt, 1969).

With this remarkable start, John joined the faculty of the University of Illinois Medical Center as an Assistant Professor of Anatomy in 1968. John and Joanie, having married in 1964, settled into the Hyde Park neighborhood of Chicago, where they continue to reside. Joanie became a Research Associate in the Department of Medicine at the University of Chicago, retiring after nearly forty years of research in the biochemistry of nutrition. John's residence in Anatomy at the University of Illinois ended in 1972 when he accepted the position of Assistant Curator of Fossil Reptiles and Amphibians at the Field Museum of Natural History, the institution from which he would retire. During his time at the Museum John retained his relationship to the University of Illinois as an Assistant Professor, then Associate Professor of Geological Sciences, and to the University of Chicago as a Lecturer in the Committee on Evolutionary Biology.

Early Research at the Field Museum

Lower Permian Tetrapods

Settled into the Field Museum, John continued work on Paleozoic amphibian-grade tetrapods (Bolt, 1974a–d, 1977a,b, 1979, 1980; Bolt & Wassersug, 1975). The 1977a and 1979 papers described the dissorophoids *Tersomius*, *Amphibamus*, and *Broiliellus* as having, at least in some specimens, bicuspid teeth, with *Amphibamus* perhaps having pedicellate teeth as well. This work provides waypoints in John's continuing interest in both the creatures bearing these teeth and their meaning in the puzzle of the origin of modern amphibians, a topic receiving additional expression in these papers, but particularly in Bolt, 1977a. During this time the extensive work on tooth replacement and structure with Bob DeMar, cited above, was also published with additional work on teeth in collaboration with Armand de Ricqlès (de Ricqlès & Bolt, 1983). These publications provided solid description, context, and interpretation for fossil structures, with their results requiring active consideration by any student of early tetrapod evolution and receiving broad citation continuing to this day. Written at the time when cladistic methodology for phylogenetic reconstruction was coming into use, and under active resistance by some, John was the first student of lower tetrapods to present morphological features in these early papers in a way consistent with this approach.

The Origin and Evolution of Tympanic Ears

R. Eric Lombard from the (then) Department of Anatomy at the University of Chicago first met John in proximity to inexpensive wine at a graduate student reception in 1976. It was at this event that they expressed mutual interest in the evolution of tetrapod hearing, establishing a lasting collaboration that extends to the present. This collaboration came to encompass not only the evolution of hearing, but of early tetrapods as well. Lombard, at that time working on the functional morphology of the ear in frogs, knew only that fossils were known to exist; John, for his part, knew only that ears must certainly function.

It was a good arrangement. Over the next fifteen years they published a series of papers that both detailed the structure of the skeletal elements of the middle ear in early tetrapods and also provided what was a radical hypothesis of otic evolution (Lombard & Bolt, 1979, 1988; Bolt & Lombard, 1985, 1992). Before their work, the tympanic ears of all tetrapods were considered to have descended from that evolved in a common ancestor. Their insight provided the framework for what has come to be the accepted alternative: that tympanic ears have evolved several times independently in tetrapods and that tympanic ears are a labile feature (for example: Christensen-Dalsgaard & Carr, 2008).

> *John and I flipped a coin to determine first author on the 1979 paper and we have alternated since, no matter what the topic.* —Eric Lombard

A Colleague

Chair 1981–1990

John's impressive body of early work and his ongoing research established him as a notable young authority both on amphibian-grade tetrapods and wider considerations of vertebrate evolution. In recognition of his accomplishments and promise, the Field Museum promoted him to Associate Curator in 1977. No good work goes unpunished though. John's reward for his promotion and scientific productivity was to be made Chair of the Department of Geology at the museum. Beyond his science, John's evenhanded and considerate manner to those around him was most surely an important determinant in his selection for this post. In retrospect, all agree that his tenure as chair was remarkably productive. Because of his care for his institution and science he was willing to take time from his own research and devote it to building the capabilities of the Field Museum, its curators, and its staff. Under John's thoughtful leadership the department metamorphosed into a research environment equaling those in the best universities.

Thirteen laboratories were renovated, including two for fossil preparation that stand out for their safety, technical equipment, and comfort. It is important to note that this could only happen in the wake of collaborative, time-consuming grant writing. The support staff was enlarged to include the illustrators and artists Lori Grove, Clara Richardson, and Marlene Donnelly, all of whose work graces the publications of the department still. William Simpson joined the department as chief preparator to later become the collections manager for vertebrate paleontology.

> … *John also greatly improved the professional staff - especially by picking Bill Simpson to lead the vertebrate prep lab. That was truly an inspired choice.* —Peter Crane

Peter Crane, John Flynn, Lance Grande, Scott Lidgard, and Olivier Rieppel were all hired as curators while John was chair (Fig. 3). This remarkable group, with John Flynn now at the American Museum of Natural History and Peter Crane at Yale University, continues to be very productive and

FIG. 3. Field Museum paleontology curators with friend, 1994. From left to right: Lance Grande, John Flynn, Olivier Rieppel, Peter Crane, John Bolt, Scott Lidgard, Matthew Nitecki. Not pictured, William Turnbull. © The Field Museum, GEO85887_3c, photographer John Weinstein.

influential, attesting to the thoughtful hiring process put in place by John.

> *I eventually took over from John as Chair at some point, but by then all of the heavy lifting had been done. As a result, the Department of Geology was just light years ahead of where it had been when he took over. John understood that making good appointments was the most important thing he could do for the future of the department and the Museum. They were the core of the renewal that John engineered and as a result, the publications, grants, and profile of the department continued to increase under John's leadership. Whatever success the department enjoyed during the 1980s, 1990s and on up to the present day, can all be traced back to John and the key decisions that he made ....* —Peter Crane

> *When I arrived at the FMNH, the Geology Department had begun to transform through his combination of vision and sensible spending—under John's nine years of leadership and fiscal responsibility, an array of new curators were hired to build on existing strengths and expand scope of research, support staff began to grow and professionalize further, and the Geology collections and labs underwent remarkable revamping. His legacy on this front will continue to be felt for many decades to come.* —John Flynn

> *[John]...really upped the metabolic rate and scientific profile of the department on a national and international level. And the higher scientific profile and relative productivity of the department ultimately led to increases in support staff (preparators and collection managers). You could say that John's early ambitions went beyond focusing on his personal career; through his leadership they centered on rebuilding the entire paleontological program of one of the world's foremost natural history museums. And he succeeded beyond anyone's dreams. It is a type of contribution to science that is at the same time both amazingly impactful and underappreciated.* —Lance Grande

> *Most will remember his chairmanship and the guidance he provided through this appointment in building the Geology Department at the Museum, but few might know that because of his personal integrity, John has regularly been called upon to serve as committee member or chair of committees that needed to be convened when delicate matters confronted the curatorial staff ....* —Olivier Rieppel

As an expression of his involvement in the important institutions of science, John's collegial leadership extended beyond the Geology Department to include journals and societies, before, during, and after his time as chair. Between 1979 and 2008 John served in an editorial capacity for varying lengths of time for the *Journal of Vertebrate Paleontology*, *Paleobiology*, and *Fieldiana*. Perhaps his most challenging contribution during this period was to assume the position of first independent treasurer of the Society of Vertebrate Paleontology in 1993—at a time when the Society was greatly enlarging in size and faced with very challenging financial circumstances.

> *In his role as SVP Treasurer, I watched John say "NO" so many times, and to so many people (but always with a sincere smile), that one might have felt that his responses were robotically thoughtless and that he had no interest in doing* anything. *But precisely the opposite was true—John listens like few others I have ever met; he thinks more deeply about the consequences of actions taken; and he cares more passionately about the most effective use of available resources.* —John Flynn

In recognition of his long and valuable service as treasurer of the Society, John was awarded the Joseph T. Gregory Award for service to the Society of Vertebrate Paleontology in 2006.

John was promoted to curator in 1989 and with gratitude and esteem allowed to "*slump back into the curatorial staff*" to paraphrase Alfred Romer with apologies.

Later Research at the Field Museum

After retiring as chair, John returned his energies to research. From an integrated whole one can tease out four foci that characterize this era, three of which continue to receive his attention and intellect: The PRESERVE project; structure of the citizens of the later Paleozoic; the origin of the Lissamphibia; and a new gift, the treasures of the Delta Locality. All of this research involved, and continues to involve, fruitful collaborative relationships with many students of the Paleozoic, a measure of John's influence on his field.

PRESERVE Project

Some things, no matter how promising, just do not work out; no active career of any length is without a dead-project file. Usually, one just lets these indurate under the weight of time and accumulated overburden, but one to which John devoted time and creative energy deserves some excavation and preparation for public view. The PRESERVE project—in theory very useful, in timing at the rising wave of the internet information age, in practice executable—died in demonstration form for lack of funding to ascend to the next level. The project was to provide a collegial web site where the core resource was a relational database of standardized characters, taxa, localities, and other things with various tools to assemble data sets for phylogenetic use. Tools for the analysis of metadata were envisioned. PRESERVE was conceived as a journal in which an editorial board would review collegial submissions of new or revised data sets to accession to the public data. Individuals would be able to form work groups and work on as many projects as they wished. They would be able to create their own project workspace and add to, and edit, any data in their own extracted set (but not the underlying public data). A demonstration data set and preliminary interface were constructed (Lombard et al., 1995; Bolt et al., 1995) and presentations were made at meetings (Clack et al., 1995a,b), the former including a somewhat anxiety-producing but successful live Internet connection. However, by the time papers introducing and using the data format were published (Lombard & Bolt, 1999; Bolt & Chatterjee, 2000) funding was expended and further professionally acceptable means were unsuccessful. Yet, a tool like PRESERVE would be useful, though the catch-up with the volume of now-published data would be a challenge.

Citizens of the Later Paleozoic and Origin of the Lissamphibia

In reflective moments, John will share that "…amphibians are fascinating in part because they are so mysterious." This challenge appears to be a strong motivation at the center of his interest. He has proven, though, not to be immune to the occasional excursion out of the Paleozoic, or away from amphibian-grade tetrapods. Like anyone with a curiosity about the evolution of life, we have all seen John exhibit stimulation and excitement in the diversity that it presents. And, after all, who would not want to know about the antecedents of Paleozoic amphibian-grade tetrapods as well as those that evolved out of them? The Mississippian locality of Goreville, Illinois, excavated by Hans-Peter Schultze and his students from the University of Kansas, produced numerous specimens of *Tranodis*, a lungfish, and John collaborated in a description of this material (Schultze & Bolt, 1996). This downstream phylogenetic excursion was, after all, devoted to a member of a possible sister taxon to the tetrapods—a hypothesis still resistant to certainty (for example, Takezaki et al., 2004)—as well as the faunal diversity of Upper Mississippian localities in North America. In upstream excursions out of the Paleozoic, Bolt and Chatterjee (2000) described a new Late Triassic temnospondyl amphibian, *Rileymillerus cosgriffi*, and in Ruta and Bolt (2008) re-considered the Middle Triassic temnospondyl *Hadrokkosaurus bradyi*. And, phylogenetically upstream and out of the water entirely, a new and better-preserved specimen collected by John in Oklahoma permitted a more detailed and useful description of the Permian early amniote synapsid *Varanosaurus*, allowing a more certain phylogenetic placement than previously possible (Berman et al., 1995).

The Goreville locality, perched on the wall of a disused limestone quarry, has also produced additional taxa more central to John's interests. These include, importantly, new specimens of the colosteid stem tetrapod *Greererpeton*. Preserved in concretions, the Goreville specimens are unusually three-dimensional (but challenging to prepare). This dimensionality reveals that *Greererpeton* possessed a much more rounded skull than previously reconstructed from the somewhat collapsed material from the type locality in West Virginia (Schultze & Bolt, 1996; Bolt & Lombard, 2000), permitted a detailed description of the jaw with a broader consideration of early tetrapod jaw evolution (Bolt & Lombard, 2001), and was a factor in a revised consideration of the colosteid skull in general (Bolt & Lombard, 2010).

The amphibian-grade tetrapods of Oklahoma were not neglected during this time and work on them continues. A study of the Permian temnospondyl *Perryella olsoni* provided stimulus for a cladistic analysis of the diverse Carboniferous and Permian temnospondyl radiation, a core interest of John's (Ruta & Bolt, 2007). Importantly, that work retrieved a single origin for temnospondyls. As this is written, Jason Anderson and John have submitted a further study of the amphibamid amphibians (which includes *Doleserpeton*) from the Dolese quarry (Anderson & Bolt, personal communication).

Microsaurs are amphibian-grade tetrapods perhaps, or not. Perhaps they are amniotes. Perhaps they are related to the origin of one or more of the modern amphibian lineages. Perhaps not. For certain they are a mystery. The "Goreville microsaur," with several specimens in a single fist-sized concretion, is at present the oldest known member of that clade (Lombard & Bolt, 1999). No autapomorphies are apparent as prepared and with current techniques the dorsum of the skull cannot be exposed without destruction, an inconsiderate circumstance. Thus there are no visible synapomorphies that would suggest a relationship with established microsaur clades (see Carroll, Chapter 2, this volume). It remains a creature waiting for a new preparation technique or additional specimens. The microsaur *Llistrofus* is found only in the fissure-fill sediments of the Dolese quarry. John and Museum colleague Olivier Rieppel recently described freshly re-prepared material of the holotype that permitted observation of the palate and lateral views of the skull for the first time (Bolt & Rieppel, 2009). Their work suggests a more certain hypothesis of relationship but indicated that the function of the lateral emargination of the skull characteristic of *Llistrofus* and some other microsaurs must remain mysterious. Microsaurs cannot be brought to a conclusion without noting *Bolterpeton carrolli* from the Dolese quarry. *Bolterpeton* was named in recognition of John's work on the Dolese taxa and Robert Carroll's (Chapter 2) on lepospondyls in general (Anderson & Reisz, 2003).

Finally, throughout this time, John has been involved in the important problem of the origin(s) of the modern amphibians, frogs, salamanders, and caecilians. As we have seen, the problem was a central element of his start in science and over the intervening years has generated a literature marked by differences in opinion and in which John has been a participant. Are the Lissamphibia a natural group sharing features in common with an identifiable common ancestral taxon? Or have they evolved separately or in some combination out of taxa which themselves are only very distantly related, that is, with a common ancestor deep in the amphibian-grade tetrapods that does not share any recognizable fossilized features with living amphibians? In Bolt (1991), Carroll et al. (2004), and Sigurdsen and Bolt (2009, 2010), as well as in passing in several of the other works already mentioned, John has offered measured argument and a steady reminder that

> *The Lower Permian amphibamid* Doleserpeton annectens *(Temnospondyli) is of great importance to our understanding of the origin of modern amphibians.... The pedicellate bicuspid dentition of* Doleserpeton *is more similar to that of modern amphibians than any other Palaeozoic form ...* Sigurdsen and Bolt (2010).

Nearly all of the research highlighted above was carried out in collegial interaction. All those who have worked closely with John around the structure and evolution of amphibians have had a common experience.

> *John's attention to anatomical detail and the complexities of comparative morphology are well known even to those who have had a casual chance to sit briefly next to him and watch him stare long and intently at fossil specimens down a microscope. The reward from such an experience is immense: as John would look up from the specimen and think hard, ideas would be communicated succinctly and effectively, the range of possibilities would be examined carefully and critically, questions would be asked, countless specimens would be scrutinized for comparisons, reprints would be browsed through, sketches would appear on scrap paper, and notes would be jotted down.* —Marcello Ruta

Delta Locality

In the early eighties, at yet another graduate student reception at which one essayed a sip of the white hoping for better, John informed Eric Lombard of a possible new fossil locality in southeast Iowa. Only days before he had been shown what clearly appeared to be tetrapod fossil fragments from this site.

> *After conveying the basic information known about the locality at that time, John added: "I've always wanted a Mississippian locality." There was no exclamation point; it was said as matter-of-fact, but with clear inner delight. It was a charged moment that I will always remember.* —Eric Lombard

Within days, the Delta site, named after a nearby hamlet, was examined on a drizzly November day and pronounced worthy of a BIG effort. Over the next couple of years, excavation produced hundreds of specimens not only of tetrapods, but also of assorted aquatic vertebrates and invertebrates (Fig. 4). This remarkable find was introduced to the world in *Nature* by John and a team from the University of Iowa (Bolt et al., 1988), and reviewed in Bolt (1990). The specimens from Delta range from lovely to dubious, with the center of distribution more towards the former. They are important not only because of their number and degree of preservation, but also because of their age, approximately 324 million years before present (fig 3., Chapter 3, this volume). Three new early tetrapods have been described so far: *Whatcheeria* (Fig. 5; Bolt & Lombard, 2000; Lombard & Bolt, 1995, 2006); *Sigournea* (Bolt & Lombard, 2006); and *Deltaherpeton* (Bolt & Lombard, 2010). *Whatcheeria,* represented by several nearly complete skeletons and numerous isolated elements or associated parts, is now the founding member of what is turning out to be a widespread family of stem tetrapods, the whatcheeriids (Clack, 2002, and see Carroll, Chapter 2, this volume). *Sigournea,* represented by an isolated jaw, is a stem tetrapod unrelated to any others known at present. *Deltaherpeton,* a complete skull and some isolated skull bones, was declared the earliest North American colosteid, a distinction challenged by the colosteid-like tetrapod described by Clack et al. (Chapter 3, this volume). A further tetrapod, an embolomere, is in preparation and

FIG. 4. John Bolt removing a specimen at the Delta quarry. Amy Nerenhausen from the University of Iowa crew supervises, summer of 1987. Photo by William Simpson.

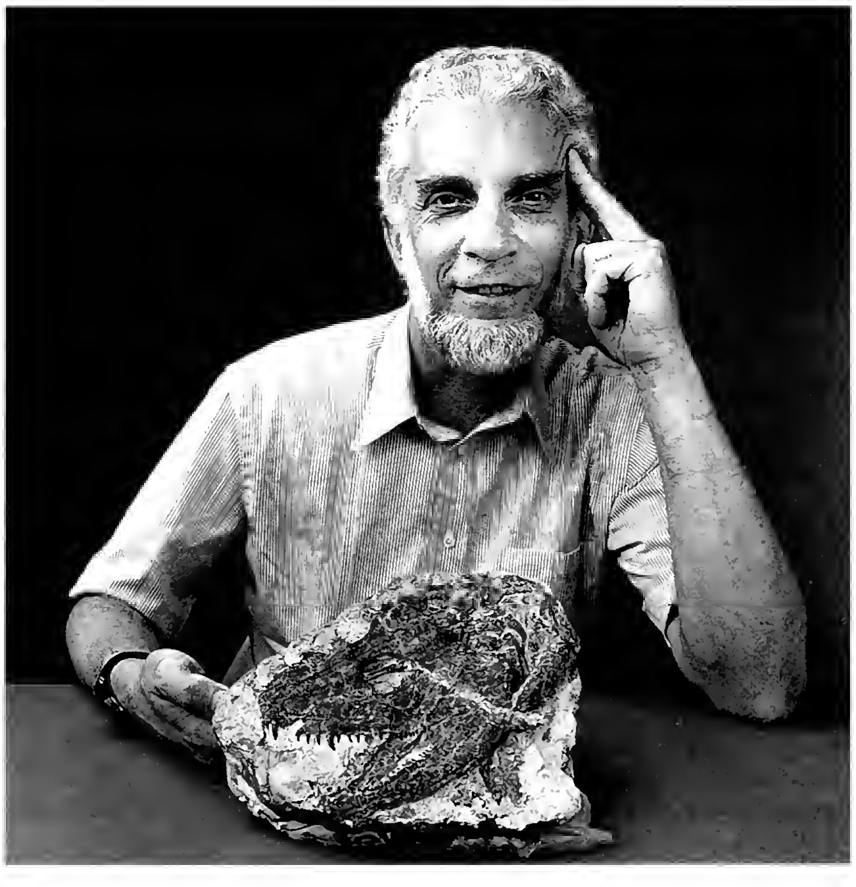

FIG. 5. John Ryan Bolt with "*Rex the wonder amphibian*" (*Whatcheeria*), July, 1997. © The Field Museum, GN88438_12, photographer John Weinstein.

detailed reconstruction of the skull of *Whatcheeria* is near completion. John's patient, careful approach to discovery is producing a descriptive literature on the Delta fauna with lasting importance.

Field, Collections, and Exhibits

In addition to research, defining roles for a museum curator are fieldwork, collection building, and participation in the design of the museum's public exhibits. Over John's career he has participated in or led prospecting or excavations broadly in the United States and these activities have resulted in major additions to the fossil vertebrate collection of the Field Museum. Already mentioned is his major work in the Permian "mud piles" of the Dolese quarry, the Mississippian Goreville and Delta quarries, and the red swath of Permian central Oklahoma. John also excavated in the Triassic of Petrified Forest National Monument, Arizona. His prospecting for new material has included the Pennsylvanian outcrops at the margins of the Illinois basin, the mountains of southern Arizona, and the front range of the Rockies in Colorado. Repeated excursions on the Permian in addition to visits to Oklahoma have included the Cutler Formation and its westward differentiated formations in Colorado and Utah. A prospect to the Upper Devonian of central Nevada produced exhilarating exercise and many flat tires, threat of extinction by lightening, but no fossils:

> *I enjoyed every field experience with John and found his stamina and excitement infectious. I also learned that he eschews Chinese food which occasionally made finding a place to stop for a meal with vegetables a challenge.* —Eric Lombard

Two major exhibits displaying the evolution of life have been mounted at the Field Museum during John's tenure: "*Life Over Time*" developed between 1984 and 1995, and its replacement "*Evolving Planet*" which opened in 2006 and is the current exhibit at this writing. John was closely involved in the conceptual and editing phases of both exhibits. The former entertained visitors with a mock-up of John's office as a way to convey the work of a curator, and though that amusing vignette is now gone, the new exhibit is far richer and informative, in part thanks to John's contributions.

John Bolt Scientist, Colleague, Mentor

> *John is one of the most straightforward people I know, always speaking his mind, always offering good advice or criticism. But he also has provided great and generous service both to the museum, and to the Society of Vertebrate Paleontology.* —Olivier Rieppel, Curator Fossil Amphibians and Reptiles, Field Museum of Natural History (see Chapter 8)

> *John and I have now worked collaboratively for over 35 years. Not having started out as a paleontologist I have learned an immense amount from him and have come to see the thoroughness with which he works as a remarkable gift. I am grateful for his forbearance with my several diversions to administrative endeavors at the University of Chicago. John is a close friend as well as colleague, and now in retirement, we enjoy our furious geriatric pace as we take the measure of the Delta fossils, which of course includes the occasional 'yummy museum hotdog' and ride on the water taxi to Navy Pier for a chocolate milkshake.*—Eric Lombard, Professor Emeritus, Organismal Biology and Anatomy, University of Chicago

> *I had the honor and pleasure to work with John on various occasions over my eight-year employment at the Field Museum. I remember his fondness for his Paleozoic 'beasties', and sincerely admire his high research standards and sense of humor. His professionalism indirectly encourages one to strive for excellence. Passion for his work is infectious, and as a preparator, I understood what was expected when dealing with delicate and often difficult fossil material.*—Lorie Barber, former Chief Preparator, Field Museum of Natural History

> *I owe John Bolt an enormous amount. He was my first contact with the Field Museum, he was Chair of the Department when I interviewed, he signed off on my appointment, and he continued as Chair as I moved through the curatorial ranks to become Curator in his Department.* — Sir Peter Crane, Dean of the School of Forestry and Environmental Studies, Yale University

> *John is one of the most altruistic scientists that I have ever known. There is no one in the museum that is more deserving of recognition than John.* —Lance Grande, Curator of Fossil Fishes and Vice President and Head of Collections and Research, Field Museum of Natural History (see Chapter 1).

> *At the end [of a research day], John would be ready for the next challenge, with laughs, shared passion for research, wit, and intellectual endeavor brightening up each moment of the day.* —Marcello Ruta, Advanced Research Fellow, School of Earth Sciences, University of Bristol, United Kingdom (see Chapter 4).

> *John taught me to operate at a new size scale and level of accuracy. As I became more accomplished at this style of preparation I saw that John was generous with encouragement, advice, and praise for a job well done. And even more than this, I saw the delight with which John observed some new bit of fine anatomy in the specimen I was preparing. John's reaction made doing preparation for him satisfying and a lot of fun. And after John had examined the newly exposed fossil, he would always explain why this new bit of morphology was interesting and important. I have always valued this aspect of working for John.* —William Simpson, Vertebrate Paleontology Collections Manager, Field Museum of Natural History

> *John listens like few others I have ever met; he thinks more deeply about the consequences of actions taken; and he cares more passionately about the most effective use of available resources. I have learned so much from John, about being an administrator, volunteer officer, and museum curator, but most importantly about how to carry oneself as a human being. It is a great thrill for me to be able to contribute some research results to this volume in his honor.* —John Flynn, Curator of Fossil Mammals and Dean of the Richard Gilder Graduate School, American Museum of Natural History (see Chapter 10)

John has been a fantastic colleague for me, especially supportive during that critical time of transition between student and professional. —Jason Anderson, Associate Professor, Biological Sciences, University of Calgary (see Chapter 5)

John was a reviewer on the very first manuscript I ever submitted. My doctoral adviser at UCLA (Peter Vaughn) said to me at the time: "Good. You will be reviewed by a sharp mind and a thorough scientist. It might look like someone bled blue on your manuscript, but this will be very good for you." It was, and the paper far better for it. Since then, as I have gone from student to postdoc to aging academic, John has set a standard for careful, thoughtful work to which I constantly aspire." — Stuart Sumida, Professor, Biology, California State University San Bernadino (see Chapter 9)

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Preface

The 11 papers in this volume are the products of 31 authors. They are arranged in a pseudo-phylogenetic sequence. Chapter 1 is devoted to some Eocene teleost osteichthyan fishes, a successful diversion in the struggle to become amphibians. Chapters 7–11 consider denizens of the Amniota, a derived group of amphibians to which we ourselves belong. In between, Chapters 2–6 consider aspects of the flower of evolution, amphibian-grade organisms themselves. This diversity of contributions, devoted to several major lineages, is a comment on John's broad interests in the evolution of vertebrates. We know he will find interest in every contribution, as we hope is true for all readers.

Novel fossil finds are always a source of progress in understanding. Localities that produce a multitude of specimens in various states of preservation are a rare occurrence, and offer insights into taphonomic patterns and processes. Taking advantage of the amazing productivity of Wyoming's Fossil Butte Member of the Green River Formation, Samuel Sullivan, Lance Grande, Adrienne Gau, and Christopher McAllister report on an impressive collection of over 1100 teleost fish specimens grouped into seven genera in Chapter 1. Nearly 70% of specimens are in near-perfect articulation; an additional 16% show some postcranial disarticulation. This bounty documents the dynamics of body disarticulation, reveals skeletal morphology in astounding detail, and is likely to cast new light on community paleoecology of the Fossil Butte Member site.

In Chapter 2, a review contribution with a point, Robert Carroll examines the astounding diversity of Paleozoic tetrapods including all amphibian-grade taxonomic groups, beginning with the earliest known limbed vertebrates at the very onset of the water-to-land transition and concluding with the sister taxa of amniotes, along the way highlighting many taxa John Bolt investigated during his career. Carroll's view is that the diversity of fossil groups is both a blessing and a curse because we struggle to understand both the relationships within and between the groups. Carroll asks us to consider that present tools are not capable of resolving many of the phylogenetic puzzles that amphibian-grade tetrapods present.

Museums often preserve long-neglected or overlooked specimens that reveal surprises long after their collection. In Chapter 3, Jennifer Clack, Florian Witzmann, Johannes Müller, and Daniel Snyder describe and re-interpret the "St. Louis tetrapod," a specimen found mislabeled as the skull of a coelacanth fish in a drawer at the Museum für Naturkunde in Berlin. Collected by Otto Jaekel in the early 1900s, this specimen closely resembles the superficially crocodile-like colosteids, a small clade of Carboniferous stem–group tetrapods. The sedimentology of the matrix would indicate it to be the oldest colosteid-like tetrapod yet found in North America.

In a wider view of the earliest amphibians, Kenneth Angielczyk and Marcello Ruta explore patterns of cranial evolution in (mostly) Paleozoic temnospondyl amphibians using geometric morphometric techniques. In Chapter 4 they introduce a new supertree of Carboniferous and Permian temnospondyls as a "backbone" for analyses of the correlation between distribution of taxa in morphological space and their phylogenetic proximity. They conclude that taxa are significantly more clustered in morphospace than expected, and that size and shape correlate strongly across their entire taxon sample, but not within a few clades, suggesting some variability in patterns of evolutionary allometry.

Two of John's favorite topics—the evolution of the amphibian ear, and the origin of the living amphibians—are considered in a detailed and visually appealing contribution by co-authors Hillary Maddin and Jason Anderson in Chapter 5. They present new data on the inner ear of the earthworm-like limbless caecilians—the least well known of the three major amphibian orders—and demonstrate that it shares more similarities to those of frogs and salamanders than formerly thought. A lissamphibian-type tympanic ear and its associated traits provide the foundations for collating novel morphological data in an expanded and revised cladistic analysis of early tetrapods. The authors conclude that lissamphibians are a monophyletic group rooted into amphibamid temnospondyls (a pattern in broad agreement with John's conclusion from over four decades ago); in addition, they support a caecilian–salamander clade with the problematic and salamander-like albanerpetontids emerging as stem-group caecilians.

In a fifth contribution devoted to amphibians, Chapter 6, Trond Sigurdsen, David Green, and Phillip Bishop, re-analyze the anterior limb and pectoral girdle anatomy of the Lower Triassic stem-group frog *Triadobatrachus massinoti.* Drawing from extensive osteological and myological investigations of various extant frogs, the authors address the evolution of locomotory adaptations in anurans, discuss features that indicate jumping abilities in this clade, and present *Triadobatrachus* as a possible short-distance jumper or a hopper.

In the first of two papers devoted to reptile-grade amniotes, Peter Makovicky, Sebastián Apesteguía, and Federico Gianechini present a new coelurosaurian dinosaur from the Cretaceous of Argentina in Chapter 7. This new species is named based on articulated hindlimbs; through careful comparative anatomical investigation it is determined the new species belongs to the Alvarezsauridae, a peculiar group of dinosaurs with highly reduced forelimbs. If their identification is correct, this specimen represents a significant range extension of the group in South America throughout the Late Cretaceous.

In Chapter 8, Olivier Rieppel considers the polarity of the ability of serpents to ingest food larger than the diameter of their heads, the "macrostomatan feeding style." Some recent studies have suggested that, since clues to the evolution of that feeding mode reside among various scolecophidian snakes, those taxa are instead regressed macrostomatans because some fossil taxa were placed in a basal-most position. Rieppel argues that this interpretation runs contrary to morphological evidence, and is not simply a question of character optimization.

In the first of three papers devoted to the mammalian lineage, Elizabeth Rega, Ken Noriega, Stuart Sumida, Adam Huttenlocker, Andrew Lee, and Brett Kennedy take on the difficult task of life history interpretation in Chapter 9. Through gross and microscopic investigation of a suspect bone fracture–healing callus in a neural spine of the early synapsid *Dimetrodon*, they report a dynamic system wherein bones were constantly remodeled to maintain a mechanically optimal configuration. This indirectly demonstrates that a soft tissue sail was present between the greatly elongate neural spines in this "sail-backed pelycosaur," but that the spines extended a ways beyond the dorsal limit of the sail. They report no histological evidence for the presence of a blood vessel along the margin of the neural spine, casting the hypothesis that the sail served a thermoregulatory function into doubt.

Recently collected and exquisitely preserved material of the traversodontid cynodont *Dadadon* from the Middle/Upper Triassic of southwestern Madagascar is described in Chapter 10, by co-authors Christian Kammerer, John Flynn, Lovasoa Ranivoharimanana, and André Wyss. New osteological features and growth series are presented, and a new cladistic analysis of traversodontids retrieves *Dadadon* as closely allied with the South American taxa *Massetognathus* and *Santacruzodon*, in the new subfamily Massetognathinae.

The evolution of key morphofunctional traits and their impact on clade diversification are core topics in current macroevolutionary research, and have informed John's own work on the origin and radiation of major early tetrapod groups. The final contribution in this volume addresses the origin of endothermy in mammals—one of the major events in the evolution of this clade. Recent works have explored enhanced parental care (from two highly contrasting perspectives) and adaptation to seasonal environments as key factors leading to endothermy. Here, James Hopson proposes that in the transition from basal synapsids to therapsids, a shift from the primitive "sit and wait mode" of predation to a "widely foraging mode" put the mammal ancestors on the path to increased aerobic capacity and consequent ability to sustain high levels of foraging activity. This in turn resulted in selection for higher body temperature.

Acknowledgments

We thank everyone who wrote to share personal experiences with John. Our requests produced such a generous response that not everything written could be included so we are grateful for the permissions given to select and lightly edit everything included in the Dedication. We are grateful to the Field Museum and the Department of Organismal Biology and Anatomy at the University of Chicago for their generous contributions towards the cost of publication. Jim Hopson, a longtime friend of John's, and Grace Krause, a new one, provided knowledgeable and insightful reviews of the Dedication. For the volume as a whole, we are indebted to numerous reviewers who acted with professionalism and competence, and whose expertise greatly improved the quality of the contributed papers. The editors are grateful to Olivier Rieppel and Janet Voight for their generous advice and assistance on numerous occasions. Janet proved herself indispensable in saving us from many lapses in the text and illustrations. Her persistence in editing, reviewing, and pushing us ever forward have resulted in a much better and more timely publication than we could have produced without her. Thank you, Janet.

Chapter 1: Taphonomy in North America's Most Productive Freshwater Fossil Locality: Fossil Basin, Wyoming

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Abstract

To determine the quality of fossil preservation in the early Eocene Fossil Butte Member (FBM) of the Green River Formation in Fossil Basin, Wyoming, we excavated 1,133 fishes from the upper 30 cm of the 45.7-cm-thick FBM. Each fossil was evaluated for its relative skeletal articulation, ranging from near perfect articulation to almost complete disarticulation, and placed into one of four stages. About 70% of the fishes have near-perfect articulation of the skeleton. Ninety-seven percent of the specimens in the sample belong to five of 19 genera known from the FBM: †*Knightia*, †*Diplomystus*, †*Cockerellites*, †*Mioplosus*, and †*Priscacara*. Finally, 97% of the specimens belong to four of 15 families known to be present in the FBM: †Paraclupeidae, Clupeidae, Latidae, and Moronidae.

Introduction

The Fossil Butte Member (hereafter termed the FBM) of the Green River Formation is located in southwestern Wyoming and contains one of North America's most complete Eocene ecosystems in terms of diversity and quality of preservation. An extremely broad sample of a 52-million-year-old community that inhabited a subtropical to warm temperate freshwater lake environment is preserved intact, with fossils ranging from a wide variety of plants, to insects, crustaceans, mollusks, fishes, amphibians, crocodiles, turtles, lizards, birds, and mammals. This early Eocene biota was recently summarized in detail by Grande (in press). Of the diverse fossil groups preserved there, the most famous are the fishes. So abundant and aesthetically beautiful are these fossils that they have been commercially mined for well over a century. The productive fossil layers are still very extensive, so even the State of Wyoming issues permits for commercial collecting of the FBM fossils on state land. The result of the many years of extensive excavation of these fossils has been an unprecedented sample of an early Eocene biota. Grande and Buchheim (1994) estimated that from 1970 through 1994 alone, more than a half million fossil fishes were excavated from the FBM. Since 1994, the rate of excavation has increased substantially. At this point, literally millions of fossil fishes (mostly clupeomorphs and percoids) have been excavated from the FBM.

The fishes are all well preserved, but the skeletons occur in various states of disassembly, which makes the FBM an ideal locality for taphonomic studies. Many fish skeletons are fully articulated, whereas others are scattered across the exposed slab surfaces. Commercial mining of the fish fossils is primarily for the well-articulated skeletons. Production from the commercial quarries is a "high-graded" sample because most disarticulated specimens are discarded in the quarry. Consequently, it has been suggested that because most museum collections of FBM fishes originated from commercial quarries, these collections are heavily biased toward well-articulated individuals (McGrew, 1975). McGrew's study evaluated the relative articulation-disarticulation of fossil fishes from the FBM based on a sample of 385 fishes that he collected in the summers of 1963 and 1964. He divided them into six categories indicating qualitative degrees of articulation, ranging from almost perfectly articulated skeletons to completely disarticulated skeletons. Tallies for McGrew's six categories were as follows: 58%, 10%, 4%, 7%, 6%, and 15%. However, some of his evaluations appeared to have been influenced by non-taphonomic factors. For example, one specimen classified as one of his Group IV disarticulations should have been classified as Group III but was misinterpreted due to damage as a result of excavation or preparation (e.g., McGrew, 1975, fig. 1). Here, we take a fresh look at his results using a much bigger study sample and consider only disarticulation that occurred during diagenesis.

McGrew's 1975 study was based on x-rays of blocks of material sent to the University of Wyoming. He did not distinguish between different genera or species of fishes in his study and, instead, considered their modalities of preservation and expressed these as percentages of the total fish count. Here, we examined and graded the state of preservation of each specimen as it was discovered in the field, breaking down the total sample at the genus level. Using a larger sample size and more consistent assessment, we sought to check McGrew's previous hypotheses on the quality of skeleton articulation and also to add to earlier collected data on relative diversity among the fish genera in the FBM.

FIG. 1. The two quarry blocks (**arrows**) from which we excavated a sample of 1,133 fossil fishes over a period of 10 days. Locality was in the James E. Tynsky 2011 quarry on Lewis Ranch, located in the SE¼, SE¼, Sec. 19, T.21N, R.117W, and NE¼, NE¼, Sec. 30, T.21N, R.117W, Kemmerer 15-minute Quadrangle (USGS). This is also known as FBM Locality A (Grande, in press).

Methods

In June and July 2011, we excavated two joint-bounded blocks within the larger quarry of James E. Tynsky in the FBM on Lewis Ranch near Fossil Butte National Monument (Fig. 1). Over 10 days, we excavated 1,133 fishes from the upper 30 cm of the 45-cm layer and recorded the state of articulation of each fish.

We ranked the quality of preservation in four different stages of disarticulation, ranging from Stage 1 (specimens with all or nearly all bones in articulation with each other, Fig. 2) to Stage 4 (specimens with nearly all bones disarticulated, commonly referred to as "blown fish" by the commercial quarriers, Fig. 5). Stages 2 and 3 were estimates of intermediate disarticulation as described in the captions of Figures 2B and 2C. Although somewhat subjective, the four categories provide a reasonable estimate of the number of well-articulated skeletons in the locality. We use the term "articulation" rather than "preservation" because even disarticulated specimens reveal extremely well preserved individual bones, serving as natural dissections for scientific study.

All specimens illustrated here are deposited in the Geology Department of The Field Museum, Chicago, Illinois (FMNH).

Results

Taxa and Stages of Disarticulation

Table 1 shows the number and proportion of fishes in each stage of disarticulation from our sample. Our results are similar to those of McGrew (1975), in that most fishes are almost completely articulated (69.9%). We found a higher proportion of almost perfect skeletons and a lower percentage of totally disarticulated skeletons than McGrew, but as indicated above, his results may have been influenced by non-taphonomic factors (post-excavation breakage). Because McGrew's original collection is mostly lost now, it cannot be recounted to look for and exclude post-excavation breakage.

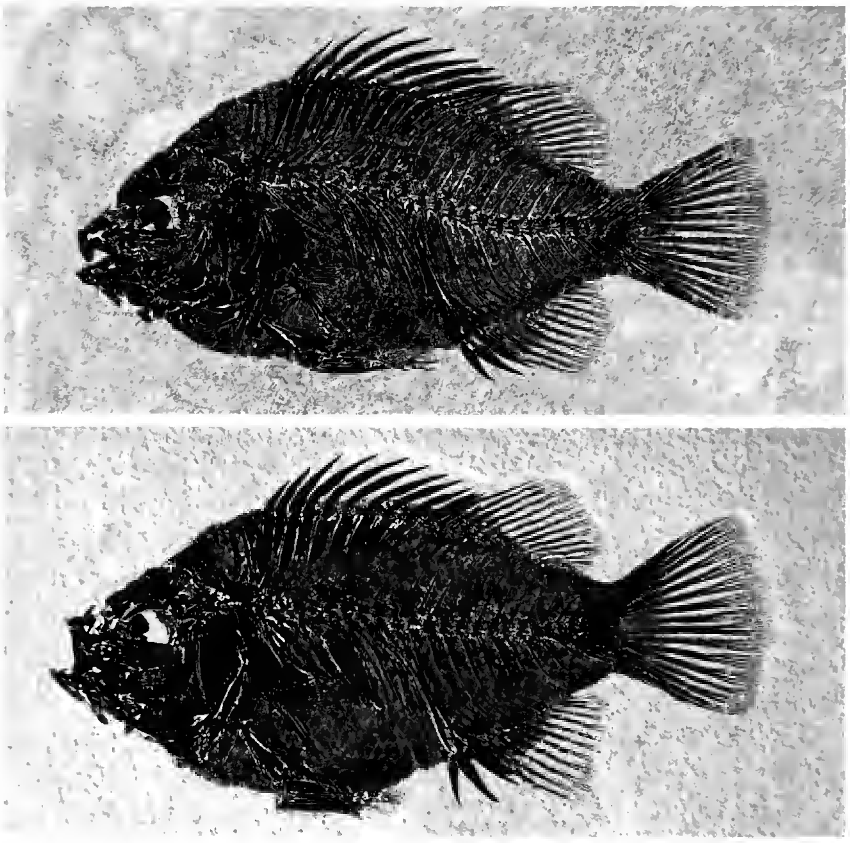

FIG. 2. Stage 1 of the articulation-disarticulation sequence of skeleton decomposition. †*Cockerellites liops* in near-perfect articulation. Specimens are FMNH PF12107 (**top**) and FMNH PF13326 (**bottom**); each fish is about 12.7 cm in total length.

TABLE 1. Numbers and percentages of each stage of articulation-disarticulation among the 1,133 fishes collected for this study. Also given are the relative abundances of each fish genus in our sample. For the purposes of this study, the closely related genera †*Priscacara* and †*Cockerellites* are grouped within the genus †*Priscacara*, as in previous studies of relative generic abundance by Grande (1984). We also found 218 non-fish fossils: 206 plants (mostly fragmentary), 11 insects, and one bird feather.

	Stages of articulation-disarticulation					
Genus	**1**	**2**	**3**	**4**	**Total**	**Percent**
†*Knightia*	384	74	40	30	528	46.60
†*Diplomystus*	260	70	11	17	358	31.60
"†*Priscacara*"	130	28	17	24	199	17.56
†*Mioplosus*	6	4	9	1	20	1.77
†*Phareodus*	5	3	5	3	16	1.41
†*Notogoneus*	7	2	1	1	11	0.97
Amia	—	—	—	1	1	0.09
Total	792	181	83	77	1,133	100.00
Proportion	69.90%	15.98%	7.33%	6.80%	100.00%	

Because we recorded each fish genus, we can add to previous studies of the relative abundance of fish genera from the 45-cm layer of the FBM (mainly by adding our data from Table 1 to the data in Grande [1984, tables II.8 and II.9]). Although we found none of the rare genera other than a disarticulated *Amia* in our sample, we can provide relative percentages of the six common genera (†*Knightia*, †*Diplomystus*, †*Priscacara*, †*Mioplosus*, †*Phareodus*, and †*Notogoneus*). (Note: In our counts, †*Priscacara* and †*Cockerellites* are combined since they

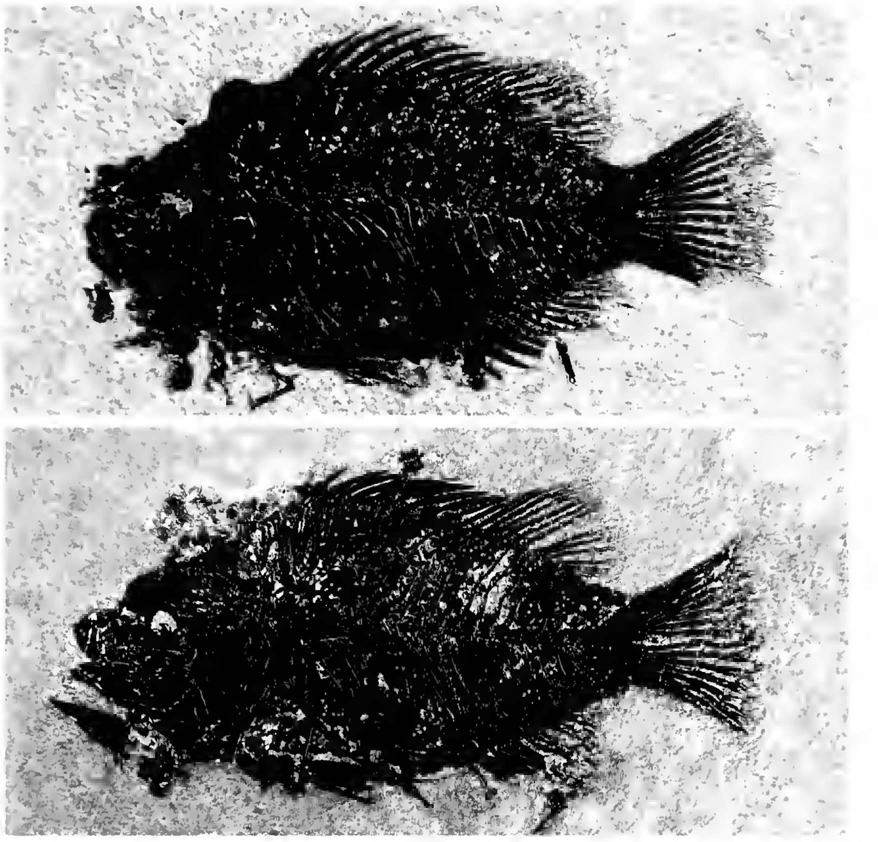

Fig. 3. Stage 2 of the articulation-disarticulation sequence of skeleton decomposition. †*Cockerellites liops* with disarticulation starting just behind the head region, displacing a few bones and scales. Specimens are FMNH PF12109 (**top**) and FMNH PF12103 (**bottom**); each fish is about 12.7 cm in total length.

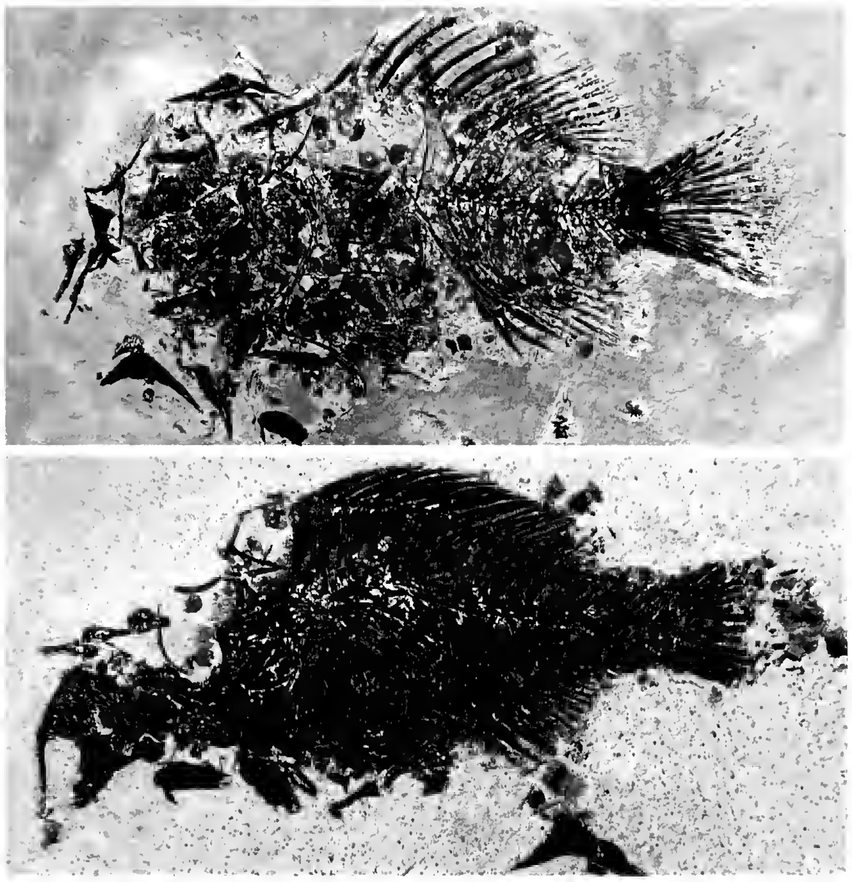

Fig. 4. Stage 3 of the articulation-disarticulation sequence of skeleton decomposition. †*Cockerellites liops* with disarticulation progressing further, primarily in the anterior region of the fish. Specimens are FMNH PF12071 (**top**) and FMNH PF15389 (**bottom**); each fish is about 12.7 cm in total length.

usually cannot be distinguished when unprepared and covered with rock.) Also adding our data to the previous data and information from Grande (1984, 1999, 2001) allows us to extrapolate percentages for other FBM genera not present in our excavated sample. We found that clupeomorphs (†*Knightia* and †*Diplomystus*) and percomorphs (†*Mioplosus*, †*Priscacara*, and †*Cockerellites*) make up 78% and 19% of our sample, respectively. Nineteen genera occur in the FBM; our counts indicate that 97% of all 45-cm-layer specimens belong to the five most common genera, †*Knightia*, †*Diplomystus*, †*Cockerellites*, †*Mioplosus*, and †*Priscacara*. This compares favorably to the other surveys of the 45-cm-layer genus diversity. McGrew (1975) found that 99% of all specimens also belong to the five most common genera based on a sample size of 385 fishes, and Grande (1984, table II.8) found that 96% of all specimens belong to the five most common genera based on a sample size of 1,049 fishes. Our sample indicates that of the 15 families of fishes that occur in the FBM, 97% belong to the four most common families, two of which are herring and herring-like fishes in Clupeomorpha (Clupeidae and †Paraclupeidae) and two of which are spiny-rayed fishes in Percomorpha (Latidae and Moronidae). The reproductive rate of living clupeomorphs and percomorphs is extremely high, which probably explains their relative dominance in Eocene Fossil Lake. They would have also been the first to recover after mass-mortality events in the lake. For a more in-depth review of the entire fish fauna and other fossils in the FBM, see Grande (in press).

The Process of Disarticulation and Decomposition

In general, disarticulation begins at the head-trunk boundary (Fig. 3). It continues gradually anteriorly into the skull region and posteriorly into the posterior abdominal region (Fig. 4). As disarticulation progresses, only the caudal region remains articulated (Fig. 5). Eventually, all bones become disarticulated, although totally disarticulated fishes are rare occurrences in the FBM. One explanation for this sequence of disarticulation could be that stomach gases released with decay accumulate in the abdominal region. As the fishes' bodies start decomposing, the connective tissues holding the bones together soften. As a result, the skeletons first began to disarticulate in the abdominal region where the gas pressure would have been greatest. In effect, the fishes' bodies slowly "exploded," first in response to gas pressure eventually rupturing the skin and anterior part of the skeleton, and later to further decomposition of soft tissues, gravity, and sediment compression.

The fishes' bodies eventually sank to the bottom of the lake, with the absence of directional sorting of disarticulated bones (Fig. 5), indicating the lack of bottom current. Lack of current sorting was also supported by McGrew's (1975) observations. In addition, the second author confirms lack of directional sorting in most of the thousands of disarticulated specimens he has collected over the last 28 years (although it is occasionally present).

One possible explanation for such a high percentage of well-articulated skeletons in the FBM is lake stratification. Subtropical lake systems often become stratified during much of the year, with only an annual mixing of bottom waters with surface waters (Bradley, 1948). If the lake was stratified for most of each year, with anoxic waters in the stagnant lake bottom, one would not expect to find signs of scavenging by organisms requiring oxygen. The fishes' bodies that settled would not become buoyant from stomach gases for at least one week, and possibly several, if temperature stayed below 15°C on the lake bottom (Smith & Elder, 1985). Given that nearly 70% of our specimens were almost perfectly articulated (Stage 1), it seems that such conditions existed. Fishes would decay untouched on the bottom, with disarticulation coming

SULLIVAN ET AL.: TAPHONOMY IN FOSSIL BASIN, WYOMING 3

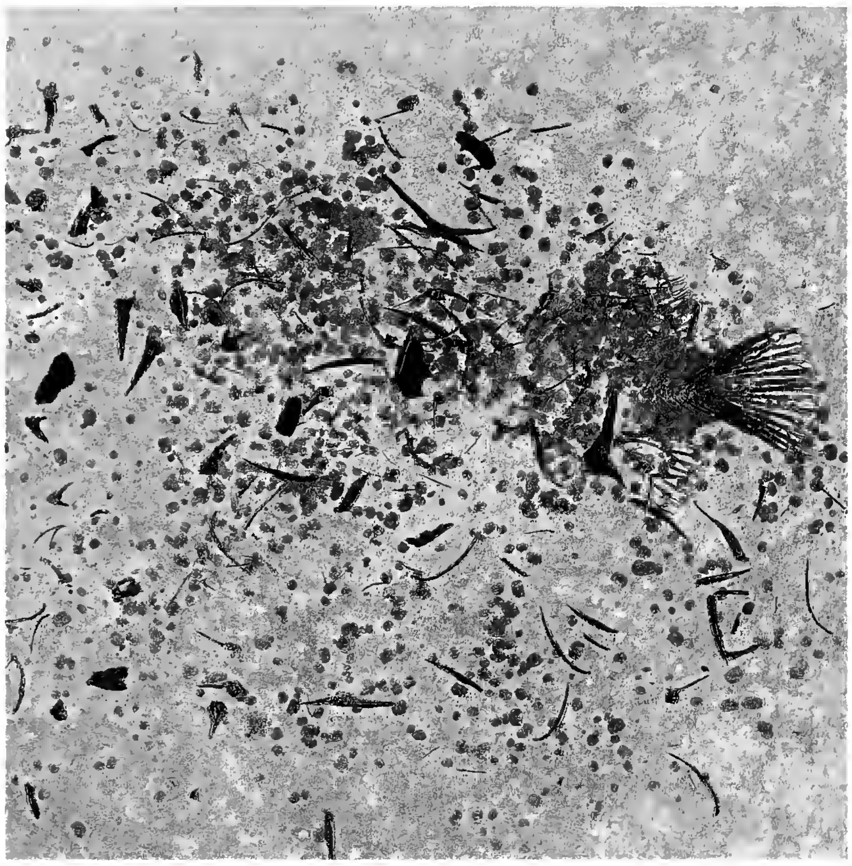

FIG. 5. Stage 4 of the articulation-disarticulation sequence of skeleton decomposition. †*Cockerellites liops* with total disarticulation of skeleton anterior to the caudal region. Specimen is FMNH PF12074 and the fish had an estimated total length of about 11.4 cm.

from connective tissue decomposition and gas build-up as described above. The stage or degree of disarticulation in the fossil would also be affected by how soon the body was buried after it settled on the lake bottom. Once buried, the bones would be held in place by the encapsulating sediments. Large fishes are commonly better articulated on the downside than on the upside, suggesting that burial was not rapid. Bottom side bones were immediately supported in place by sediment, while upside bones had time before burial to disarticulate due to the effects of tissue decomposition and gravity.

Although macroscopic scavengers would be unable to reach the dead fishes on the lake bottom, anaerobic bacteria could survive in such conditions. McGrew (1975) attributed the disarticulation of his specimens to these bacteria and reasoned that they would gain access to the interior of the fish carcass through the opercular opening, which would explain why connective tissues first decomposed just posterior to the skull. While Wilson and Barton (1996) agree that the lake bottom was stagnant, they reject the hypothesis that anaerobic bacteria caused the disarticulation found in the FBM and other Green River localities. Instead, they concluded that disarticulation resulted for the most part from macroscopic scavengers, such as fishes and other animals. We do not believe this is plausible due to the random sorting pattern of small bones and the fact that disarticulated specimens usually retain all bones. Even individual scales appear to be randomly sorted, as one would expect if gravity, gas escape through tissues, and low energy conditions on the lake bottom were solely responsible for bone displacement.

It has also been suggested that lake stratification could have been due to salinity gradients rather than temperature differences. Buchheim (1994) proposed that the deep region near the lake's center may have been saline, with the overlying and marginal regions of the lake consisting of freshwater. Although this is possible, the abundance and diversity of the freshwater organisms inhabiting the lake make it seem unlikely.

The FBM is an ideal stratigraphic horizon for continued studies of taphonomy and Eocene biodiversity. The preservation, as indicated here and elsewhere, is amazingly good, with nearly 70% of the fish skeletons almost perfectly articulated. Our sample size was not large enough to compare inter-generic variability in articulation, and this might be an area of future study after further collecting. The variation in relative abundance of genera in the FBM is also remarkable, ranging from 46.6% for the most common genus (*Knightia*) to 0.00005% for the least common (*Esox*) (Grande, 1999). This has significant implications for adequate sample sizes for measuring biodiversity based on fossil localities.

Acknowledgments

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Chapter 2: The Importance of Recognizing Our Limited Knowledge of the Fossil Record in the Analysis of Phylogenetic Relationships among Early Tetrapods

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Abstract

This chapter is a critical review of the problems presented by our current knowledge of the early fossil record of tetrapods. This record is marked by two major features. The first is a significant absence of preserved fossils between the Upper Devonian and the end of the Lower Carboniferous: Romer's Gap. The second is that the numerous lineages that appear at the end of the Lower Carboniferous are diverse and distinct from one another and do not present features that permit the confident assignment of relationships either to the Devonian taxa or among the several lineages themselves. Furthermore, convergence in anatomical characteristics is common. Phylogenetic systematics, also termed cladistics, currently plays a major role in the analysis of relationships and patterns of evolution among vertebrates. This mode of analysis does not consider the relative incompleteness of the fossil record, the relative frequency of convergence in the evolution of character changes that may occur independently in more than a single major lineage, development, or body function, none of which can be readily categorized with standard data matrices. These problems in the available data and its mode of analysis are discussed in the context of the early stages in the evolution of terrestrial vertebrates.

The Ancestry of Tetrapods

A key area of inquiry in the study of fossil vertebrates is the resolution of the affinities of several late Devonian to middle Carboniferous tetrapod groups. Both the mutual relationships of these groups and their phylogenetic placement relative to extant tetrapods are vexing problems. The great anatomical diversity of early tetrapods and the shortcomings of the fossil record limit our knowledge of the evolutionary routes leading from the earliest known tetrapods in the Upper Devonian to the most primitive members of the tetrapod crown-group—some 60 million years later (Fig. 1).

The greatest morphological divide is between the "labyrinthodonts" and the "lepospondyls," each term referring to a collection of widely disparate groups. The former were characterized by a generally large body, relatively short trunk, and conspicuous appendicular skeleton, whereas the latter were characterized by loss or fusion of several skull bones, a usually elongate trunk, and highly reduced appendages. These two major tetrapod categories are readily distinguished, but as yet lack any obvious intermediates. Not only is it difficult to establish specific phylogenetic affinities for each of these categories, there remain equally serious problems of determining affinities among the major groups of labyrinthodonts and lepospondyls. These groups are also clearly distinct when they first appear in the fossil record.

These problems can be attributed to our very limited knowledge of tetrapod remains between the late Devonian and the middle Carboniferous, mostly due to the limited number of collecting horizons and the destructive action of geomorphologic and tectonic processes. Fossils from this crucial time interval are from a few scattered localities representing a wide range of depositional environments located primarily in the Northern Hemisphere. As a result, they may provide few and patchy clues to the ancestry of the approximately 16 anatomically distinct lineages that were in place by the late Carboniferous. Therefore, even the oldest known members of nearly all of these advanced groups differ greatly from each other in anatomy and probable ways of life, making it extremely difficult to establish reliable sister group relationships. Further complicating the recognition of valid sister-taxa is the apparently high degree of convergence in many aspects of the anatomy of the recognized major groups. This makes it difficult to identify which apparently synapomorphic character changes actually link such groups (Carroll, 2009). For example, trunk elongation certainly occurred in many otherwise distinct lineages of lepospondyls associated with limb reduction or loss, often with great modifications of the skull and vertebral anatomy. The specific combinations of these characters certainly distinguish different lepospondyl groups from their first appearance in the fossil record some millions of years after their divergence from as yet undetermined ancestral groups in the late Devonian or early Carboniferous.

In fact, we must go back to the early and middle Devonian to pick up the first evidence of the origin of tetrapods (Zhu & Yu, 2004). It has long been recognized that their ancestry can be ultimately traced to sarcopterygian fishes, clearly distinguished from actinopterygians by the lobate configuration of the paired fins supported by an internal skeleton readily recognizable as homologous with the limb bones of tetrapods. Their muscular paired fins indicate that most members of this

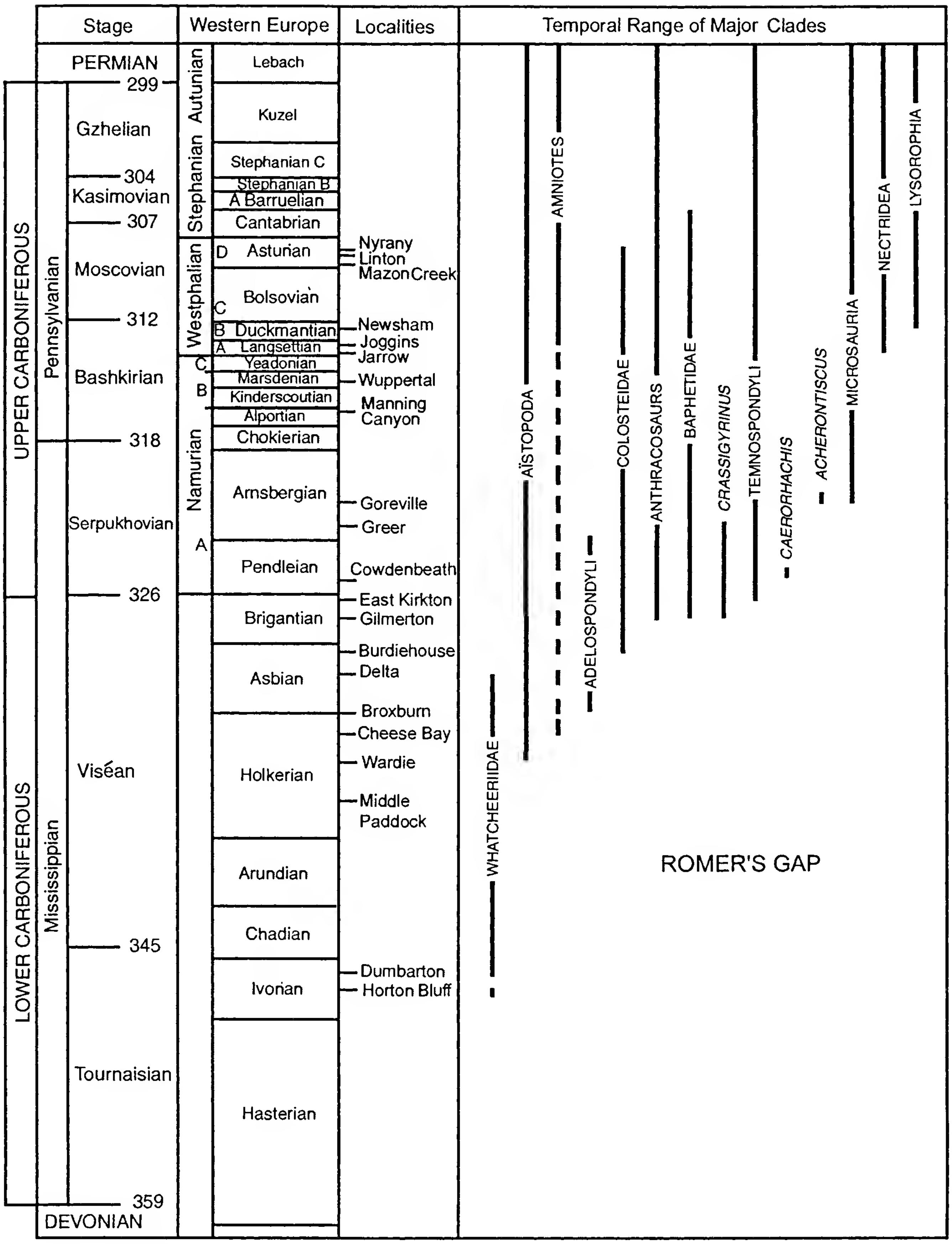

FIG. 1. Temporal ranges of Carboniferous tetrapods. Geological time scale based on Gradstein et al. (2004). Relative sequence of Scottish amphibian localities from Smithson (1985a). Romer's Gap refers to the paucity of amphibian fossils from the first half of the Carboniferous. Ages given in millions of years.

group lived close to the bottom and probably near shore. Judging from the palatal position of their internal nares, sarcopterygians had probably also evolved lungs homologous with those of tetrapods.

By the Upper Devonian, several taxa have been recognized as near-tetrapod relatives, including *Panderichthys*, *Elpistostege*, *Tiktaalik*, and *Elginerpeton* (Carroll, 2009). It has long been recognized that osteolepiforms such as *Eusthenopteron* formed a grade group along the tetrapod stem. *Eusthenopteron* retained dorsal fins and a vertical, trifid tail, indicating that it swam in the manner of fish in fairly deep water, but *Panderichthys* and *Tiktaalik* had lost their dorsal fins. *Tiktaalik*, however, was divergent in having a very long trunk region with at least 46 presacral vertebrae, not counting those in the neck or just anterior to the pelvic fins, and the vertebrae do not appear to be ossified (Daeschler et al., 2006). However, the bones of the pectoral fin were well ossified, suggesting that it might have pulled itself onto land.

Elginerpeton predates by some 12 million years the first appearance of unquestionably limbed tetrapods, the best known of which were *Acanthostega* and *Ichthyostega* from east Greenland. Unfortunately, *Elginerpeton* is known only from dissociated jaw and scattered postcranial remains, which do not provide sufficient characters for establishing a useful data base (Ahlberg, 2011). In fact, none of these genera share a sufficient number of derived character states comparable with the known early tetrapods to establish specific, reliable sister-group relationships with of any tetrapod taxa known from the

Upper Devonian or later. This is hardly surprising in view of the long gaps in time, the great change in their anatomy, and the relatively small number of adequately known taxa involved.

The Oldest Amphibians

Throughout, the term "amphibians" is used in the generic sense of early limbed vertebrates, without necessarily implying a close relationship to crown-group amphibians (frogs, salamanders, caecilians). The oldest vertebrates for which there is direct evidence of limbs with digits, *Ichthyostega* and *Acanthostega,* are known from nearly complete skeletons from shortly below the Devonian-Carboniferous boundary in East Greenland (Säve-Söderbergh, 1932; Coates, 1996; Clack, 2002). Their skulls had lost the bony connection with the shoulder girdle common to rhipidistians. The number of digits, however, was greater than in early Carboniferous tetrapods, with seven in *Ichthyostega* and eight in *Acanthostega*, clearly a primitive condition for tetrapods. Both had lateral line canals and pit lines. *Acanthostega* had a large, vertically oriented caudal fin, demonstrating that it must have spent much of its life in the water. In addition, the vertebral column retained the primitive feature (shared with *Eusthenopteron*) of paired neural arches, intercentra, and pleurocentra. *Ichthyostega* also retained long dorsal fin rays in its tail, which would have been useful in aquatic locomotion, but the configuration and attachment of the pelvis strongly suggest that the trunk could have been held above the ground when on land. These features certainly support the intermediate nature of both genera between water and land. However, one character, the loss of the intertemporal bone, was derived, relative to that of early labyrinthodonts. The occurrence of these two genera is estimated at about five million years prior to the end of the Devonian.

Acanthostega and *Ichthyostega* appear as nearly ideal intermediates between rhipidistian fish and later tetrapods, but the retention of many primitive features makes it difficult to determine specific affinities with any of known Carboniferous tetrapod lineages. Recent work by Callier et al. (2009) helps to specify changes in the configuration of the humeri during the ontogeny of these two genera that point to *Ichthyostega* as the more probable sister-taxa of tetrapods. Ironically, the humeri of juvenile ichthyostegids appear more primitive than do those in *Acanthostega* in their simplicity. However, changes during early growth show progressive modification in both the humerus and the scapula that indicate transition from an aquatic way of life in the hatchling to effective terrestrial locomotion in the adult. In contrast, the humeri of juvenile *Acanthostega* appear more advanced than do those of *Ichthyostega*, but they changed very little during ontogeny and probably remained primarily aquatic in their habits.

The most important ontogenetic change in *Ichthyostega* was the elaboration of the pectoral process of the humerus, which was not apparent in the most juvenile specimens. In the adults, it would have served as the area of insertion of the pectoralis musculature to lift the body above the substrate. As pointed out by Callier et al. (2009), a homologous structure was not present in any osteolepiform fish. During development, the elaboration of the pectoral process of the humerus and the associated oblique ventral ridge were coupled with changes in the shoulder girdle. The posterodorsal supraglenoid process of the scapula had an anterolaterally facing extension of the glenoid surface, which appears to have formed a locking contact for a posterior-facing extension of the articular head of the humerus. The resulting humeral pronation would have rotated the forearm ventrally-posteriorly and thus both lifted the body off the ground and contributed to the stride. Changes in the configuration of the shoulder girdle and humerus may also have been associated with the breakup of large muscles sheets common to fish, into the several discrete flexor muscles of more derived tetrapods. This would have provided the more effective movement of the humerus that is necessary for locomotion on land. Callier et al. (2009) also noted that, although *Ichthyostega* underwent great locomotory terrestrialization during ontogeny, it could have been phylogenetically more basal than *Acanthostega.* This is supported by the juvenile *Ichthyostega* appearing more primitive than the sarcopterygians *Tiktaalik* and *Panderichthys* in the configuration of the forelimb. Callier et al. (2009, pg. 364–367) further argued for "...a scenario of rapid early terrestrialization rather different from the currently predominant 'aquatic Devonian tetrapods' model." Such early achievement of a fully terrestrial way of life also supports an early radiation of fully terrestrial vertebrates during the period of Romer's Gap, further complicating the phylogenetic analysis of later Paleozoic tetrapods. This study demonstrates the importance of ontogenetic change and locomotor functions in establishing phylogenetic affinities, factors rarely considered in establishing data bases for cladistic analyses.

Two less well known tetrapods occur later in the Upper Devonian, *Ventastega* and *Tulerpeton. Ventastega* is an unquestioned tetrapod from the latest Devonian of the Baltic region, which is known from much of the skull and lower jaw, dermal elements of the shoulder girdles, and an ilium that differs from those in other Devonian or Lower Carboniferous tetrapods in possessing a single, posteriodorsally directed, paddle-shaped iliac process, rather than distinct dorsal and posterior processes common to most other early tetrapods, including *Acanthostega* and *Ichthyostega* (Ahlberg et al., 1994). *Tulerpeton*, from the Tula region of central Russia, is the only Devonian amphibian that is a plausible sister-taxon of any of the later tetrapods (Lebedev & Coates, 1995). The vertebral intercentra are fully crescentic, in contrast with most of those in *Acanthostega,* in which all but those of the axis and the sacral vertebra were paired. The phalangeal formula is 2,3,4,5,4,2, compared with seven digits in *Ichthyostega*, eight in *Acanthostega,* and five in early Carboniferous labyrinthodonts. An intertemporal bone, lost in *Acanthostega* and *Ichthyostega*, is retained, as in early Carboniferous labyrinthodonts, including anthracosaurs and early temnospondyls.

The End of Romer's Gap

Horton Bluff

The oldest known tetrapods after Romer's Gap that can be associated with the major radiation in the later Carboniferous have been collected from Horton Bluff, Nova Scotia, Canada, on the shore of the Bay of Fundy (Carroll, 2009). This was a biologically rich locality, with remains of diverse plants, fish, and amphibians, suggestive of a nearshore environment in which the remains of tetrapods were disarticulated by scavengers and swept into rivers or streams, discharging into a lake or marine environment occupied by gyracanths and gigantic rhizodontids. Thousands of individual bones have been collected, but almost none in articulation. On the other hand, many are extremely well preserved and can be compared with individual skeletal elements of later Carboniferous tetrapods. Their certainly tetrapod nature can be attested to by a myriad of footprints and trackways, some extending for hundreds of feet on bedding planes.

Many isolated bones can be attributed to known amphibians represented by complete skeletons from later beds in the Carboniferous, whereas one well-preserved scapulocoracoid has several features resembling those of *Ichthyostega* (Carroll, 2009). Numerous well-preserved humeri can be compared with those in a number of tetrapods that have been described from later in the Carboniferous, including the colosteid *Greererpeton* and the anthracosaurs *Eoherpeton* and *Tulerpeton* from the late Devonian of Russia (Clack, 2000). An ilium very closely resembles that of *Pederpes*, described from beds only about two million years later in the Lower Carboniferous of Scotland (Clack & Finney, 2005). There are also a number of extremely well-preserved interclavicles broadly resembling those of anthracosaurs described from later Carboniferous and Permian deposits. A partial jaw exhibits highly rugose angular and splenial bones, in marked contrast with the rudimentary striations of the adjacent surangular and dentary, which closely resemble the lower jaws of early temnospondyls such as *Dendrerpeton*.

These scattered, but well-preserved elements indicate the wide spectrum of labyrinthodont lineages that had almost certainly appeared by the base of the Lower Carboniferous. So far, no bones resembling those of lepospondyls have been recognized at the Horton Bluff locality; however, representatives of two groups appear toward the end of the Lower Carboniferous, the aïstopods and adelospondyls. These fossils demonstrate the difficulty of constructing an informative character base for meaningful phylogenetic analysis of the interrelationships of the early tetrapods without much more complete evidence from the early fossil record.

The Whatcheeriidae

Pederpes—Three other, much more completely known genera from later in the Carboniferous have retained similarities with specimens from Horton Bluff. These were united by Clack (2002) within the family Whatcheeriidae. The oldest is *Pederpes*, from beds only one or two million years younger than those of the Horton Bluff locality. It is known from a single nearly complete skeleton collected at a locality north of Dumbarton, Scotland (Clack & Finney, 2005), but only three bones, the humerus, ilium, and femur, can be directly compared with those of Horton Bluff specimens.

This genus provides the best known basis for comparison of a well-established labyrinthodont with *Acanthostega* and *Ichthyostega* from the Upper Devonian and the great diversity of tetrapods from the upper portion of the Carboniferous. *Pederpes* is unquestionably a labyrinthodont (based on the labyrinthine infolding of the tooth enamel, the pattern of the cranial bones, and the multiple vertebral elements), above the level of *Acanthostega* and *Ichthyostega*, but with suggested ties to two other genera from the later Carboniferous, *Ossinodus* (Warren, 2007) from the mid-Visean (~337 million years) of Australia and *Whatcheeria* from the Asbian (about 330 million years) of Iowa, all tentatively included in the family Whatcheeriidae. The skull is about 15 cm long, with a distance from the snout to the base of the tail of about 60 cm. It differs in several respects, including the retention of an intertemporal bone lost in the Devonian genera but retained in early temnospondyls and anthracosaurs. The dermal bones of the skull are sculptured with conspicuous pits and extended grooves. Lateral line tubes are present, but no obvious lateral line grooves. The cheek is attached firmly to the skull table and the orbits are very large, extending almost the entire height of the cheek. The jaw articulation extends well behind the skull table, and there is a deep squamosal notch. A canine-like tooth is present in the anterior portion of the maxilla. The palate is closed, as in anthracosaurs, but there are paired fangs on the vomer, palatine, and ectopterygoid, as in temnospondyls, in contrast with the loss of the vomerine fangs in anthracosaurs. The vertebral centra resemble those of later temnospondyls, with paired, elongate, rhomboidal dorsal pleurocentra and medial crescentic intercentra, but the neural arches are not firmly attached at the midline. There are approximately 28 presacral vertebrae. The ribs in the region of the shoulder girdle are exceptional among all early tetrapods in being greatly expanded and overlapping. The scapula and coracoid ossified separately. The ilium has a well-developed dorsal process anteriorly and a short posterior extension, as in most early labyrinthodonts. The limbs are well developed, but the femur differs from most temnospondyls in being slightly longer than the humerus and without a slender shaft. The manus is poorly known, but the pes has a digital count of 2,3,4,4?, not easily comparable with later labyrinthodonts.

Ossinodus—Described by Warren (2007) as the only known early tetrapod from Gondwana, *Ossinodus* appears quite different from the earlier *Pederpes* or the later *Whatcheeria*. Several specimens have been collected from the Mid-Viséan Ducabrook Formation, Middle Paddock site, Queensland, Australia, some nine million years younger than *Pederpes*. Most of the skull is known, but the vertebral column is incomplete, precluding determination of the length of the trunk. The entire skull roof is ornamented with a relatively uniform pattern of pits and grooves, common to much later temnospondyl labyrinthodonts, but clearly distinct from other labyrinthodont genera from the Lower Carboniferous. The orbits are somewhat anterior to the mid-length of the skull and much smaller than those of *Pederpes*. In common with *Acanthostega* and *Ichthyostega*, the intertemporal is missing, in contrast with early temnospondyls and anthracosaurs. The marginal dentition differs from that of most labyrinthodonts in the presence of larger teeth at the anterior end of the maxilla and premaxilla. A large fang occurs at the anterior end of the palatine bone, but fangs are not present on the ectopterygoid or the vomer. Otherwise, the palate is primitive in being closed and having a uniform covering of denticles. There are 27 neural arches preserved in sequence, with the most anterior identified as the axis. None are well attached at the midline. The 29th is tentatively identified as the sacral. The centra are typically rhachitomous, with wedge-shaped intercentra and pleurocentra that are rhomboidal and elongate in outline. A distinctive feature is seen in the anterior trunk ribs, which have conspicuously expanded flanges. Only the base of the tail is preserved. The scapulocoracoid is ossified as a unit and associated with a typical clavicle and cleithrum. The pubis remains unossified. In contrast with *Pederpes*, the femur has as substantial shaft. The limbs are only incompletely known but appear small relative to the size of the skull. In an effort to establish the phylogenetic position of *Ossinodus*, Warren (2007) ran a number of phylogenetic analyses on the early Carboniferous tetrapods. She concluded that the Whatcheeriidae may be a grade rather than a clade. She goes on to say: "It is likely that the scarce tetrapod material from Romer's Gap represents a 'grade' of tetrapod evolution more derived than the Devonian taxa but still with many plesiomorphies, as suggested by Clack and Finney (2005). The few apomorphies are insufficient to outweigh this general primitiveness and cannot relate the single Gondwanan taxon to any of the later Euramerican taxa" (Warren, 2007, pg. 850-862)

Whatcheeria—The latest of the genera placed in the Whatcheeridae, from about four million years prior to the end of the Lower Carboniferous, is *Whatcheeria*, from southeastern Iowa, near the town of Delta. All specimens of *Whatcheeria* were collected from a single lacustrine locality, about 16 m in diameter. This was probably a sinkhole, but the remains of chondrichthyans, osteichthians, rhizodonts, lungfish, acanthodians, and at least three other types of labyrinthodonts suggest that it was probably connected with a larger body of water. Several mostly complete and mostly articulated skeletons, about 50 partial remains and a few hundred isolated elements, make this genus the most completely known Lower Carboniferous tetrapod (Bolt & Lombard, 2000). *Whatcheeria* is certainly not closely related to any labyrinthodonts currently known from later in the Carboniferous. It might have some affinities with *Pederpes* or *Ossinodus*, but no uniquely shared derived characters have been recognized. One of the best studied specimens has a skull length of 16.5 cm, with the combined length of skull and trunk approximately 40 cm. The skull is narrow, with a steep cheek region firmly sutured to the skull table. Except for the lateral margin of the skull table, premaxilla, and maxilla, which have a scattering of small pits, the surface of the skull bones is nearly smooth, in sharp contrast to the conspicuous, regular pitting of *Ossinodus*. In addition, the orbits are clearly much more extended dorsoventrally and more posterior in position. The bones of the skull table are clearly defined. An intertemporal bone is present, as in primitive labyrinthodonts, but not *Acanthostega* or *Ichthyostega*. The parietal does not reach the tabular—a character shared with *Acanthostega*, *Pederpes*, temnospondyls, and baphetids—but it does in early anthracosaurs. There is a massive canine-like tooth at an anterior position in the maxilla. The pterygoids are separated by small interpterygoid vacuities. Each of the lateral paired bones of the palate bears an alternatively replacing pair of fangs, as common to temnospondyls, whereas most anthracosaurs lack fangs on the vomers. There are about 30 presacral vertebrae. Their most striking feature, unknown in any other early tetrapod, is the fusion of the otherwise paired pleurocentra at the dorsal midline. The ventral intercentra are crescentic in shape, as in other early labyrinthodonts. The scapula and coracoids ossify separately. The pelvis has the typical dorsal iliac and postiliac processes of most other early tetrapods. During early growth, the anterior margin of the acetabulum retains unfinished bone. As in *Ossinodus*, the femur has a distinct shaft. The proximal portions of fore and hind limbs have similar proportions. No wrist or ankle bones have been identified, suggesting that they may have remained unossified. The digits, however, are well developed with short, flat phalanges that give the hand and foot a paddle-like appearance, indicative of a predominately aquatic mode of life.

The Appearance of Highly Derived Tetrapods

After the first 75% of the Lower Carboniferous duration, eight clearly distinct lineages of much more highly derived vertebrates appeared in a period of only eight million years, prior to the beginning of the Upper Carboniferous. It is difficult to account for the relatively sudden appearance of so many highly divergent lineages over a relatively short period of time. Geological or climatic differences in the earth's environment either masked an earlier period of more modest change and radiation or opened up new environments and ways of life. In the later part of the Lower Carboniferous and throughout the Upper Carboniferous, eastern North American and western Europe were united into a single continent, Pangaea, that spanned the equator, resulting in a long-lasting, relatively uniform, tropical climate. Over hundreds of thousands of square kilometers, extensive lowlands and swamps provided a rich environment for both terrestrial and aquatic vertebrates that differentiated extensively in their anatomy and ways of life, as well as radiating geographically. The long-lasting wet and tropical environment also led to the growth and persistence of extensive forests, whose trees, ferns and other vegetation lead to the accumulation of huge amounts of plant material that eventually consolidated into the vast coal fields that continue to be mined in both North America and Europe. In contrast, land masses that were the antecedents of the current southern continents of South America, Africa, and Australia were located close to the South Pole, which was covered by an extensive ice sheet, and they have yielded almost no fossil tetrapods from this period of time.

Lepospondyls

Instead of a progressive appearance of successively more highly derived descendants of the few tetrapods (primarily whatcheeriids) from earlier in the Lower Carboniferous, a series of much more highly derived amphibians appeared suddenly in the latter half of the Viséan, most without any plausible antecedents or sister-taxa from the earlier Lower Carboniferous. The most distinctive was an assemblage termed the lepospondyls, which are distinguished from all labyrinthodonts in having holospondylous (spool-shaped), rather than multipartite, vertebrae and a snake-like body with little if any trace of limbs. Cranial features were also clearly distinctive, with the absence of the squamosal notch, labyrinthine infolding of the teeth, and loss of fangs on the lateral bones of the palate. Many had greatly reduced limbs or lost their limbs completely.

Aïstopods—The first and most extremely modified lepospondyls to appear in the fossil record were the aïstopods. The earliest known species, *Lethiscus stocki*, is based on a single specimen from the mid-Viséan Wardie Shales near Edinburgh (Wellstead, 1982). As preserved, the trunk region is 49 cm long, with a total of 78 vertebrae. The orbits are in the anterior third of the skull, behind which are very large temporal fenestrae. The parietals and very large postparietals are fused at the midline, except anterior to the pineal opening. As in all other members of this order, the intertemporal is absent, and there is no squamosal notch. A single, displaced centrum, shorter than any in the trunk region, may be from the tail. The hourglass-shaped, deeply amphicoelous trunk centra are fused seamlessly to the unpaired neural arches. The anterior trunk vertebrae bear transverse processes on the neural arches, rather than on the centra, as in later aïstopods. There are traces of the pectoral girdle, but no pelvis or limbs are preserved. *Lethiscus* and many other Carboniferous aïstopods are also unique from all other Paleozoic tetrapods in possessing specialized dorsal ossifications in the form of numerous tiny polygonal osteoderms. The aïstopod families Ophiderpetontidae and Phlegethontiidae (with up to 230 vertebrae) extended into the coal swamps of the Upper Pennsylvanian and Lower Permian of both Europe and North America.

ADELOSPONDYLI—The Adelospondyli span the boundary between the late Lower Carboniferous and the early Upper Carboniferous, a period of approximately 10 million years, but their known remains are limited to a small area near Edinburgh, Scotland. Four very similar genera have been named. *Palaeomolgophis* was collected from the Viséan Boxburn locality and an unnamed larval specimen from the lower Namurian of Loanhead (Andrews & Carroll, 1991). The orbits are far forward, as in aïstopods, but the skull lacks temporal openings. In contrast with other lepospondyls, a notch at the back of the cheek superficially resembles the squamosal notch of labyrinthodonts, except that it occurs within a single bone that was presumably formed by the fusion of several separate elements (supratemporal, intertemporal, tabular, and squamosal) in more primitive tetrapods. There is thus no line of mobility between the skull table and the cheek, as is evident in anthracosaurs. The palate is closed, and there is no evidence of palatal fangs. The marginal teeth are columnar, not pointed, but with the tips laterally compressed and hooked posteriorly. Surprisingly, the occipital surface had paired openings resembling the posttemporal fenestrae of some other early tetrapods, including microsaurs and temnospondyls, but there is no evidence as to whether these openings were homologous. In common with aïstopods, adelospondyls have long bodies with 50 to 70 trunk vertebrae. The cleithrum, clavicle, and interclavicle are well ossified, but there is no evidence of the endochondral bones of the pectoral and pelvic girdles, nor do they show limbs. Unlike the aïstopods, the neural arches are not fused to the long, cylindrical centra. This is presumably associated with an aquatic way of life, which is supported by the presence of lateral line canal grooves on the skull and massive hyoid elements, as well as the association of their remains with a diverse fish fauna.

ACHERONTISCUS—After a temporal hiatus, the lepospondyl record is continued by the occurrence of *Acherontiscus* (Carroll, 1969b), known from only a single specimen from the Namurian A of Scotland. In common with the aïstopods and adelospondyls, this genus has a long trunk region and no evidence of limbs, although it retains the dermal bones of the shoulder girdle. The orbits are small and positioned far anteriorly, as in *Adelospondylus*, but there is no temporal fenestra or squamosal notch. The posterior cheek teeth are widely expanded at the base.

Most significantly, *Acherontiscus* differs from all other "lepospondyls" in having two cylindrical vertebral elements for each segment of the trunk region posterior to the neck. These were presumably homologous with the pleurocentra and intercentra of labyrinthodonts, although their individual configuration differs. There are approximately 64 vertebrae in the specimen as preserved, with the caudal region beginning at about the 37th. Unlike aïstopods, the caudal vertebrae have haemal arches. The conspicuous lateral line canals on the skull and the presence of massive hyoid elements likely supported a permanently aquatic way of life. The Adelospondyli and *Acherontiscus* constitute isolated groups limited to Scotland, which have been associated with aïstopods based on little but their great elongation and absence of limbs, as well as the obvious distinction of their vertebral anatomy from that of any labyrinthodonts. Whether or not they belong to a single assemblage requires evidence of intermediate forms from earlier in the Carboniferous. Three other groups, the Microsauria, Nectridea, and Lysorophia, whose known fossil record is limited to the Upper Carboniferous and Lower Permian, have long been classified within the Subclass Lepospondyli on the basis of the similarity of vertebral structure, absence of labyrinthine enfolding of the teeth, reduction of the number of bones making up the skull roof, and absence of a squamosal notch. However, in contrast with aïstopods, adelospondyls, and *Acherontiscus*, all have well-developed, but in some genera, shortened, limbs.

MICROSAURIA—The earliest known and most diverse group is the Microsauria (Carroll & Gaskill, 1978), with 27 genera in 11 families. In common with other lepospondyls, all have cylindrical pleurocentra. Some retain crescentic intercentra. In the Pennsylvanian and Lower Permian, they evolved in a broad range of habitats, from perennibranchiate genera, somewhat resembling the living salamanders *Necturus* or *Cryptobranchus*, to agile lizard-like genera and a variety of large and small burrowing forms. None express the unique features that differentiate the nectrideans, aïstopods, lysorophids, or adelogyrinids, but together they express a higher degree of variability than labyrinthodonts; for example, the number of presacral vertebrae varies from 19 to 45 and the number of sacral vertebrae from 1 to 3. The tails may be long or short. Whereas at least some microsaurs have five digits on the rear limb, the forelimb is not known to have more than four. Within the Microsauria, two suborders are recognized, Tuditanomorpha, consisting of seven distinct families, and Microbrachomorpha, which includes only four. The lizard-like Tuditanomorpha were primarily terrestrial and showed well-developed limbs. These features have been used to support their relationships to reptiles, but this is refuted by many other characters (e.g., mode of articulation between occiput and first cervical vertebra, limiting movement of the skull to a primarily dorsoventral arc; reduction in the number of skull table bones; lack of transverse flange on pterygoid). Among Tuditanomorpha, the postfrontal and postorbital are of subequal size, and both are typically in contact with the large tabular. Microbrachomorpha were less uniform than tuditanomorphs in the pattern of the skull table. The parietal is substantially wider than the frontal, extending laterally to reach the postorbital, whereas the postfrontal may be reduced or lost. Microbrachomorpha were more highly adapted to an aquatic way of life, with smaller limbs and the manus having only three toes. No trunk intercentra are known.

The oldest known microsaurs are represented by eight specimens from a mudstone nodule collected from a limestone quarry in Goreville, Illinois, dated as Namurian A (Lombard & Bolt, 1999). From the same quarry have come a lungfish and an aquatic labyrinthodont. The skull surface lacks the conspicuous sculpturing of most labyrinthodonts and all traces of lateral line canals, suggesting a terrestrial way of life. The frontal appears to enter the margin of the orbit, but little else is known of the distribution of the skull table bones. The configuration of the occipital condyles and anterior surface of the atlas favor dorsoventral flexion of the skull on the trunk and greatly limit lateral bending or rotation, which is in common with other microsaurs but in strong contrast with labyrinthodonts and early amniotes, where there is some degree of bending or rotation in all directions. As in labyrinthodonts, the atlas arch bears prezygapophyses for paired proatlantes, but these are not known in later microsaurs. In common with microbrachomorphs, they have a fairly long trunk region, with 34 vertebrae and relatively short limbs, but the vertebrae have crescentic intercentra that resemble those of tuditanomorphs, as well a cylindrical pleurocentra. It is not yet possible to place these specimens with either tuditanomorphs or microbrachomorphs, but they are plausible antecedents of both. They certainly do not share any of the unique synapomorphies of other lepospondyls, nor can they be associated with whatcheeriids or later labyrinthodonts.

Microsaurs diversified throughout the Upper Carboniferous and Lower Permian in North America and Europe, but none have been described from later in the fossil record, and there is no evidence of their having given rise to any other tetrapod groups. All of the then known microsaur species were described in detail by Carroll and Gaskill (1978) and further discussed by Carroll (2009).

NECTRIDEANS—Nectrideans (Bossy & Milner, 1998) are among the most readily characterized of the small Paleozoic tetrapods. The primitive genera broadly resembled newts, with short bodies, small limbs, and a long, laterally compressed tail. Most appear habitually aquatic. The oldest known nectrideans, in the families Diplocaulidae and Urocordylidae, are known from the 314-million-year-old Jarrow locality in Ireland at the base of the Westphalian. These families were already well differentiated from one another, suggesting a considerable period of prior evolution. None have any obvious synapomorphies that would support a sister-group relationship with other lepospondyls, except for the presence of cylindrical pleurocentra fused to the neural arches and the loss of intercentra, which occur variably in that assemblage. The haemal arches are fused to the caudal centra. The presacral vertebral count for the order ranges from 19 to 26.

The primitive genus *Urocordylus* retains five toes in the manus with a phalangeal count of 2,3,4,3,2; later genera lose one toe. The tarsals are not ossified. The prefrontal extends into the margin of the external nares. There is no squamosal notch. Most nectrideans have interpterygoid vacuities, in common with temnospondyls and some microsaurs, as well as a movable basicranial articulation, in common with all early tetrapods. The occipital-cervical articulation is like that of other lepospondyls, permitting only dorsoventral hinging on the skull. The tabular is shorter than the medial edge of the postparietal but reaches the parietal laterally, distinguishing it from both anthracosaurs and other early labyrinthodonts. There is no intertemporal. *Diplocaulus*, known from the Lower and Upper Permian of North America, has a highly integrated skull, with the back of the cheeks extending beyond the outstretched forelimbs. It is a very flattened form, associated with aquatic adaptation, which is further supported by the presence of lateral line canal grooves. The jaw articulation is very far forward. The cheek and table are not firmly attached in more primitive genera, but they are in *Diplocaulus*. The last family to appear in the fossil record was the Scincosauridae, characterized by the genus *Scincosaurus* from the Westphalian D of Nýřany in the Czech Republic and in France. It seems the least specialized of the group, with a relatively small skull lacking the postparietal and supratemporal and well-developed limbs. The tail is long, but the neural and haemal arches were not expanded as in the other families, and the carpals and tarsals are ossified. These features suggest a terrestrial way of life. Its presence in the aquatic deposit of Nýřany may be attributed to breeding habits.

LYSOROPHIA—The latest lepospondyls to appear in the fossil record were the Lysorophia, known first from the Westphalian B of Newsham, England. They are not known later in Europe but were common in North American localities, including those of the Upper Carboniferous of Linton, Ohio; Mazon Creek, Illinois; and in the Lower Permian redbeds of Texas. Lysorophids were the last of the lepospondyls to appear in the fossil record. They resembled other lepospondyls in having greatly elongated bodies, with 69 to 97 presacral vertebrae (cylindrical pleurocentra but no intercentra; haemal arches present in the tail) and reduced limbs, but can be clearly distinguished from other orders by the configuration of the skull and the retention of paired neural arches, even in the most mature individuals. The skulls were highly fenestrate, and the jaw suspension was angled far forward, a unique feature relative to all other early amphibians. The presence of a well-developed hyoid apparatus suggests that they were gape and suck feeders. The clavicle and interclavicle were retained, but the pelvic elements were not co-ossified. The phalangeal counts of the manus and pes were 3,3,3,2 and 2,3,3,3,2. No dorsal or ventral scales are known.

SUMMARY OF LEPOSPONDYLS—The Aïstopoda, Adelospondyli, *Acherontiscus*, Microsauria, Nectridea, and Lysorophia show collectively the greatest amount of anatomical change between the Late Devonian and early Viséan tetrapods on one hand and late Westphalian tetrapods on the other. This is demonstrated by the very small number of shared derived characters in common between any of the lepospondyl orders, aside from the cylindrical configuration of the pleurocentra and the tendency for an elongate trunk and short limbs. The overall differences from the earlier Whatcheeriidae are even more striking, precluding any suggestion of ancestor-descendant relationships. In fact, there are few if any synapomorphies shared between these late-appearing families and any of the Lower Carboniferous and Upper Devonian genera that preceded them.

In contrast, the anatomy and presumably the ways of life of the individual species and genera within each of the families and orders are sufficiently similar that there have not been major changes in classification at this level over the last 20–30 years. Absence of knowledge of any plausible antecedents from the fossil record over a span of 25–45 million years, between the beginning of the Lower Carboniferous to the first appearance of the oldest known lysorophids, makes it nearly impossible to determine the specific sister-group relationships.

Labyrinthodonts

In marked contrast with the lepospondyls are five groups of labyrinthodonts known from the Upper Carboniferous, which can be compared with the Lower Carboniferous Whatcheeriidae and even the Upper Devonian genera. These groups retain a common suite of distinctive traits that can be traced back to the Upper Devonian and Lower Carboniferous, including labyrinthine infolding of the teeth, primitively much larger body size than lepospondyls, and complex, multipartite vertebrae consisting of separate neural arches, paired dorsal pleurocentra, and paired or median ventral intercentra. Most labyrinthodonts retain extensive rugose sculpturing of the skull and a fairly consistent number and pattern of dermal skull roof bones. These features have provided an effective means of recognizing or distinguishing members of the various clades and tracking their evolutionary sequences more effectively than is possible among the lepospondyls. The fact that labyrinthodonts are generally much larger also makes it easier to discover their fossils and to describe their skeletons, especially the skulls, in much greater detail.

COLOSTEIDAE—The Colosteidae are the first of the primarily Upper Carboniferous labyrinthodonts to appear in the fossil record. Their earliest record is from the freshwater Burdiehouse locality in the late Viséan of Scotland, represented by the ventral surface of a poorly preserved skull roof of *Pholidogaster*, known from more complete skeletons from later in the Carboniferous. Three other genera of colosteids are recognized (Bolt & Lombard, 2010): *Greererpeton,* from the Upper Mississippian of West Virginia and Illinois, *Deltaherpeton* from the Upper Mississippian of Iowa, and *Colosteus* from the Middle Pennsylvanian of Ohio. In Chapter 3, Clack et al. describe a new colosteid-like tetrapod from the St. Louis Limestone of Missouri that they indicate may be the oldest colosteid. Of these, *Greererpeton* is the best known, represented by 60 well-preserved, complete specimens, and best characterized of the family (Godfrey, 1989).

The skulls have a low profile, with the orbits becoming more anteriorly located within their evolutionary history. Well-developed lateral line canals indicated that they were primarily aquatic in habit, as supported by the coal swamp and lake deposits in which they have been discovered. In contrast with other labyrinthodonts, the squamosal notches occur in only the most immature specimens. A small intertemporal is retained in *Greererpeton*, but not in other genera. As in later temnospondyls, there are clearly defined interpterygoid vacuities and conspicuous fangs on the palatine, ectopterygoid, and vomer. However, they are distinguished from all later labyrinthodonts in having a greatly enlarged marginal tooth at the posterior end of the premaxilla that fits into a groove in the lateral surface of the dentary. An important feature that unites them with later labyrinthodonts, but clearly distinguishes them from lepospondyls, is the configuration of the back of the skull. In contrast with lepospondyls, the occipital surface of the skull is wide and typically low, with the cheeks extended laterally from the surface for articulation with the vertebral column. This is associated with a relatively narrow occipital condyle formed by the fused or tightly sutured basioccipital and exoccipital, which form the joint between the skull and the anterior elements of the atlas-axis complex. Instead of the unipartite atlas common to lepospondyls, the atlas-axis complex of labyrinthodonts consisted of a paired proatlas anteriorly, followed by a paired atlantal neural arch, supported by paired pleurocentra and medioventral, crescentic intercentra, providing flexibility between the skull and the neck. The shoulder girdle retains all the basic elements of earlier labyrinthodonts: the dermal cleithrum, clavicle, interclavicle, and endochondral scapulocoracoid of whatcheeriids and their late Devonian antecedents, going back to the ichthyostegids, in contrast with the great reduction or loss of these bones in lepospondyls. As in later labyrinthodonts, the trunk vertebrae consisted of paired, dorsal pleurocentra and crescentic ventral intercentra, but in contrast with most later temnospondyls, colosteids had a long trunk region, with up to 40 vertebrae, and small limbs. *Greererpeton* reached 1.4 meters in total body length. The humerus is small and incompletely ossified, resembling that of an isolated bone from the Horton Bluff locality (Carroll, 2009). The ilium differs from that of many other labyrinthodonts in the absence of a dorsally directed anterior process. The phalangeal formula of colosteids, like that of later temnospondyls, was 2,2,3,3 for the manus and 2,2,3,4,3+ in the pes.

Among later labyrinthodonts, the closest resemblance of colosteids is with the temnospondyls rather than the anthracosaurs (Clack, 2003; Ruta & Bolt, 2006) based primarily on primitive characters, including the general configuration of the skull roof and palate and more specifically the configuration of the vertebrae, with small paired pleurocentra dorsally and large ventrally crescentic intercentra. However, none of the known colosteids are plausible sister-taxa of specific later temnospondyls. This is emphasized by evidence of aquatic adaptation, indicated by elongation of the trunk, relative shortness of the limbs, presence of conspicuous lateral line canals, and incomplete ossification of the carpals and tarsals.

The small size and general configuration of an isolated humerus from the Lower Carboniferous Horton Bluff locality and those of the slightly later *Pederpes* (Clack & Finney, 2005) are similar to those of *Greererpeton*, suggesting a very early time of divergence from other labyrinthodonts.

TEMNOSPONDYLS—Temnospondyls are the most diverse and long-lived of all early amphibian groups, with 12 superfamilies and a record that extends into the Cretaceous. The Lower Carboniferous genus *Balenerpeton* from the Scottish locality of East Kirkton is the earliest documented member of this group. Temnospondyls superficially resemble colosteids and may share a common ancestor with them. The group as a whole exhibits multipartite vertebral centra: the pleurocentra are generally small, paired, and dorsal in position, whereas the intercentra remain median and crescentic, except among the derived stereospondyls of the Triassic. Extensive growth series, particularly common in several Upper Carboniferous coal swamp taxa, indicate consistent differences from lepospondyls, especially in the very slow vertebral central ossification. The very early ossification of fully cylindrical centra in lepospondyls is a fundamental difference between these two major Paleozoic groups.

The skull roof of temnospondyls can be readily distinguished from that of anthracosaurs in the separation of the tabular from the parietal by the supratemporal, and in the strong sutural attachment of the skull table and cheek. The sculpturing pattern is also more consistent than that of anthracosaurs in the relative uniformity of close-set pitting over the entire skull roof. Primitive temnospondyls retain an intertemporal, as in all anthracosaurs, but this bone is lost in most of the more derived taxa. The configuration of the ear region in several small terrestrial temnospondyls, including *Balanerpeton,* is very similar to that of modern anurans, suggesting that they had already evolved an impedance-matching middle ear. In the temnospondyl palate, large fangs are uniformly observed on the vomers, palatines, and ectopterygoids. In contrast, anthracosaurs tend to lose vomerine fangs as the snout becomes narrower. In all anthracosaurs, the pterygoids are close to the midline on either side of the cultriform process of the parasphenoid, but all known temnospondyls have conspicuous interpterygoid vacuities. Both groups initially had a mobile articulation between the braincase and the pterygoids (the basicranial articulation), but this area of articulation becomes fused in later temnospondyls. The dorsal process of the ilium is reduced or lost in temnospondyls but is retained in anthracosaurs. The number of phalanges shows the general pattern of colosteids, with a typical count of 2,3,3,3 (manus) and 2,3,3,3,3 (pes). Like anthracosaurs, many later temnospondyls became specialized toward an aquatic way of life, with greatly elongated skulls and retention of conspicuous lateral line canal systems in adults. Despite their anatomical differences, temnospondyls and anthracosaurs clearly show the greatest number of similarities among the major groups of early tetrapods.

BAPHETIDAE—The Baphetidae (formerly referred to as loxommatids because of the keyhole-shaped orbits) are represented by five genera from Europe and North America (Clack, 2001, 2003; Ruta, 2009). The oldest is from the same locality, Gilmerton, Scotland, as are the first known anthracosaur and the enigmatic tetrapod *Crassigyrinus*, near the end of the Lower Carboniferous. Most baphetids are known primarily by their skulls, but *Eucritta* from East Kirkton has contributed substantial data on the postcranial anatomy.

The large orbits of *Eucritta* lack the keyhole shape of other baphetids, perhaps as a result of immaturity, independently suggested by the lack of carpal and tarsal ossifications. The pes phalangeal count, 2,2,3,4,3,? suggests temnospondyl rather than anthracosaur affinities. As in early temnospondyls and anthracosaurs, but in contrast to lepospondyls, an intertemporal bone is retained and the tabular does not reach the parietal. There is also a conspicuous squamosal notch. The trunk is relatively short, with approximately 24 vertebrae.

ANTHRACOSAURIA—This is a diverse assemblage of superficially amniote-like early tetrapods. From their first appearance they document patterns in vertebral structure that distinguish them from nearly all previously described groups. In contrast with temnospondyls, anthracosaurs elaborated their pleurocentra at the expense of the intercentra. The primitively paired pleurocentra fused ventrally to form horseshoe-shaped structures that extended above the intercentra to help support the neural arches. The crescent-like intercentra remained small, for the most part, and ventrally located. In contrast with temnospondyls, the ilium retained both dorsal and posterior processes. The oldest known anthracosaur (suborder Embolomeri) is *Eoherpeton* from Gilmerton, near Edinburgh, very close to the end of the Mississippian, about 328 million years ago. In contrast with Upper Devonian amphibians, whatcheeriids, and temnospondyls, the posterolateral corner of the parietal contacted the tabular, eliminating the primitive sutural connection between the postparietal and supratemporal. This derived character is shared by all anthracosaurs. The intertemporal is primitively retained. In addition, the occipital lappet of the tabular increases in depth relative to the postparietal and articulates with the otic capsule. In contrast with most other labyrinthodonts, the skull table is not firmly attached to the cheek. A further distinction from temnospondyls is that anthracosaurs did not develop interpterygoid vacuities. They did retain fangs on the ectopterygoid and palatine, but these are lost from the vomers in most genera in relationship to the narrowing of the snout. Some large embolomeres replaced the vomerine fangs functionally by developing large marginal teeth at the front of the maxilla and the premaxilla. Two exceptions to the loss of vomerine fangs include the earliest known genus *Eoherpeton* and the Upper Permian *Chroniosaurus* (Klembara et al., 2010), a member of the enigmatic chroniosuchians. *Eoherpeton* also stands out from other early anthracosaurs in having larger limbs relative to the length of the trunk, suggesting a more terrestrial way of life. A closely related North American genus, *Proterogyrinus*, has 32 presacral vertebrae (Holmes, 1984).

Embolomeres were widespread in Europe and North America during the late Carboniferous and Permian. Two major adaptive groups were the large aquatic genera common during the Upper Carboniferous and Lower Permian—including *Anthracosaurus*, *Eogyrinus*, and *Palaeoherpeton* in Europe and *Archeria* in North America—and the more terrestrial, short-bodied Gephyrostegidae from North America and Europe. The terrestrial seymouriamorphs common in North America and Europe spread to Asia as well, continuing into the Upper Permian, but without giving rise to any known descendants.

CRASSIGYRINUS—The superficially anthracosaur-like *Crassigyrinus* stands alone anatomically. Its remains are known primarily from Great Britain, with less complete material from the Upper Carboniferous of North America, about five million years later than the British localities. The oldest known fossils of *Crassigyrinus* were collected from the Gilmerton Ironstone near Edinburgh dated from approximately 328-million-year-old deposits within the Brigantian, just prior to the end of the Viséan. This deposit also contained the earliest known anthracosaur, *Eoherpeton*, and the earliest known baphetid, *Loxomma*. The common occurrence of these three lineages in the same locality suggests an unusual environment of deposition and preservation not encountered earlier in the Carboniferous. This may explain why the earlier history of these taxa remains unknown. In addition to Gilmerton, *Crassigyrinus* also occurs in the Lower Namurian of the Dora opencast mine, Cowdenbeath, near Edinburgh, where Panchen (1985) collected new material that provided knowledge of almost the entire skeleton.

Crassigyrinus is so distinctive that it is the only recognized member of its own family. Size was its most conspicuous character, with a 30-cm-long skull capable of a wide gape and a trunk-tail complex in excess of 90 cm. Large fangs on its vomers, palatines, and ectopterygoids made *Crassigyrinus* one of the most ferocious freshwater predators of its time. However, *Crassigyrinus* appears very primitive for a labyrinthodont, with the vertebrae lacking postzygapophyses and pleurocentra having paired rather than fused neural arches. The intercentra are barely attached at the midline. *Crassigyrinus* also retained a sarcopterygian-like notochordal articulation between the vertebral column and the skull. The bones of the forelimb were so shortened that the humerus was initially identified as a stapes, whereas the rear limbs were somewhat larger for sculling. Many other elements of the postcranial skeleton have not been recognized, presumably because they remained cartilaginous to reduce their weight and thereby increase their buoyancy in the water. The scapulocoracoids, pubis, carpals, and tarsals remained unossified. Their huge orbits suggest the necessity of sight through deep, dark waters.

Classification of *Crassigyrinus* has been based primarily on the skull, which shows features common to early embolomeres, but many can also be traced to *Eusthenopteron* and *Panderichthys*, especially the comparable pattern of the dermal bones of the skull roof, with the tabulars being small and separated from the parietals by a large supratemporal. In addition, the squamosal notch was deep, and the cheek was mobile relative to the skull table. The anterior portion of the skull is also unique. The nares face dorsally as well as laterally, and there is a large median opening in the position of the internasal bone of baphetids, somewhat like the median antorbital area in *Acanthostega*. *Crassigyrinus* may share more similarities with primitive anthracosaurs such as *Eoherpeton* than with whatcheeriids, colosteids, baphetids, and primitive temnospondyls, but few if any are shared derived characters that support a sister-group relationship. Hence, it remains the only recognized representative of a family of its own.

No definitive temnospondyls or anthracosaurs are known prior to the Brigantian, but tantalizing individual limb bones resembling those of anthracosaurs and a lower jaw having derived characteristics of temnospondyls have been found in the lowermost Carboniferous of the Horton Bluff Formation in eastern Canada, suggesting a much earlier divergence (Carroll, 2009). An even earlier genus, *Tulerpeton*, from the Upper Devonian of Europe also shares characters with anthracosaurs. Unfortunately, none of these early remains provide evidence of specific synapomorphies that support affinities between Upper Devonian and late Lower Carboniferous temnospondyls and anthracosaurs, and no suggestions of lepospondyl characters.

Amniota

Earliest Definitive Amniotes—The earliest definitive remains of crown amniotes are from Joggins and Florence in Nova Scotia, Canada, and dated as Westphalian A and D. In both localities, the skeletons have been found in considerable number within the hollow, upright stumps of giant *Sigillaria* trees, into which they had either crawled or fallen (Carroll, 1964, 1969). Their fully terrestrial mode of life may explain their absence from any of the earlier European deposits that were dominated by fish and aquatic tetrapods. However, closely related amniotes were apparently capable of living in and around water bodies, as indicated from their articulated remains in the aquatic environments of Linton, Ohio; Mazon Creek, Illinois; and Nýřany, Czechoslovakia (Carroll, 2009). The Nova Scotia taxa can be unequivocally identified as early amniotes not only by the presence of a transverse flange of the pterygoid and canine teeth in the maxillae, but also by the absence of palatal fangs and labyrinthine infolding in their teeth. The structure of the occipital condyle and atlas-axis complex, the general configuration of the vertebral column, the phalangeal count of the manus and pes, and the basic configuration of the carpals and tarsals are of particular taxonomic significance, as they closely resemble those of Paleozoic embolomeres and living amniotes. The very elongate limbs (relative to trunk length) and the clawed digits suggest a habitually terrestrial way of life.

Possible Sister Taxa of Amniotes—Three genera from Europe and central Russia have been suggested as having amniote affinities. *Casineria kiddi,* from the Cheese Bay Shrimp Beds, middle upper Viséan, the coast of Scotland (Paton et al., 1999), consists of a nearly complete small skeleton measuring 80 mm from the neck to the base of the tail, but lacking the skull and most of the tail. It is the only known tetrapod from a deposit with a fauna otherwise consisting of excellently preserved shrimp, scorpions, and fish. The high degree of ossification of the limbs and girdles suggests that it was a fairly mature animal. The vertebral count is approximately 25, with a vertebral configuration similar to that of primitive anthracosaurs. The manus phalangeal count has been reconstructed as 2,3,4,5,4, comparable to embolomeres and early amniotes, with curved terminal elements, as in both anthracosaurs and amniotes, but certainly distinct from that of any temnospondyls or lepospondyls.

This phalangeal count is also roughly similar to that of *Tulerpeton* from the Upper Devonian of Central Russia (Lebedev & Coates, 1995) in which there are six digits in the manus with a count of 2,3,4,5,4,2, and a similar number in the pes. *Casineria* is the oldest known plausible antecedent of the amniotes, but the absence of the skull makes it impossible to make specific comparisons with the oldest adequately known specimens from Joggins.

Westlothiana, a further tantalizing specimen from the late Viséan of East Kirkton, is approximately eight million years younger than *Casineria* (Smithson, 1994). It is known from an almost complete skeleton, lacking only the end of the tail. The skull is somewhat flattened and there is apparently no squamosal notch, but most of the bones of the skull roof and palate can be recognized. The intertemporal, common to anthracosaurs, has been lost, as in all amniotes, as are the fang-like teeth on the marginal palatal bones, present in both anthracosaurs and temnospondyls. However, a transverse flange of the pterygoid and canine teeth, characteristic of all early amniotes, are not present. Individually, the vertebrae are almost identical to those of later amniotes, with the cylindrical pleurocentra solidly fused to the neural arches and the presence of short, crescentic intercentra. However, they number 36, much longer than any other early amniotes. This and the shortness of the limbs might be interpreted as adaptation to either an aquatic way of life or sinusoidal locomotion close to the ground, which are not expressed in any other known amniotes from the Carboniferous or early Permian. On the other hand, the configuration of the ilium is advanced over those of early anthracosaurs in the reduction of the anterior dorsal process. The humerus is almost identical to that of early amniotes and the phalangeal count is a reptilian 2,3,4,5,4. These amniote features, however, do not preclude *Westlothiana* from having diverged from an early member of a clade leading from ancestral anthracosaurs toward amniotes, but having become extinct without leaving descendants. Unfortunately, this cannot be demonstrated without the discovery of earlier intermediates in the fossil record.

Footprints

Falcon-Lang et al. (2007) described superficially amniote-like trackways from a horizon in New Brunswick, not far from Joggins, that they argued were about a million years older than the earliest known skeletal remains of amniotes. These relatively small footprints gave indication of a phalangeal count of 2,3,4,5,3 in the manus, and 2,3,4,5,4 in the pes. This, however, is also the phalangeal count of anthracosaurs, including the enigmatic *Westlothiana*. A later paper by Keighley et al. (2007) questioned both the dating of these trackways and their specific affinities with amniotes.

Tetrapod trackways from the Middle Devonian (Eifelian stage) of Poland, approximately 18 million years older than the earliest known skeletal remains of tetrapods (Niedźwiedzki et al., 2010), have been interpreted as having as many as seven digits and reconstructed as having a phalangeal count of approximately 2,3,3,3,?,2,2, roughly comparable with those of *Acanthostega* or *Ichthyostega*, but less than that in *Tulerpeton*. This, however, is based on footprint casts that are very difficult to interpret. In most cases, the linear series of "footprints" are more or less circular in outline and might have been made by the ends of fins. The ancestors of tetrapods may have diverged from sarcopterygians at such an early date, but these trackways do not provide sufficient evidence to establish the pattern of subsequent phylogenetic divergence.

Summary

Available knowledge of the fossil record of early tetrapods is shown in Figure 1. The illustrated durations of all the lineages are governed by the relative completeness of the fossil record, but the pattern and timing of their phylogenetic divergence remain unresolved. The poor record of the Lower Carboniferous and the difficulty in identifying shared derived features between groups make it arduous to infer early stages of evolution. The fossil record of both sarcopterygian fish and primitive tetrapods in the Upper Devonian does establish the probable sequence of origin of early land vertebrates, but various aspects of the anatomy of the best known Devonian taxa, *Ichthyostega* and *Acanthostega*, preclude establishing their immediate sister-group relationship with any of the later tetrapod groups. However, the later Devonian *Tulerpeton* does exhibit a phalangeal count that is a plausible antecedent to that of Carboniferous labyrinthodonts.

Formed about 12 million years after the beginning of the Lower Carboniferous, the Horton Bluff locality has yielded numerous disarticulated bones of early tetrapods, several of which resemble those of later labyrinthodonts. Several of these resemble those of the family Whatcheeriidae, known from three, more or less complete skeletons from later in the Lower Carboniferous. If one were to accept whatcheeriids as the only known labyrinthodonts from this time period, then they might be considered the sister-taxa of one or another of the two major groups of subsequent labyrinthodonts, the temnospondyls and anthracosaurs. In fact, they do not share any key derived characters of the later groups and are considered to have died without descendants (Clack & Finney, 2005).

Five major labyrinthodont groups—Colosteidae, Anthracosauria, Baphetidae, Crassigyrinidae, and Temnospondyli—all appeared suddenly, without known antecedents, within a period of about five million years near end of the Lower Carboniferous without obvious immediate ancestors or close sister-taxa. The fact that the oldest known members of four of these linages were collected from a single fossil locality in Great Britain strongly suggests that some significant changes had occurred in the climate or other aspects of the environment that enabled them to prosper in this area and time, but not in earlier Carboniferous beds.

Unquestioned amniotes are not known until about 314 million years ago. Their oldest known fossil remains consist of nearly complete skeletons that are clearly recognizable on the basis of numerous unique, derived characters shared with living lizards and other early reptilian-grade amniotes. Among other Carboniferous tetrapods, they share the greatest number of unique derived characters with anthracosaurs, specifically the nature of the vertebral column and the digital and phalangeal counts that clearly distinguish them from temnospondyls.

Unlike anthracosaurs, temnospondyls, and amniotes, the lepospondyls share no unique derived characters with early labyrinthodonts and have only rarely been grouped with them cladistically. They differ most strikingly in the nature of articulation between the occipital condyle and the first cervical vertebra, but also the early ossification of the entire column. Nearly all have a large number of trunk vertebrae, and the limbs are commonly short or may be missing entirely. No lepospondyls are known before late in the Lower Carboniferous, leaving a huge gap subsequent to the origin of the oldest known labyrinthodonts. The earliest known forms are the aïstopods, which were already among the most highly derived members of this group. There is little consistency in the phylogenetic arrangement of the lepospondyl groups seen in recent cladograms (Carroll, 2009). In common with advanced labyrinthodonts, there remains an enormous temporal gap in the fossil record prior to the appearance of the oldest lepospondyls. This must reflect the absence of any known deposits where they could have been preserved and recovered in any readily accessible areas of the Earth as we know it. No amount of phylogenetic analysis will resolve this problem.

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Chapter 3: A Colosteid-Like Early Tetrapod from the St. Louis Limestone (Early Carboniferous, Meramecian), St. Louis, Missouri, USA

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Abstract

We report the discovery of an early tetrapod skull from the St. Louis Limestone of Missouri, USA. It was found among a collection of coelacanths in the Museum für Naturkunde in Berlin, Germany, part of a larger collection donated to that institution by Jaekel containing other fish fossils from the same locality. The exact locality remains uncertain, but sedimentological analysis suggests that the specimens derive from the lower or middle part of the Upper St. Louis Limestone. The lithology is consistent with a deeper water marine setting, suggesting that the tetrapod specimen is an erratic. The skull is a natural mold exposed in palatal view, showing good detail of the bones preserved. Phylogenetic analysis shows it to be most closely related to colosteids, though retaining some plesiomorphic characters. Stratigraphic correlation shows that the St. Louis Limestone is older than the Verdi and Waugh Members of Iowa, here assigned to the Ste. Genevieve Formation, from which other colosteid specimens and *Whatcheeria* were found. The new specimen is thus both the earliest post-Devonian tetrapod from North America, and also the oldest colosteid-like tetrapod known.

Introduction

Between the end of the Devonian and the mid-Viséan, only a few localities have been known to yield fossils of tetrapods. This period of about 20 million years has been termed "'Romer's Gap' Gap" (Coates & Clack, 1995), but it is probably during this time that fully terrestrial tetrapods evolved. Therefore, the description of any tetrapods from this period is important: such remains should increase our knowledge both of the origin of major tetrapod clades and the acquisition of terrestriality.

The preponderance of Early Carboniferous localities from the Scottish Midland Valley (e.g., Smithson, 1985) may skew or bias the record, making those from other parts of the world of particular interest. They include a few records from North America (e.g., Thomson et al., 1998; Bolt & Lombard, 2000; Clack & Carroll, 2000; Anderson et al., 2009) and a single record from Australia (e.g., Thulborn et al., 1996; Warren & Turner, 2004; Warren, 2007). We describe here a small skull of a previously undescribed colosteid-like tetrapod from the St. Louis Limestone in St. Louis, Missouri. The St. Louis Formation is Meramecian (Early Carboniferous, mid-Viséan) in age. This formation underlies the upper "St. Louis" Formation of Iowa (actually the Ste. Genevieve Formation, as outlined below). Thus, the skull to be described here is the earliest Carboniferous tetrapod known from the United States and predates the fossils of Delta, Iowa (Bolt et al., 1988).

Materials and Methods

Specimen Preservation and Preparation

The specimen was discovered housed among a collection of fossil coelacanths in the Museum für Naturkunde in Berlin, Germany, under inventory number MB.f.17811 and labeled "Skull of a crossopterygian" (*Crossopterygier Schädel*), "St. Louis limestone, St. Louis, Missouri" (Figs. 1 and 2). According to the old label, the specimen originally belonged to the paleontological collection in Greifswald, Germany. Specimen MB.f.17811 is an incomplete skull that consists of a natural mold with no original bone preserved. It was brought to Berlin by Otto Jaekel at the beginning of the 20th century, with a few other fish specimens from the same locality, mainly chondrichthyan teeth and spines (e.g., *Helodus*, *Psammodus*, *Deltodus*, *Cladodus*, *Polyrhizodus*, *Ctenacanthus*). The old labels show that the tetrapod skull was found in the "upper Coal Measures" of the St. Louis Limestone. Subsequently, the specimen was transferred to the fossil amphibian collection of the Museum für Naturkunde Berlin and has the new inventory number MB.Am.1441.

The description of the specimen is based on a latex peel and a positive silicone cast produced in 2009 by the preparators of the Museum für Naturkunde Berlin. Thin sections and faunal identifications from other material of the Jaekel collection were made by DS using the following specimens: MB.f.9511 *Ctenacanthus dentatus*, *Spirifer* impressions from this

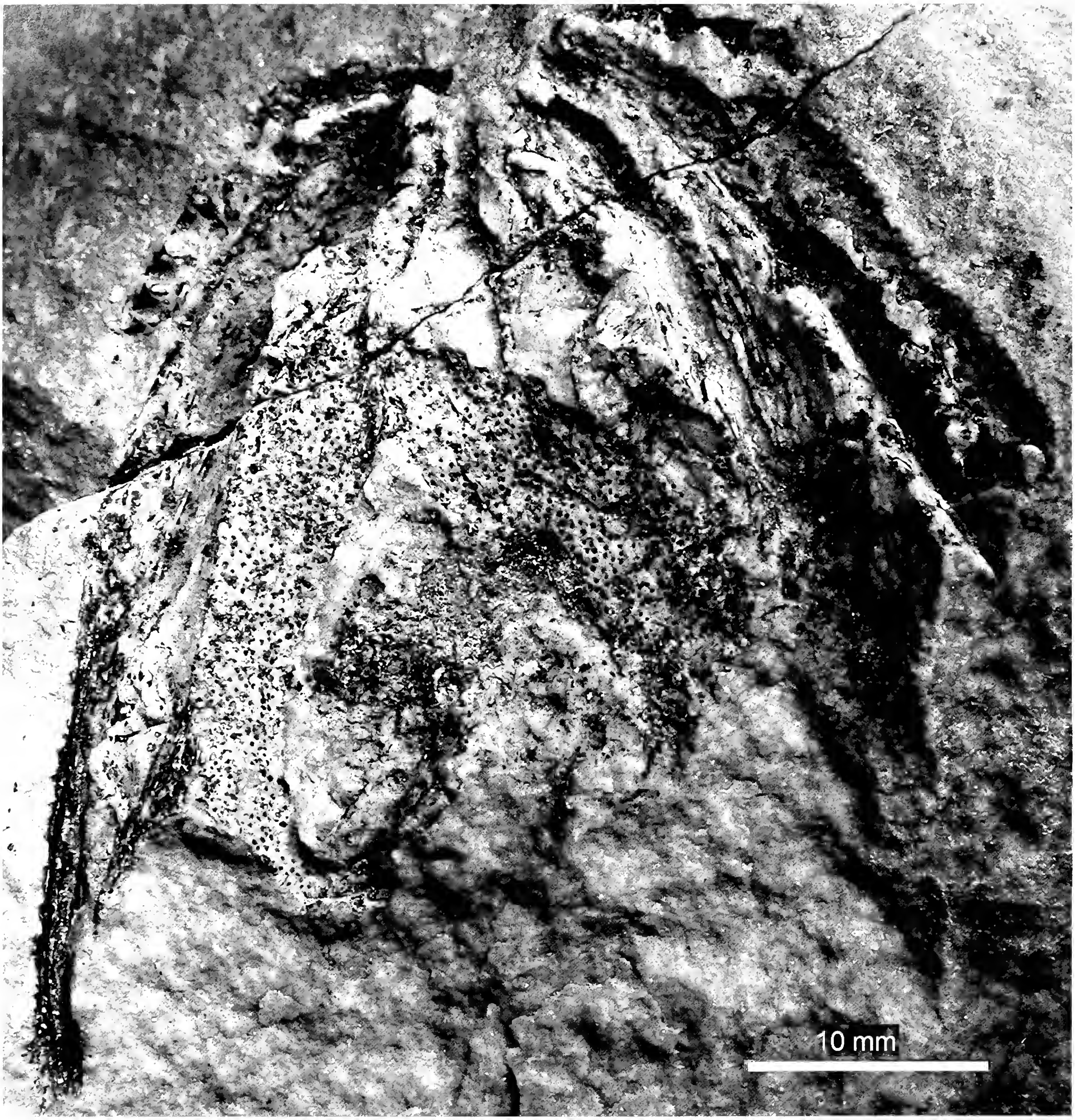

Fig. 1. MB.Am.1441. Photograph of the specimen.

specimen; MB.f.9227 a–c *Cladodus* sp/C. *ferox* [sic] tooth bases, thin sections from 9227a, *Spirifer* impressions from 9227b; MB.f.1168 *Cladacanthus* [sic], head spine, *Composita* from this specimen.

Geological Setting, Locality, and Age

Specimen MB.Am.1441 is from the upper St. Louis Limestone, but the exact locality from which it was collected cannot be determined. The St. Louis Limestone (Engelmann, 1847; Buckley & Buehler, 1904) is a marine limestone body exposed across much of the central United States, originally described from exposures along the Mississippi River (Figs. 3 and 4). The underlying boundary with the Salem Formation is gradational in the type area (Lasemi et al., 1999) but can be erosional elsewhere (Witzke & Bunker, 2005). The upper boundary with the Ste. Genevieve Formation is marked by the "Lost River" chert, a bed of dark blocky chert frequently associated with bryozoan-dominated facies and contemporaneous with an overturn in the conodont fauna (Elrod, 1899; Rexroad et al., 1990; Lasemi et al., 1999). The St. Louis Limestone itself is heterogeneous vertically as well as laterally,

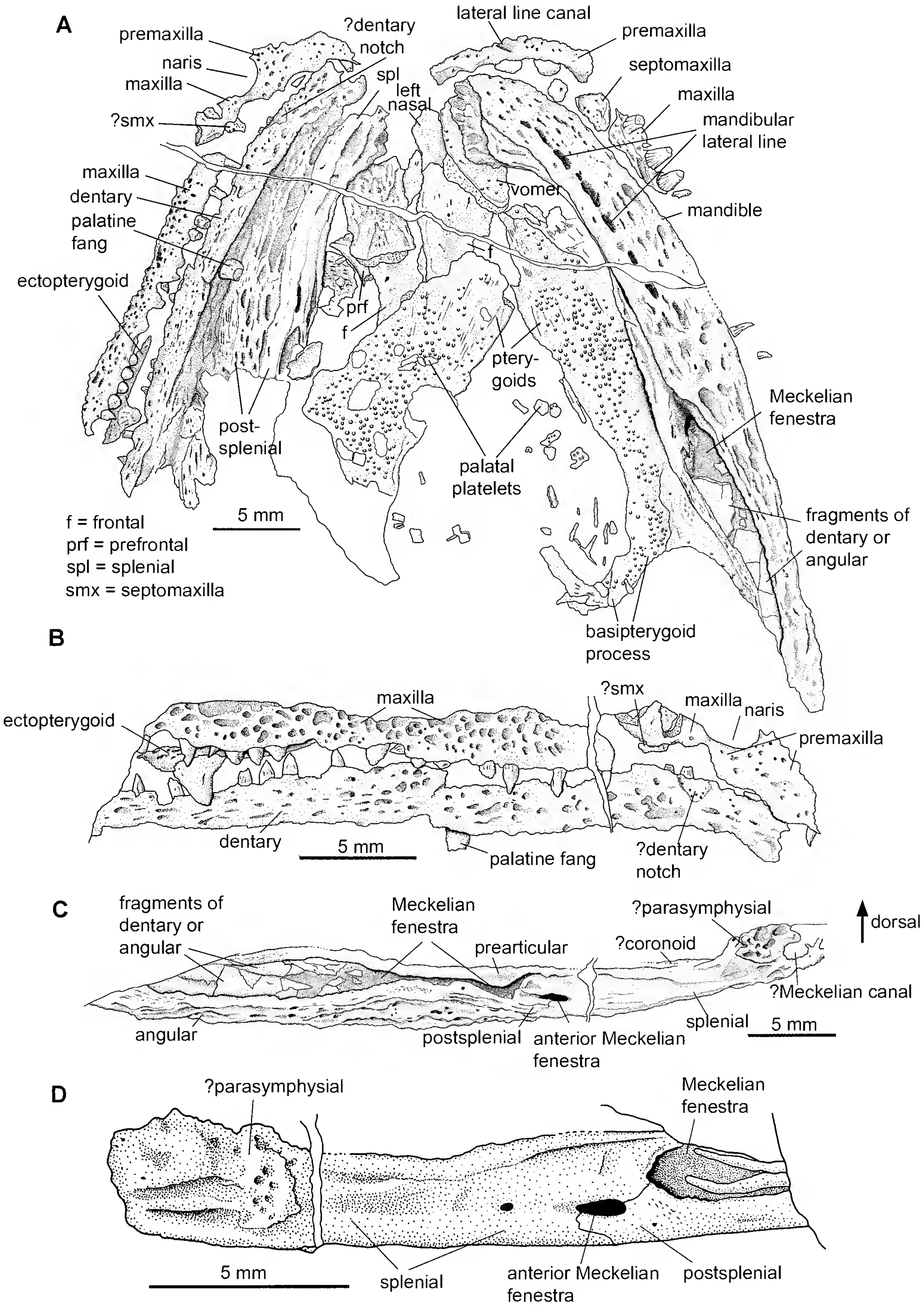

FIG. 2. MB.Am.1441. Interpretive drawings. (**A**) Drawing of the whole specimen. (**B**) Close-up drawing of the right premaxilla, maxilla, and dentary, showing the naris, possible dental notch, a palatine fang, and a partial ectopterygoid. (**C**) Close-up of the ventral view of the left lower jaw showing the Meckelian fenestrae. (**D**) Close-up of the right splenial showing possible parasymphysial brassicate structure.

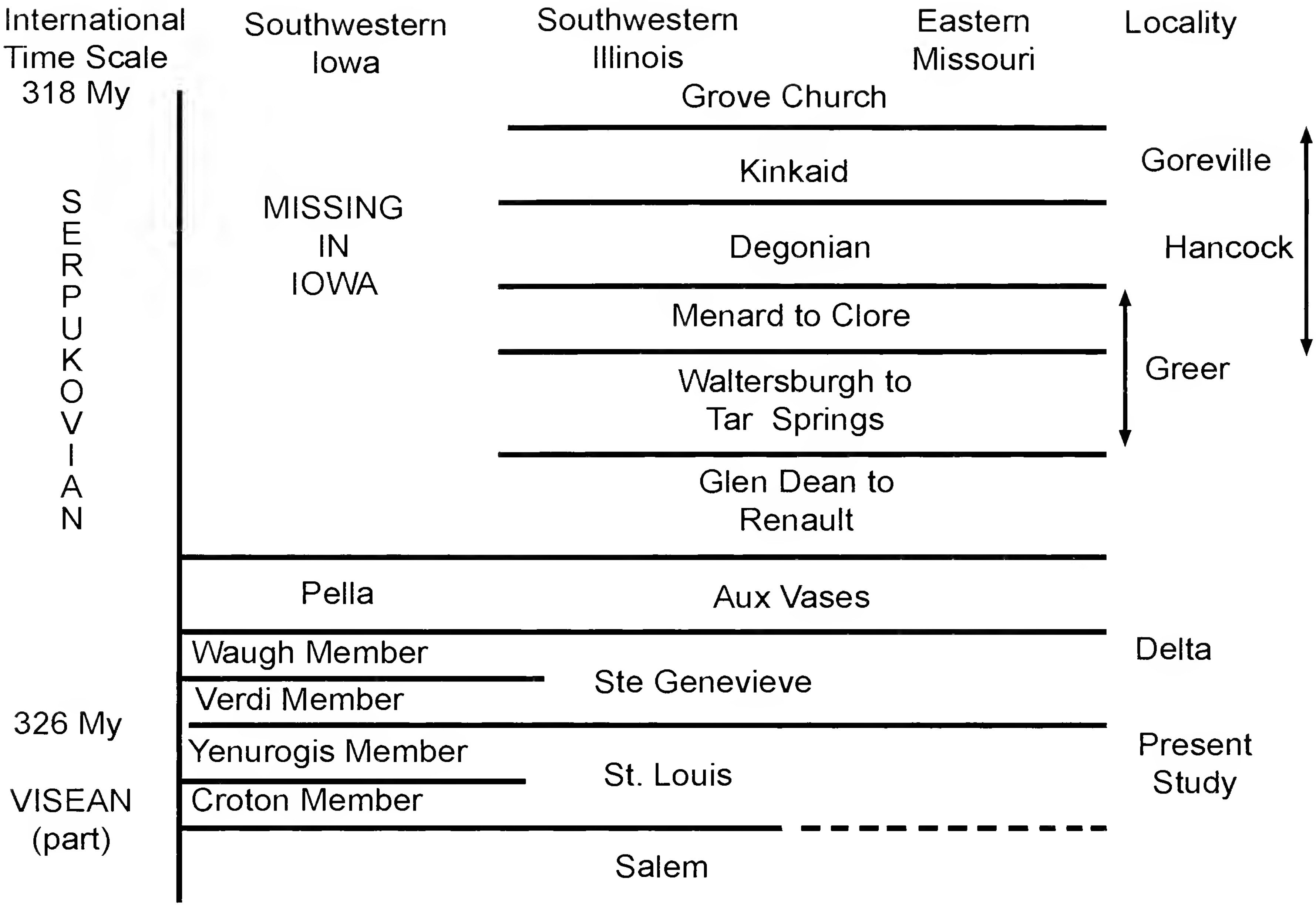

FIG. 3. Stratigraphic column of ages and formations discussed in this paper, with reference to other Mississippian tetrapod localities in the Midwestern United States, after Schultze and Bolt (1996). Absolute age dates from Gradstein et al. (2004). Stratigraphy from Parker (1973), Maples and Waters (1987), Smith and Read (1999), and Brenkle et al. (2005). Additional locality data from Bolt et al. (1988), Schultze and Bolt (1996), Chesnutt et al. (2002), and Maynard et al. (2006).

making lithologic and biostratigraphic inferences difficult (McKay et al., 1987; Lasemi et al., 1999). The diverse fauna includes echinoderms, bryozoans, brachiopods, and corals, found in strata throughout the St. Louis Limestone (Witzke et al., 1990; Lasemi et al., 1999; Brenckle et al., 2005). The foraminifera and conodonts have been studied in great detail (Lane & Brenckle, 2005, and references therein).

The St. Louis Limestone is often divided lithologically and paleontologically into upper and lower members (Weller & St. Clair, 1928; Pinsak, 1957; Lasemi et al., 1999; Witzke & Bunker, 2005). In the St. Louis metropolitan area, the sedimentology of the lower St. Louis Limestone is consistent with a nearshore, restricted circulation, and evaporitic marine environment of deposition (Brill et al., 1960; Lasemi et al., 1999; Brenckle et al., 2005). These include lime mudstone, wackestone, grainstone, and packstone; microcrystalline dolomite and collapsed evaporites; peloids, oncolites, and stromatolites; mudcracks and birdseye fenestrae; and bioturbation. The lower member also includes the coral *Acrocyathus floriformis* (Sando, 1983; Witzke et al., 1990; but see Weller, 1931; Fedorowski et al., 2007), which is thought to be a guide fossil for the St. Louis Limestone, and the first appearance of the foraminifer *Eostaffella* Rausen, 1948 (Brenckle et al., 2005).

The boundary between the lower and upper St. Louis Limestone is marked by "a light greenish gray, argillaceous limestone and/or shaley bed … at or just above [the boundary]" (Lasemi et al., 1999, p. 10). The transition to the upper St. Louis marks a significant faunal turnover. The conodont assemblage that characterized the Salem and lower St. Louis is replaced with a new assemblage that continues to the Ste. Genevieve boundary (Rexroad & Collinson, 1963; Norby &

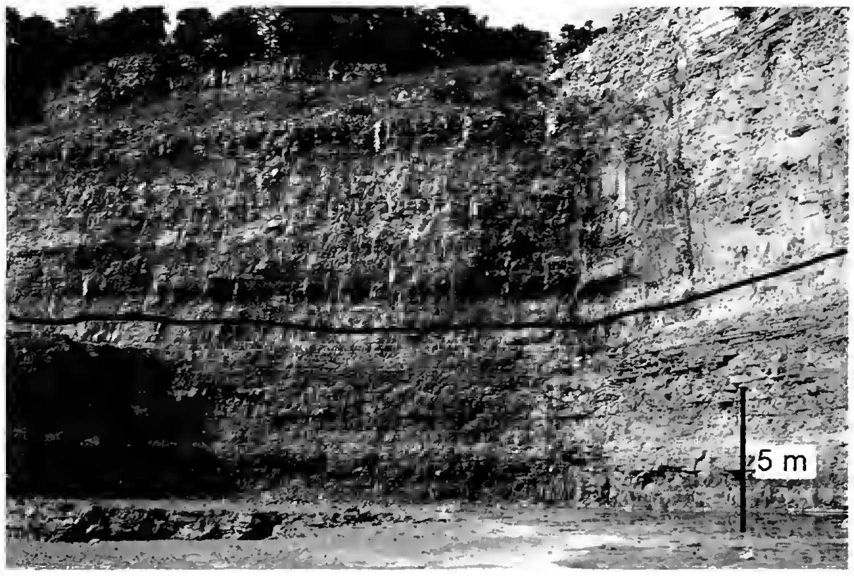

FIG. 4. Photograph of St. Louis Limestone as exposed in the Casper Stolle Quarry, southeast of St. Louis, in Dupo, Illinois. The black line indicates the contact between the Upper and Lower St. Louis Limestone, marked following Lasemi et al. (1999).

Lasemi, 1999). Encrusting foraminifera appear (Brenckle et al., 2005). Higher in the section, mudstone and dolomite are present, but the dominant lithologies are peloidal–bioclastic wackestone, packstone, and grainstone (Lasemi et al., 1999; Brenckle et al., 2005). Chert is present, and bryozoan macrofossils become dominant at the "Lost River" chert bed. These changes are consistent with a rise in sea level and the commencement of open marine circulation (Maples & Waters, 1987; Lasemi et al., 1999; Smith & Read, 1999).

Specimen MB.Am.1441 is preserved in a heterogeneous lime grainstone to packstone. The grains are very poorly sorted, ranging from submillimeter to centimeter scale. They are primarily bioclastic, as fragments of a diverse fauna are clearly preserved and dominant, whereas ooids are trace and lithics are essentially absent. There are significant numbers of mud peloids and intraclasts. Many grains are still intact, however a significant number have micritic envelopes. In addition, neomorphic spar is present throughout the grumous micrite, especially as growth across echinoderm fragments. Blocky void-filling calcite is found in the centers of some foram microfossils. It is not clear at present whether this calcite grew as a result of the neomorphism or at a different time.

This lithology is consistent with deposition in a deeper water marine setting, perhaps a short distance down the reef front. Mud and clasts were redeposited from shallower waters, likely in debris flows, though without more information on the bed structure, it is not possible to say for certain. The tetrapod represented in MB.Am.1441 may have died in the shallows or nearshore and then been re-deposited downslope, where diagenesis took place. The burial environment was deep enough to inhibit pore fluid flow that would have caused more widespread neomorphism. Consistent with this interpretation, we conclude that MB.Am.1441 is from the lower or middle part of the upper St. Louis Limestone.

Identified macrofauna includes isolated cladodont teeth, the distal tip of a spine of *Ctenacanthus denticulatus*, *Composita* species, and impressions of *Spirifer* brachiopod shells. The microfauna includes fragmentary brachiopods, bryozoans, echinoderms including crinoids, and rare trilobites and pelecypods. Conodonts have not been identified, but many calcareous microfossil taxa are present, including at least one species of *Eostaffella*. This is an important observation, as *Eostaffella* has not been found in either the Salem or Ste. Genevieve Formations.

Description

The preserved portion of the skull is approximately 40 mm in length, measured from the tip of the premaxillae to the posterior end of the preserved part of the left mandible. It has a blunt, parabolic outline and is visible in ventral view with the lower jaw preserved. The orbits are relatively anteriorly situated, so that the snout of the animal is rather short. The premaxillae and the right maxilla have been rotated outward from their life position, so that their sculptured external surfaces are visible. A small septomaxillary bone is present between premaxilla and maxilla. Of the remaining dermal skull roof, only parts of the ventral surface of the nasal, frontal, and prefrontal bones are visible; all other parts are obscured by palatal bones and the rami of the lower jaws or have been concealed by sediment. The preserved palatal elements consist of the pterygoids, the vomer, palatal platelets of the interpterygoid vacuities, and parts of the palatine and ectopterygoid.

Skull Roofing Bones

Premaxilla—Both left and right premaxillae are preserved. They are short and possess an irregular sculpture of small deep pits. The right premaxilla shows the anteroventral margin of the external naris, indicating that this opening was rounded and situated close to the jaw margin. In most early tetrapods, the junction between the premaxilla and maxilla is situated beneath the lower margin of the external naris, but a suture in this position is not visible in MB.Am.1441. It is not clear whether this is an artifact of preservation or represents an unusual condition in this specimen (Fig. 2B).

The posterior end of the right premaxilla is inturned and connected with the anterior part of the maxilla by a narrow strut. The contact between the left premaxilla and maxilla is not preserved. On the left premaxilla, a deeply incised groove runs in a ventral direction toward the jaw margin. It probably represents a part of the supraorbital line.

Maxilla—The maxilla is a long, slender bone that bears an irregular reticulate sculpture. It forms the posteroventral rim of the external naris. Similar to the posterior end of the premaxilla, the anterior end of the maxilla appears to be inturned, suggesting that it is unlikely that the two bones were joined by an interdigitating suture. The anterior portion of the left maxilla bears a longitudinal groove on its medial surface.

Septomaxilla—On the left side of the skull, an isolated trapezoidal bone is visible between premaxilla and maxilla. Its surface is slightly sculptured with a few small pits. From its position and size, it can be interpreted as a septomaxilla (Fig. 2B). A similar bone is present on the right side of the skull, also possibly a septomaxilla, but is largely obscured by the anterior portion of the maxilla.

Nasal, Frontal, and Prefrontal—The left nasal is partly visible in internal view, mainly posterior to but partly overlain by the right vomer. Posteriorly, the paired frontals are visible, though the posterior portions are obscured by the right pterygoid. The preserved parts of the frontals are distinctly longer than the nasal. They possess a smooth, slightly concave ventral surface, with a smooth, slightly concave ventral surface. The right prefrontal is partly visible in internal view, but its anteromedial portion is obscured by a quadrangular element that may be a displaced part of the right frontal (itself obscured by sediment) or an inverted right nasal, so that the anterior extent of the frontal is not obvious. Its medial margin is thickened. The posterior part of the frontal has broken off; the width of the prefrontal, however, suggests that it precluded the frontal from participation in the orbital margin and contacted the postfrontal posteriorly, a condition found in most primitive tetrapods.

Palatal Bones

Pterygoids—The pterygoids are the most conspicuous of the palatal bones preserved. They are densely covered by denticles and fine, radial striae on their ventral surface. The pterygoids form interpterygoid vacuities of moderate size. The vacuities taper anteriorly and have thus a teardrop-shaped or triangular appearance. It is possible that the pterygoids in MB.Am.1441 have been splayed apart, as the lower jaws were disarticulated: this might have exaggerated the width of the interpterygoid vacuities posteriorly. The broad palatal rami meet anteriorly, where they seem to wedge between the vomers. The outline of the narrow, medially directed denticulated part of the left basipterygoid process can be seen, but not the articular surface. Given its disarticulated condition, the process appears not to have been sutured to the basisphenoid. The quadrate ramus is not preserved. Small palatal platelets of irregular outline, some of which appear to bear denticles, are present in the interpterygoid vacuities and scattered on the ventral surface of the right pterygoid, as they are in some temnospondyls (e.g., *Platyrhinops*; Clack & Milner, 2010).

Vomer—The left vomer is a short element whose ventral surface is covered by denticles. It appears slender; however, its lateral extent cannot be determined. Vomerine fangs are not visible but might be obscured by the symphysial region of the left lower jaw ramus. The posterior margin of the vomer is aligned anteromedially, supporting the possibility that the pterygoid wedged between the paired vomers (see above).

Palatine and Ectopterygoid—Parts of the right palatine are visible in a slit between the dentary and the postsplenial of the right lower jaw ramus, from which the dentary has become detached (see below). Its length and outline cannot be determined, but a single fang is visible. Further palatine teeth are not preserved. A part of the right ectopterygoid, exposed between the maxilla and the dentary (Fig. 2B), bears a fang, but no other teeth are visible. The ectopterygoid appears to contribute to the margin of the adductor fossa.

Lower Jaw

The lower jaw rami are visible in ventral view. Because they are preserved three-dimensionally (albeit somewhat dorsoventrally compressed), their medial side can also be studied. Most parts of the left ramus are preserved, but the adductor fossa and the area of the glenoid are missing. In contrast, the right ramus is preserved posteriorly up to the anterior part of the large Meckelian fenestra (see below).

Lateral and Ventral View—The lateral and ventral parts of the lower jaw are distinctly sculptured by irregular ridges and furrows. These parts probably represent the dentary, the splenials, and the angular, but the sutures between these bones are difficult to follow. On the anterior part of the right dentary, approximately on the level of the naris, is a small recess that might represent a dental notch. If this interpretation is correct, then this notch is proportionally shallower and smaller than that described for *Greererpeton* (Smithson, 1982; Bolt & Lombard, 2001) and *Colosteus* (Hook, 1983). However, there seems to be no strong evidence of an enlarged premaxillary tooth to match it. The mandibular line (sulcus mandibularis) is present on the anterior part of the lower jaw, exposed on the ventral surface of the splenial and postsplenial. It does not consist of a continuous furrow, but of individual oval or oblong, moderately deep depressions, a condition similar to that in *Acanthostega* (Ahlberg & Clack, 1998) and colosteids (Smithson, 1982; Bolt & Lombard, 2001). The symphysis is formed by the dentary and the splenial, as exposed by the right lower jaw ramus in which the dentary is slightly dislocated and detached from the splenial.

Medial View—In the symphysial region, the mesial lamina of the splenial bears a rounded buttress dorsally. Anterodorsal to the buttress, a region of bone bears a highly sculptured surface bearing distinct projections and recesses. If it were a separate ossification distinct from the dentary and splenial, this bone might be interpreted as a parasymphysial plate (or adsymphysial of authors, e.g., Bolt & Lombard, 2001), which is common in tetrapodomorph fishes and early tetrapods (Ahlberg & Clack, 1998). The sculptured medial surface somewhat resembles the "brassicate" structure of the parasymphysial plate described in baphetids (Ahlberg & Clack, 1998) and *Greererpeton* (Bolt & Lombard, 2001) (Fig. 2D). Sutures with the splenial and the dentary are unfortunately not detectable.

Anteroventral to the possible parasymphysial plate, there is a hollow that might represent the Meckelian canal (Fig. 2C). Posterodorsal to the buttress of the splenial, a fragment of the first coronoid, bearing denticles, is visible. The remaining dorsomedial region of the ramus is not preserved. Posterior to the buttress, at the boundary between the splenial and postsplenial, both rami are pierced by a small anterior Meckelian foramen. In the right lower jaw ramus, an additional, small oval opening is situated on the splenial anterior to the anterior Meckelian foramen. On the left ramus, slightly posterior to the anterior Meckelian foramen, a long slit extends posteriorly, and after approximately 6 mm length, this slit widens into a large, long-oval fenestra, whose posterior end is not preserved. This opening is placed too far anterior and ventrad, and is too large, to be reasonably interpreted as the adductor fossa. The slit and the fenestra are interpreted here as a single, large Meckelian fenestra, whose anterior portion is crushed (Fig. 2C). The broken bone visible within the Meckelian fenestra might be the inner surface of the dentary or angular.

Dentition

The marginal teeth and fangs of the palate are of the "labyrinthodont" type. Tooth bases are ovoid in cross section, with the longitudinal axis oriented mesiodistally. There is no evidence of carinae or keels such as those present in baphetids. Only the bases of the premaxillary teeth are visible, and they seem to be distinctly larger than the maxillary teeth. There is space for five or six teeth on the premaxilla, but the number of maxillary teeth is uncertain. The preserved part of the right maxilla has spaces for about 21 or 22 teeth as a minimum number. We are unable to estimate the full length of the maxilla or its tooth row. Single, apparently unpaired fangs about the same size as the teeth on the premaxilla, are visible on the palatine and ectopterygoid. Although it is possible that more were present in the intact skull (Fig. 2B), the right ectopterygoid is preserved in such a way that additional teeth would very likely have been evident if present.

In the lower jaw, 10 or 11 partial teeth or tooth spaces can be made out on the right ramus, though the full complement was obviously higher. There is no clear discrepancy in tooth size between upper and lower jaw rami as there is in some early tetrapods such as *Ichthyostega* (Jarvik, 1996), colosteids (Smithson, 1982; Hook, 1983), or *Balanerpeton* (Milner & Sequeira, 1994).

Discussion

Tetrapod Assignment of MB.Am.1441

Although originally labeled a "crossopterygian," the skull MB.Am.1441 can unambiguously be assigned to a tetrapod for the following reasons. First, interpterygoid vacuities of this size and shape are unknown in any fish. Second, the postsplenial possesses a mesial lamina which is not present in tetrapodomorph fishes and the most primitive tetrapods (Ahlberg & Clack, 1998). Third, the external surface of the dermal bones of the lower jaw and the skull roof (at least premaxilla and maxilla) are distinctly sculptured by ridges, pits, and furrows. Godfrey (1989a, p. 127) considered dermal sculpture that "consists of deep polygonal pits or troughs surrounded by raised ridges" a tetrapod autapomorphy. Fourth, the lateral line (sulcus mandibularis) is not enclosed in bone but consists of a series of long oval depressions in the dermal bone sculpture. In the fish-like relatives of tetrapods, the lateral lines ran in true canals within the bone rather than in open sulci (Clack, 2002). Fifth, there is an elongate basipterygoid process of the pterygoid by which the palate would attach to the braincase. This is not seen in tetrapodomorph fish such as *Tiktaalik* (Downs et al., 2008).

Affinities of MB.Am.1441 to Major Tetrapod Clades

Because the skull is incompletely preserved, it is difficult to assess to which group of early tetrapods MB.Am.1441 belongs. It shows a number of plesiomorphies that could be expected in an early tetrapod: ventrally placed external naris, premaxilla and maxilla not firmly sutured, lateral line in separate short grooves rather than a single fully open one, a large Meckelian fenestra. The moderately sized, teardrop-shaped interpterygoid vacuities are striking, and preclude an assignment of this specimen to baphetids, in which these vacuities are absent (Beaumont, 1977; Clack, 1994), or to anthracosaurs (Holmes, 1984, 1989; Clack, 1987) and whatcheeriids (Clack & Finney, 2005), in which these vacuities are small and narrow. Similar interpterygoid vacuities to those in MB.Am.1441 occur in the basal temnospondyl *Edops* (Romer & Witter, 1942), colosteids (Smithson, 1982; Hook, 1983), *Caerorhachis* (Holmes & Carroll, 1977; Ruta et al., 2002), and even some nectrideans and microsaurs such as *Micraroter*, *Rhynchonkos*, *Microbrachis*, *Hyloplesion* (Carroll et al., 1998). However, microsaurs have jaws whose dermal bones are rarely sculptured and the dentary is generally smooth, and no palatine or ectopterygoid fangs have ever been described for nectrideans. Furthermore, labyrinthine infolding of teeth is not present in microsaurs and was only reported for one very large urocordylid specimen (Carroll et al., 1998). For these reasons, it is most probable that MB.Am.1441 represents either a colosteid or a basal temnospondyl.

Is the St. Louis Tetrapod MB.Am.1441 a Colosteid or a Temnospondyl?

The St. Louis tetrapod bears some colosteid-like characters, some of which are derived and others primitive for early tetrapods.

The following characters of MB.Am.1441 are derived and shared with colosteids:

(1) The orbits are positioned far forward in the skull, associated with short nasal bones and an apparently long postorbital region of the skull. This is especially similar to *Colosteus* (Hook, 1983). In basal temnospondyls, the postorbital region is proportionally shorter (e.g., Holmes et al., 1998), and this is the case even in *Balanerpeton* which has very short preorbital region (Milner & Sequeira, 1994).

(2) The brassicate splenial boss in the symphysis is described in *Greererpeton* (Bolt & Lombard, 2001), but is unknown in temnospondyls. It occurs also in baphetids (Ahlberg & Clack, 1998).

(3) The presence of a single, large, elongate Meckelian fenestra is regarded as a key feature for colosteids (Smithson, 1982; Bolt & Lombard 2010). This character has not been described in temnospondyls, but elongate Meckelian fenestrae also occur in some embolomeres (Clack, 1987; Holmes, 1984, 1989), in *Crassigyrinus* and *Gephyrostegus* (Ahlberg & Clack, 1998). It is not possible to say whether the fenestra in MB.Am.1441 was single or not: a second may have been present further posteriorly than the ramus is preserved.

(4) Supraorbital line deeply incised on premaxilla and directed towards the jaw margin, regarded by Bolt and Lombard (2010) as unique to colosteids. This character is shared with juvenile *Greererpeton* (Godfrey 1989b, fig. 4a) and with *Colosteus* (Hook 1983, fig. 1c). In basal temnospondyls, lateral lines are either absent (*Dendrerpeton*, *Balanerpeton*, Carboniferous edopoids), or if present, are not directed towards the jaw margin on the premaxilla.

(5) Possible presence of a weakly developed dental notch. A dental notch with premaxillary tusk is found in colosteids (Smithson, 1982; Bolt & Lombard 2010), though it is also present in *Erpetosaurus*, a trimerorhachid temnospondyl (Romer 1930). However, no premaxillary tusk is preserved in MB.Am.1441.

(6) The largest marginal teeth are present on the premaxilla and correspond in size to the palatine and ectopterygoid fangs. This somewhat resembles the condition in colosteids, in which some premaxillary teeth are developed as fangs and are of approximately the same size as the palatal fangs (Smithson, 1982; Hook, 1983). In basal temnospondyls, the premaxillary teeth do not reach the size of the palatine and ectopterygoid fangs (Romer & Witter, 1942; Holmes et al., 1998; Milner & Sequeira, 1994)

The following characters of MB.Am.1441 are primitive and shared with colosteids:

(1) The naris is located ventrally, and maxilla and premaxilla are not firmly sutured. This character was described for Devonian tetrapods (Säve-Söderbergh, 1932; Jarvik, 1952), whatcheeriids (Lombard & Bolt, 1995; Clack & Finney, 2005), embolomeres (Panchen, 1964, 1967) as well as colosteids (Schultze & Bolt, 1996, fig. 8b). This character is unknown in temnospondyls.

(2) The pterygoids are wedged between the small vomers. A similar condition was illustrated for *Colosteus* (Hook, 1983, fig. 1b) and *Greererpeton* (Smithson, 1982, fig. 11). In basal temnospondyls, the pterygoids do not form a wedge, or they do not contact the vomers (Romer & Witter, 1942; Holmes et al., 1998; Milner & Sequeira, 1994, 1998; Sequeira, 2005).

(3) Presence of a septomaxilla with fine external sculpture. The septomaxilla, as a dermal element bearing ornament, is present in a few primitive tetrapods, for example

in *Acanthostega* and *Ichthyostega*, where it is known as the anterior tectal (Jarvik, 1996; Clack, 2002), and in baphetids (Panchen, 1967; Beaumont, 1977). In temnospondyls, where it occurs, the septomaxilla is usually more internally placed (e.g., Panchen, 1967; Holmes et al., 1998; Schoch, 2001), although Langston (1953) described and illustrated ornamented septomaxillae in *Chenoprosopus*, an edopoid temnospondyl. Smithson (1982), Hook (1983) and Godfrey (1989b) did not detect a septomaxilla in the colosteids *Greererpeton* and *Colosteus*, respectively. In the colosteid *Pholidogaster*, however, Panchen (1975) described and illustrated a septomaxilla posteroventral to the naris. Its surface bears fine, irregular sculpture, and Panchen (1975) suspected a septomaxilla of similar type being present also in *Greererpeton*. Schultze and Bolt (1996, fig. 8b) figured a septomaxilla ventral to the naris in *Greererpeton* from Goreville but did not describe it. This septomaxilla apparently has an internal process, thus resembling the situation in temnospondyls. Bolt and Lombard (2010) concluded that no known specimen of a colosteid is sufficiently well preserved to confirm the presence or absence of a septomaxilla (their anterior tectal).

(4) The mandibular line consists of short sections. This character is known from Devonian tetrapods (Ahlberg & Clack, 1998) and colosteids (Bolt & Lombard, 2001), but not in basal temnospondyls, in which lateral lines are either lacking or more continuous.

The St. Louis tetrapod MB.Am.1441 shares the following characters with basal temnospondyls:

(1) Presence of possibly denticulate palatal platelets within the interpterygoid vacuities. This is a character of uncertain polarity. Denticulate or sculptured palatal platelets are known in a variety of temnospondyls (e.g., van Hoepen, 1915; Boy, 1988; Cox & Hutchinson, 1991; Milner & Sequeira, 1998; Witzmann, 2006; Witzmann & Schoch, 2006; Clack & Milner, 2010) and have not been described in other basal tetrapods. However, similar denticulate palatal plates ("upper oral dental plates") are present in the porolepiform *Glyptolepis groenlandica* (Jarvik, 1972, fig. 30). They are spread on the ventral side of the posterior part of the vomer, the ethmosphenoid, the parasphenoid, the entopterygoid and the anterior part of the roof of the pharynx. Given their appearance in such dispersed groups, the palatal plates are not a strong phylogenetic character.

(2) Except for the fangs on the palatine and ectopterygoid, additional smaller teeth are probably, but not certainly, absent in MB.Am.1441, similar to basal temnospondyls (Romer & Witter, 1942; Milner & Sequeira, 1994; Holmes et al., 1998; Sequeira, 2005) and baphetids (Beaumont, 1977). The presence of additional teeth on palatine and ectopterygoid is a primitive character in tetrapods (Jarvik, 1996; Clack, 1994) and occurs also in colosteids (Smithson, 1982; Hook, 1983).

Characters of the St. Louis tetrapod MB.Am.1441 that are consistent with both the colosteid and temnospondyl interpretations:

(1) The size and the teardrop-shape of the interpterygoid vacuities as preserved in MB.Am.1441 are consistent with the interpterygoid vacuities as reconstructed for *Colosteus* (Hook, 1983, fig. 1b) and *Edops* (Romer & Witter, 1942, fig. 3), but contrast with all other, more derived temnospondyls in which the vacuities are proportionally larger and more rounded. However, given the possible displacement of the pterygoids, the interpterygoid vacuities could have been more slender, similar to those of *Greererpeton* (Smithson, 1982, fig. 11), supporting the hypothesis of colosteid relationships.

(2) The basipterygoid process of the left pterygoid in MB.f.1441 closely resembles that of *Greererpeton* and *Colosteus* in size and shape, but similar to those of *Edops*, the processes were probably not sutured to the basisphenoid. They are shorter than that of more derived temnospondyls.

Phylogenetic Analysis

To test the hypotheses of colosteid or temnospondyl affinity of MB.Am1441, we ran a cladistic analysis using the dataset from Clack and Klembara (2009), which is based on Ruta and Clack (2006). In total, 35 taxa were entered in the data set. The following 4 new characters were added, which resulted in a total of 331 characters (278 of which being parsimony-informative): 328, preorbital region of skull longer than or equal in length to postorbital region (0), or postorbital region of skull longer than preorbital region (1); 329, brassicate splenial boss in symphysis of the lower jaw absent (0) or present (1); 330, supraorbital line on premaxilla runs parallel to the jaw margin (0), is directed towards the jaw margin (1), or supraorbital line is absent (2); 331, pterygoids not deeply wedged between vomers (0), or deeply wedged (more than half the length of the vomers) (1). For the character list and data matrix, see Appendices I and II.

The analysis was run with PAUP*4.0 (Swofford, 2003) using the heuristic search option (random stepwise addition, TBR branch swapping, multistate taxa treated as polymorphism) with all characters unordered. Ten most parsimonious trees were recovered (TL=1004, CI=0.3606, HI=0.6773, RI=0.5485, RC=0.1978) in which MB.Am.1441 always clusters as sister to a clade consisting of *Ptyonius* and *Adelogyrinus*/*Greererpeton* (Fig. 5). The grouping is supported by the following synapomorphies, present under both ACCTRAN and DELTRAN character optimization: 90, 1→0 Palatine without (0) or with (1) denticles; 93, 1→0 Ectopterygoid without (0) or with (1) denticles; 329, 0→1 brassicate splenial boss in symphysis of the lower jaw absent (0) or present (1); 331, 0→1 pterygoids not deeply wedged between vomers (0) or deeply wedged (more than half the length of the vomers) (1). Bootstrap support (1000 replicates), however, is low for this grouping (<50%) (Fig. 5).

Taxonomic Assignment of the St. Louis Tetrapod

Four derived characters are definitely present in MB.Am.1441 that are shared with colosteids: the position of the orbits, the brassicate splenial boss (also in baphetids), the large Meckelian fenestra (also in embolomeres, *Crassigyrinus* and *Gephyrostegus*), and the course of the supraorbital line on the premaxilla. One further derived character of colosteids that might be present in MB.Am.1441 is the dental notch. In addition, the size of premaxillary and palatal teeth of this

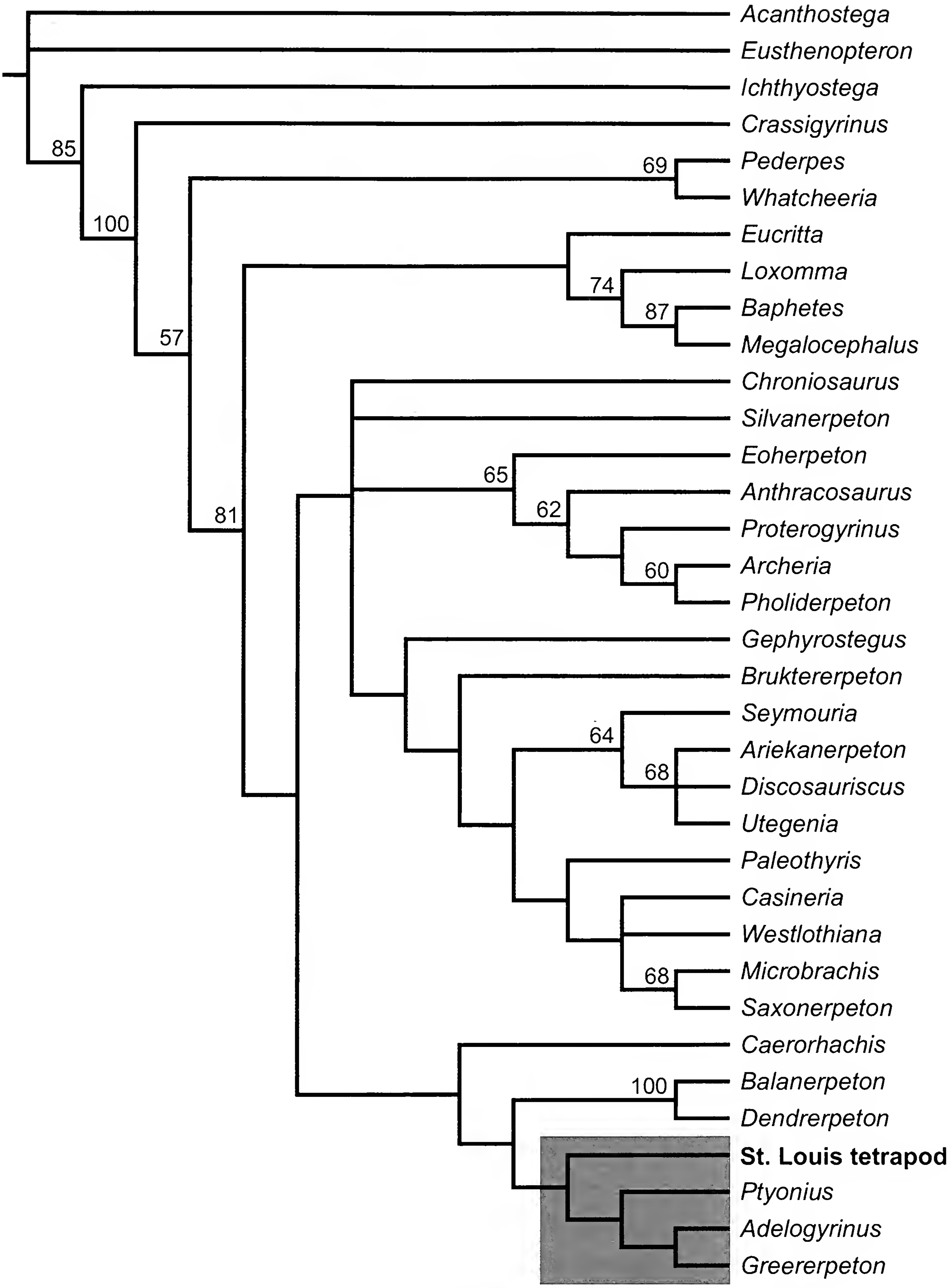

Fig. 5. Strict consensus of 10 most parsimonious trees showing the phylogenetic position of the St. Louis tetrapod within early terrestrial vertebrates. Bootstrap values >50% are indicated. For further details, see text.

specimen resembles the derived situation in colosteids, though not as strongly expressed. Further characters shared with colosteids, albeit plesiomorphic, are the ventrally located naris, the premaxilla and maxilla being not firmly sutured, the wedging of pterygoids into the vomers, the septomaxilla with fine external sculpture, and the mandibular line that consists of short sections. These characters are not reported in basal temnospondyls, with the exception of an ornamented septomaxilla in one temnospondyl, *Chenoprosopus* (Langston 1953).

The only derived character shared with basal temnospondyls is the probable lack of additional teeth on the palatine and ectopterygoid (also a feature of baphetids). The further characters shared with basal temnospondyls (and some other basal tetrapods) are either of ambiguous phylogenetic value (presence of palatal platelets), or they are likewise present in colosteids (teardrop-shaped interpterygoid vacuities, probably unsutured basipterygoid process). For this reason, it is most probable that MB.f.Am.1441 represents a relative of colosteids. Because the dermal skull roof, which bears many significant characters (Hook, 1983), and the postcranium are not preserved, we cautiously designate MB.Am.1441 as a "colosteid-like early tetrapod." This view is supported by the phylogenetic analysis performed on the basis of the data matrix of Ruta and Clack (2006). The St. Louis tetrapod clusters as the sister taxon to a *Ptyonius–Adelogyrinus–Greererpeton* clade, indicating closer affinities of the specimen to colosteids than to temnospondyls.

Colosteids were formerly regarded as basal temnospondyls (e.g., Smithson, 1982; Hook, 1983; Godfrey, 1989a,b) or as the sister group of temnospondyls (Carroll, 1995). In recent phylogenetic analyses (e.g., Ruta et al., 2003), however, colosteids appear as stem-tetrapods. The basal position of this specimen among colosteids is not only indicated by its early stratigraphic date, but also by the premaxillary teeth, whose size is not as pronounced as in other known colosteids, and by the possible dental notch, which is correspondingly shallow and small. The small size of its skull might suggest that MB.Am.1441 represents a juvenile, because colosteids generally have much larger skulls; however, there is insufficient information to compare it to the sequence of size and ossification changes documented in colosteid ontogeny by Godfrey (1989b).

The Relative Ages of Colosteids and Other Tetrapods in the United States

Colosteids have been found in North America, Ireland, and Scotland. The oldest material attributed to the group, represented by small fragments from the mid-Viséan of Australia (Thulborn et al., 1996), now appear to pertain to a whatcheeriid, *Ossinodus pueri* (Warren & Turner, 2004; Warren, 2007). Colosteids are definitely known from the mid-Viséan Burdiehouse Limestone in Scotland, in which remains of *Pholidogaster* were found (Panchen, 1970, 1975). The geologically youngest known colosteid is *Colosteus* from the "uppermost Westphalian D" (Moscovian) Freeport Coal of Ohio (Hook, 1983).

In North America, several Mississippian colosteid localities are known. Among the oldest colosteids of North America are specimens reported by Bolt et al. (1988) and Bolt and Lombard (2001, 2010) from the site in Delta, Iowa. Further Mississippian colosteid remains are known from the Mauch Chunk Group at Greer, West Virginia, which is uppermost Viséan and Serpukhovian in age (327–316 Ma; Maynard et al., 2006; Fillmore et al., 2010). *Greererpeton* remains from Goreville, Illinois, cannot be assigned to the Mauch Chunk Group and are of slightly later age (Schultze & Bolt, 1996). Garcia et al. (2006) reported colosteid remains in the Mississippian (Chesterian) Buffalo Wallow Formation, Hancock County, Kentucky.

Specimen MB.Am.1441 is slightly older than the tetrapod remains reported from the Jasper Hiemstra Quarry (a.k.a. the "Pink Floyd Quarry") at Delta, Iowa (Fig. 3). Recent research has shown that the Upper St. Louis Formation of Missouri is stratigraphically below the Upper "St. Louis" Formation of Iowa (Witzke & Bunker, 2005; see also the review in Anderson & Langel, 2004). The Croton of Iowa's Lower "St. Louis" Formation has been correlated with St. Louis Limestone beds in Missouri and Illinois by three criteria: the brecciated facies, the lower massive carbonate facies, and the coral *Acrocyathus* (Maples & Waters, 1987; Witzke et al., 1990). Witzke et al. (1990) suggested that the Croton and the overlying Yenruogis Member represent a single depositional sequence. The Croton Member was deposited in the main marine transgression, whereas the Yenruogis Member is the highstand and regressive sequence (sensu Catuneanu et al., 2009). This correlates with the eustacy curve of Ross and Ross (1987), where the St. Louis Formation in the Illinois Basin is a single system. The differences in lithology between the Croton, Yenruogis, and St. Louis sensu stricto (Parker, 1973; Witzke et al., 1990) could be explained by the up-sequence position of the former two bodies, closer to a sediment source (Witzke & Bunker, 2005).

As the Verdi and Waugh Members of the "St. Louis" Formation of Iowa (Fig. 3) preserve the sediments of the Delta, Iowa, fossil site (Bolt et al., 1988; Schultze & Bolt, 1996), their age is of great interest to paleobiologists. Like the Croton and Yenruogis, the Verdi and Waugh Members go through facies changes consistent with a single transgressive/regressive cycle. The Verdi is a marine limestone that becomes nearshore up-section, and the overlying Waugh is brackish/freshwater sediments capped by paleosols (D. Snyder and B. J. Witzke, pers. observ.). It follows that Verdi and Waugh Members' sediments can be matched with the first transgressive/regressive cycle of the Ste. Genevieve Formation of Missouri (Smith & Read, 1999).

The absence of the Lost River chert in southeastern Iowa, the sea level curve, and the ecological turnover at the St. Louis/Ste. Genevieve boundary may be explained by the same mechanism. It has been hypothesized that nodular cherts can form during marine regression (Knauth, 1994). The Illinois Basin seaway's withdrawal was simultaneously exposing Iowa and changing habitats. Organisms that could not adapt went extinct at the boundary, leading to the observed faunal turnover (Maples & Waters, 1987). The source of silica for the chert and the paleohydrology of southeastern Iowa remain unknown.

As a consequence of this stratigraphic reassignment, MB.Am.1441 is the oldest known post-Devonian tetrapod in the United States, and if our interpretation as a basal colosteid is correct, it is ranked as the earliest known colosteid.

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Appendix I: Character List

1. Absence (0) or presence (1) of alary process. PREMAX 1.
2. Alary process less than (0) or at least one-third as wide as premaxillae (1). PREMAX 3.
3. Premaxillae more (0) or less than (1) two-thirds as wide as skull. PREMAX 7.
4. Absence (0) or presence (1) of shelf-like premaxilla–maxilla contact mesial to tooth row on palate. PREMAX 9.
5. Presence (0) or absence (1) of anterior tectal. TEC 1.
6. Presence (0) or absence (1) of lateral rostral. LAT ROS 1.
7. Absence (0) or presence (1) of septomaxilla. SPTMAX 1.
8. Septomaxilla not a detached ossification inside nostril (0); detached (1). SPTMAX 2.
9. Absence (0) or presence (1) of paired dorsal nasals. NAS 1.
10. Nasals more (0) or less than (1) one-third as long as frontals. NAS 2.
11. Absence (0) or presence (1) of condition: nasals' broad plates delimiting most of nostril posterodorsal and mesial margins, with lateral margins diverging abruptly anteriorly. NAS 5.
12. Parietal-nasal length ratio less than (0) or greater than 1.45 (1). NAS 6.
13. Prefrontal less than (0) or more than (1) three times longer than wide. PREFRO 2.
14. Prefrontal not sutured with premaxilla (0) or sutured (1). PREFRO 6.
15. Prefrontal without (0) or with (1) stout, lateral outgrowth. PREFRO 7.
16. Absence (0) or presence (1) of condition: prefrontal entering nostril margin. PREFRO 8.
17. Prefrontal not sutured with maxilla (0) or sutured (1). PREFRO 9.
18. Lacrimal without (0) or with (1) dorsomesial digitiform process. LAC 4.
19. Lacrimal without (0) or with (1) V-shaped emargination along posterior margin. LAC 5.
20. Absence (0) or presence (1) of condition: portion of lacrimal lying anteroventral to orbit abbreviated. LAC 6.
21. Total length of lacrimal less than (0) or more than (1) two and a quarter times its maximum preorbital depth. LAC 7.
22. Maxilla extending behind level of posterior margin of orbit (0); terminating anterior to it (1). MAX 3.
23. Maxilla not entering (0) or entering (1) orbit margin. MAX 5.
24. Frontal unpaired (0) or paired (1). FRO 1.
25. Frontal shorter than (0), longer than (1), or subequal to (2) parietals. FRO 2.
26. Absence (0) or presence (1) of condition: anterior margin of frontals deeply wedged between posterolateral margins of nasals. FRO 6.
27. Absence (0) or presence (1) of parietal-tabular suture. PAR 1.
28. Absence (0) or presence (1) of parietal-postorbital suture. PAR 2.
29. Anterior margin of parietal lying in front of (0), level with (1), or behind (2) orbit midlength. PAR 4.
30. Anteriormost third of parietals not wider than frontals (0); at least marginally wider (1). PAR 5.
31. Parietals more than two and a half times as long as wide (0) or less (1). PAR 6.
32. Parietal-frontal suture not strongly interdigitating (0); strongly interdigitating (1). PAR 8.
33. Parietal–postparietal suture not strongly interdigitating (0); strongly interdigitating (1). PAR 9.
34. Postparietals paired (0) or unpaired (1). POSPAR 2.
35. Postparietal less than (0) or more than (1) four times wider than long. POSPAR 3.
36. Postparietals without (0) or with (1) median lappets. POSPAR 4.
37. Absence (0) or presence (1) of postparietal–exoccipital suture. POSPAR 5.
38. Nasals not smaller than postparietals (0) or smaller (1). POSPAR 10
39. Postfrontal not contacting tabular (0) or contacting it (1). POSFRO 3.
40. Absence (0) or presence (1) of condition: posterior margin of postfrontal lying flush with posterior jugal margin. POSFRO 4.
41. Intertemporal present (0) or absent (1) as a separate ossification. INTEMP 1.
42. Intertemporal not interdigitating with cheek (0) or interdigitating (1). INTEMP 2.

43. Intertemporal not contacting squamosal (0) or contacting it (1). INTEMP 3.
44. Absence (0) or presence (1) of condition: intertemporal shaped like a small, subquadrangular bone, less than half as broad as the supratemporal. INTEMP 4.
45. Presence (0) or absence (1) of supratemporal. SUTEMP 1.
46. Absence (0) or presence (1) of condition: supratemporal forming anterior edge of temporal notch. SUTEMP 2.
47. Absence (0) or presence (1) of condition: supratemporal narrow and strap-like, at least three times as long as wide. SUTEMP 3.
48. Supratemporal contact with squamosal smooth (0) or interdigitating (1). SUTEMP 4.
49. Tabular present (0) or absent (1) as separate ossification. TAB 1.
50. Absence (0) or presence (1) of rounded, subdermal, button-like posterior process of tabular. TAB 3.
51. Tabular contacts squamosal on dorsal surface of skull table (0) or not (1). TAB 4.
52. Tabular contact with squamosal smooth (0) or interdigitating (1). TAB 5.
53. Parietal–parietal width smaller than (0) or greater than (1) distance between posterior margin of skull table and posterior margin of orbits measured along the skull midline. TAB 7.
54. Postorbital without (0) or with (1) ventrolateral digitiform process fitting into deep vertical jugal groove. POSORB 2.
55. Postorbital contributing to (0) or excluded from (1) margin of orbit. POSORB 3.
56. Postorbital irregularly polygonal (0) or broadly crescentic and narrowing to a posterior point (1). POSORB 4.
57. Postorbital not contacting tabular (0) or contacting it (1). POSORB 5.
58. Postorbital not wider than orbit (0) or wider (1). POSORB 6.
59. Absence (0) or presence (1) of condition: postorbital at least one-fourth the width of the skull table at the same transverse level. POSORB 7.
60. Anteriormost part of dorsal margin of postorbital with sigmoid profile absent (0) or present (1). POSORB 8.
61. Anterior part of squamosal lying behind (0) or in front (1) of parietal midlength. SQU 1.
62. Squamosal without (0) or with (1) broad, concave semicircular embayment. SQU 3.
63. Absence (0) or presence (1) of "squamosotabular" in place of squamosal and tabular. SQU 4.
64. Jugal not contributing (0) or contributing (1) to ventral margin of skull roof. JUG 2.
65. Jugal not contacting (0) or contacting (1) pterygoid. JUG 3.
66. Jugal depth below orbit greater (0) or smaller (1) than half orbit diameter. JUG 4.
67. Jugal without (0) or with (1) V-shaped indentation of dorsal margin. JUG 7.
68. Jugal not extending (0) or extending (1) anterior to anterior orbit margin. JUG 8.
69. Absence (0) or presence (1) of condition: quadratojugal much smaller than squamosal. QUAJUG 2
70. Absence (0) or presence (1) of condition: quadratojugal an anteroposteriorly elongate and dorsoventrally narrow splinter of bone. QUAJUG 3.
71. Quadrate without (0) or with (1) dorsal process. QUA 1.
72. Absence (1) or presence (0) of preopercular. PREOPE 1.
73. Absence (0) or presence (1) of internarial fenestra. INT FEN 1.
74. Interorbital distance greater than (0), smaller than (1), or subequal to (2) half skull table width. ORB 1.
75. Interorbital distance greater than (0), smaller than (1), or subequal to (2) maximum orbit diameter. ORB 2.
76. Absence (0) or presence (1) of angle at anteroventral orbit corner. ORB 3.
77. Absence (0) or presence (1) of condition: in lateral view, orbit deeper than long. ORB 4.
78. Position of pineal foramen behind (0), at the level of (1), or anterior to (2) interparietal suture midlength. PIN FOR 2.
79. Fossa at dorsolateral corner of occiput, not bordered laterally, roofed over by skull table and floored by dorsolateral extension of opisthotic (0); fossa near dorsolateral corner of occiput, roofed over by occipital flanges of tabular and postparietal and bordered laterally and ventrally by dorsolateral extension of opisthotic meeting ventromedial flange of tabular (1); small fossa near ventrolateral corner of occiput bordered laterally by ventromedial flange of tabular, roofed over by dorsal portion of lateral margin of supraoccipital–opisthotic complex and floored by lateral extension of opisthotic (2); absence of fossa (3). PTF 1.
80. Absence (0) or presence (1) of abbreviated skull roof postorbital region. SKU TAB 1
81. Lateral line system on skull roof totally enclosed (0), mostly enclosed with short sections in grooves (1), mostly in grooves with short sections enclosed (2), entirely in grooves (3), absent (4). SC 1.
82. Mandibular canal totally enclosed (0), mostly enclosed, short sections in grooves (1), mostly in grooves, short sections enclosed (2), entirely in grooves (3), absent (4). SC 2.
83. Absence (0) or presence (1) of condition: ventral, exposed surface of vomers (i.e., excluding areas of overlap with surrounding bones) narrow, elongate, and strip-like, without extensions anterolateral or posterolateral to choana and two and a half to three times longer than wide. VOM 1.
84. Vomer without (0) or with (1) denticles. VOM 4.
85. Vomer excluded from (0) or contributing to (1) interpterygoid vacuities. VOM 5.
86. Vomer not forming (0) or forming (1) suture with maxilla anterior to choana. VOM 7.
87. Vomer with (0) or without (1) toothed lateral crest. VOM 8.
88. Vomer with (0) or without (1) anterior crest. VOM 9.
89. Palatine with (0) or without (1) fangs. PAL 1.
90. Palatine without (0) or with (1) denticles. PAL 2.
91. Palatine with (0) or without (1) tooth row (3 or more teeth). PAL 4.
92. Ectopterygoid with (0) or without (1) fangs. ECT 2.
93. Ectopterygoid without (0) or with (1) denticles. ECT 3.
94. Ectopterygoid longer than/as long as palatines (0) or not (1). ECT 4.
95. Ectopterygoid with (0) or without (1) tooth row (3 or more teeth). ECT 5.
96. Absence (0) or presence (1) of pterygoid flange oriented transversely. PTE 3.

97. Pterygoid without (0) or with (1) posterolateral flange. PTE 9.
98. Pterygoids not sutured with each other (0) or sutured (1). PTE 10.
99. Pterygoid without (0) or with (1) distinct, mesially directed process for the basipterygoid recess. PTE 13.
100. Palatal ramus of pterygoid without (0) or with (1) distinct, anterior, unornamented digitiform process. PTE 16.
101. Presence (0) or absence (1) of interpterygoid vacuities. INT VAC 1.
102. Absence (0) or presence (1) of condition: interpterygoid vacuities occupying at least half of palatal width. INT VAC 2.
103. Absence (0) or presence (1) of condition: interpterygoid vacuities concave along their whole margins. INT VAC 3.
104. Absence (0) or presence (1) of condition: interpterygoid vacuities together broader than long. INT VAC 4.
105. Presence (0) or absence (1) of anterior palatal vacuity. ANT VAC 1.
106. Anterior palatal vacuity single (0) or double (1). ANT VAC 2.
107. Supraoccipital absent (0) or present (1) as separate ossification. SUPOCC 1.
108. Absence (0) or presence (1) of condition: exoccipitals enlarged, about as broad as high and forming stout, double occipital condyles. EXOCC 3.
109. Absence (0) or presence (1) of condition: exoccipitals forming continuous, concave, strap-shaped articular surfaces with basioccipital. EXOCC 4.
110. Basioccipital notochordal (0) or not (1). BASOCC 1.
111. Absence (0) or presence (1) of condition: basioccipital circular and recessed. BASOCC 6.
112. Absence (0) or presence (1) of condition: opisthotic forming thick plate with supraoccipital, separating exoccipitals from skull table. OPI 2.
113. Parasphenoid without (0) or with (1) elongate, strut-like cultriform process. PASPHE 1.
114. Parasphenoid without (0) or with (1) posterolaterally directed, ventral thickenings (ridges ending in basal tubera). PASPHE 3.
115. Parasphenoid without (0) or with (1) single median depression. PASPHE 6.
116. Parasphenoid without (0) or with (1) paired lateral depressions. PASPHE 7.
117. Ventral cranial fissure not sutured (0), sutured but traceable (1), absent (2). PASPHE 9.
118. Parasphenoid without (0) or with (1) triangular denticle patch with raised margins at base of cultriform process. PASPHE 12.
119. Jaw articulation lying behind (0), level with (1), or anterior to (2) occiput. JAW ART 1.
120. Presence (0) or absence (1) of parasymphysial plate. PSYM 1.
121. Parasymphysial plate without (0) or with (1) paired fangs. PSYM 2.
122. Parasymphysial plate without (0) or with (1) tooth row. PSYM 3
123. Parasymphysial plate with (0) or without (1) denticles. PSYM 4.
124. Dentary with (0) or without (1) anterior fang pair. DEN 2.
125. Dentary with (1) or without (0) chamfered ventral margin. DEN 3.
126. Dentary without (0) or with (1) U-shaped notch for premaxillary tusks. DEN 4.
127. Absence (0) or presence (1) of condition: rearmost extension of mesial lamina of splenial closer to anterior margin of adductor fossa than to anterior end of jaw. SPL 2.
128. Absence (0) or presence (1) of suture between splenial and anterior coronoid. SPL 3.
129. Absence (0) or presence (1) of suture between splenial and middle coronoid. SPL 4.
130. Postsplenial without (0) or with (1) mesial lamina. POSPL 2.
131. Postsplenial with (0) or without (1) pit line. POSPL 3.
132. Angular without (0) or with (1) mesial lamina. ANG 2.
133. Angular contacting prearticular (0) or not (1). ANG 3.
134. Angular not reaching (0) or reaching (1) posterior end of lower jaw. ANG 4.
135. Surangular with (0) or without (1) pit line. SURANG 3.
136. Prearticular sutured with splenial (0) or not (1). PREART 5.
137. Anterior coronoid with (0) or without (1) fangs. ANT COR 2.
138. Anterior coronoid with (0) or without (1) denticles. ANT COR 3.
139. Anterior coronoid with (0) or without (1) tooth row. ANT COR 4.
140. Middle coronoid present (0) or absent (1). MID COR 1.
141. Middle coronoid with (0) or without (1) fangs. MID COR 2.
142. Middle coronoid with (0) or without (1) denticles. MID COR 3.
143. Middle coronoid with (0) or without (1) marginal tooth row. MID COR 4.
144. Posterior coronoid with (0) or without (1) fangs. POST COR 2.
145. Posterior coronoid with (0) or without (1) denticles. POST COR 3.
146. Posterior coronoid with (0) or without (1) tooth row. POST COR 4.
147. Posterior coronoid without (0) or with (1) posterodorsal process. POST COR 5.
148. Posterior coronoid not exposed (0) or exposed (1) in lateral view. POST COR 6.
149. Posterodorsal process of posterior coronoid not contributing (0) or contributing (1) to tallest point of lateral margin of adductor fossa ("surangular" crest). POST COR 7.
150. Adductor fossa facing dorsally (0) or mesially (1). ADD FOS 1.
151. Dentary teeth not larger (0) or larger (1) than maxillary teeth. TEETH 5.
152. Marginal tooth crowns not chisel-tipped (0) or chisel-tipped (1). TEETH 6.
153. Marginal tooth crowns without (0) or with (1) dimple. TEETH 7.
154. Cleithrum with (0) or without (1) postbranchial lamina. CLE 2.
155. Cleithrum co-ossified with (0) or separate from (1) scapulocoracoid. CLE 3.
156. Clavicles meet anteriorly (0) or not (1). CLA 3.

157. Absence (0) or presence (1) of condition: posterior margin of interclavicle drawn out into parasternal process. INTCLA 1.
158. Absence (0) or presence (1) of condition: parasternal process elongate and parallel-sided for most of its length. INTCLA 2.
159. Absence (0) or presence (1) of condition: interclavicle wider than long. INTCLA 3.
160. Interclavicle rhomboidal with posterior half longer (0) or shorter (1) than anterior half. INTCLA 4.
161. Absence (0) or presence (1) of separate scapular ossifications. SCACOR 1.
162. Glenoid subterminal (0) or not (1) (scapulocoracoid extending ventral to posteroventral margin of glenoid). SCACOR 2.
163. Presence (0) or absence (1) of enlarged glenoid foramen. SCACOR 3.
164. Absence (0) or presence (1) of ventromesially extended infraglenoid buttress. SCACOR 4.
165. Presence (0) or absence (1) of anocleithrum. ANOCLE 1.
166. Latissimus dorsi process offset anteriorly (0) or aligned with ectepicondyle (1). HUM 1.
167. Absence (0) or presence (1) of distinct supinator process projecting anteriorly. HUM 2.
168. Presence (0) or absence (1) of ventral humeral ridge. HUM 3.
169. Latissimus dorsi process confluent with (0) or distinct from (1) deltopectoral crest. HUM 4.
170. Presence (0) or absence (1) of entepicondylar foramen. HUM 5.
171. Presence (0) or absence (1) of ectepicondylar foramen. HUM 6.
172. Presence (0) or absence (1) of distinct ectepicondyle. HUM 7.
173. Absence (0) or presence (1) of condition: ectepicondylar ridge extending distally to reach distal humeral end. HUM 8.
174. Distal extremity of ectepicondylar ridge aligned with ulnar condyle (0), between ulnar and radial condyles (1), or aligned with radial condyle (2). HUM 9.
175. Humerus without (0) or with (1) expanded extremities (waisted). HUM 10.
176. Radial condyle terminal (0) or ventral (1). HUM 11.
177. Posterolateral margin of entepicondyle lying distal with respect to plane of radial–ulnar facets (0) or not (1). HUM 13.
178. Posterolateral margin of entepicondyle markedly concave (0) or not (1). HUM 14.
179. Width of entepicondyle greater (0) or smaller (1) than half humeral length. HUM 15.
180. Portion of humeral shaft length proximal to entepicondyle smaller (0) or greater (1) than humeral head width. HUM 16.
181. Presence (0) or absence (1) of accessory foramina on humerus. HUM 17.
182. Humerus length greater (0) or smaller (1) than the length of two and a half midtrunk vertebrae. HUM 18.
183. Radius longer (0) or shorter (1) than humerus. RAD 1.
184. Radius longer than (0), as long as (1), or shorter than (2) ulna. RAD 2.
185. Absence (0) or presence (1) of olecranon process. ULNA 1.
186. Absence (0) or presence (1) of dorsal iliac process. ILI 3.
187. Supra-acetabular iliac buttress less (0) or more (1) prominent than postacetabular buttress. ILI 6.
188. Absence (0) or presence (1) of transverse pelvic ridge. ILI 7.
189. Acetabulum directed posteriorly (0) or laterally (1). ILI 10.
190. Ischium not contributing (0) or contributing (1) to pelvic symphysis. ISC 1.
191. Absence (0) or presence (1) of distinct process on internal trochanter. FEM 1.
192. Absence (0) or presence (1) of condition: internal trochanter separated from femur by distinct trough-like space. FEM 2.
193. Absence (0) or presence (1) of distinct rugose area on fourth trochanter. FEM 3.
194. Proximal end of adductor crest of femur not reaching (0) or reaching (1) midshaft length. FEM 4.
195. Femur shorter than (0), as long as (1), or longer than humerus (2). FEM 5.
196. Without (0) or with (1) flange on posterior edge. TIB 7.
197. Fibula not waisted (0) or waisted (1). FIB 1.
198. Absence (0) or presence (1) of ridge near posterior edge of fibula flexor surface. FIB 3.
199. Absence (0) or presence (1) of rows of tubercles near posterior edge of flexor surface of fibula. FIB 4.
200. Absence (0) or presence (1) of ossified tarsus. TAR 1.
201. Absence (0) or presence (1) of one proximal tarsal ossification, or presence of more than two ossifications (2). TAR 2.
202. Tarsus without (0) or with (1) L-shaped proximal tarsal element. TAR 3.
203. Absence (0) or presence (1) of distal tarsals between fibulare and digits. TAR 4.
204. Absence (0) or presence (1) of distal tarsals between tibiale and digits. TAR 5.
205. Cervical ribs with (0) or without (1) flattened distal ends. RIB 2.
206. Ribs mostly straight (0) or ventrally curved (1) in at least part of the trunk. RIB 3.
207. Absence (0) or presence (1) of triangular spur-like posterodorsal process in at least some trunk ribs. RIB 5.
208. Absence (0) or presence (1) of condition: elongate posterodorsal flange in midtrunk ribs. RIB 6.
209. Axial arch not fused (0) or fused (1) to axial (pleuro)centrum. CER VER 3.
210. Absence (0) or presence (1) of extra articulations above zygapophyses in at least some trunk and caudal vertebrae. TRU VER 1.
211. Absence (0) or presence (1) of condition: neural and hemal spines rectangular to fan-shaped in lateral view. TRU VER 2.
212. Absence (0) or presence (1) of condition: neural and hemal spines facing each other dorsoventrally. TRU VER 3.
213. Hemal spines not fused (0) or fused (1) to caudal centra. TRU VER 4.
214. Absence (0) or presence (1) of extra articulations on hemal spines. TRU VER 5.
215. Absence (0) or presence (1) of ossified pleurocentra. TRU VER 7.
216. Trunk pleurocentra not fused midventrally (0) or fused (1). TRU VER 8.

217. Trunk pleurocentra not fused middorsally (0) or fused (1). TRU VER 9.
218. Neural spines without (0) or with (1) distinct convex lateral surfaces. TRU VER 10.
219. Neural spines of trunk vertebrae not fused to centra (0) or fused (1). TRU VER 11.
220. Presence (0) or absence (1) of trunk intercentra. TRU VER 13.
221. Trunk intercentra not fused middorsally (0) or fused (1). TRU VER 14.
222. Absence (0) or presence (1) of lateral and ventral carinae on trunk centra. TRU VER 15.
223. Absence (0) or presence (1) of condition: tallest ossified part of neural arch in posterior trunk vertebrae lying above posterior half of vertebral centrum. TRU VER 19.
224. Absence (0) or presence (1) of prezygapophyses on trunk vertebrae. TRU VER 20.
225. Absence (0) or presence (1) of postzygapophyses on trunk vertebrae. TRU VER 21.
226. Absence (0) or presence (1) of prezygapophyses on proximal tail vertebrae. TRU VER 22.
227. Absence (0) or presence (1) of postzygapophyses on proximal tail vertebrae. TRU VER 23.
228. Absence (0) or presence (1) of prezygapophyses on distal tail vertebrae. TRU VER 24.
229. Absence (0) or presence (1) of postzygapophyses on distal tail vertebrae. TRU VER 25.
230. Absence (0) or presence (1) of capitular facets on posterior rim of vertebral midtrunk centra. TRU VER 26.
231. Height of neural arch in midtrunk vertebrae greater (0) or smaller (1) than distance between pre- and postzygapophyses. TRU VER 27.
232. Absence (0) or presence (1) of digits. DIG 1.
233. Absence (0) or presence (1) of no more than four digits in manus. DIG 2.
234. Absence (0) or presence (1) of no more than five digits in manus. DIG 3.
235. Absence (0) or presence (1) of no more than three digits in manus. DIG 4.
236. Presence (0) or absence (1) of dorsal fin. DOR FIN 1.
237. Presence (0) or absence (1) of caudal fin. CAU FIN 1.
238. Presence (0) or absence (1) of basal scutes. BAS SCU 1.
239. Anterior tectal: narial opening ventral to it (0); narial opening anterior to it (1).
240. Basioccipital: indistinguishable from exoccipitals (0); separated by suture (1).
241. Basioccipital: ventrally exposed portion longer than wide (0); shorter than wide (1).
242. Lacrimal contributes to narial margin: no, excluded by anterior tectal (0); yes (1); no, excluded by nasal/maxillary or prefrontal/maxillary suture (2).
243. Maxilla external contact with premaxilla: narrow contact point not interdigitated (0); interdigitating suture (1).
244. Median rostral (= internasal): mosaic (0); paired (1); single (2); absent (3).
245. Nasals contribute to narial margin: no (0); yes (1).
246. Opisthotic paroccipital process ossified and contacts tabular below posttemporal fossa: no (0); yes (1); posttemporal fossa absent (2).
247. Postparietal occipital flange exposure: absent (0); present (1).
248. Prefrontal–postfrontal suture: anterior half of orbit (0); middle or posterior half of orbit (1); absent (2).
249. Premaxilla forms part of choanal margin: broadly (0); point (1); excluded by vomer (2).
250. Squamosal suture with supratemporal position: at apex of temporal embayment (0); dorsal to apex (1); ventral to apex (2).
251. Tabular emarginated lateral margin: no (0); yes (1).
252. Tabular facets/buttresses for braincase ventrally: no (0); single (1); double (2).
253. Tabular occipital flange exposure: absent (0); extends as far ventrally as does postparietal (1); extends further ventrally than does postparietal (2).
254. Ectopterygoid reaches adductor fossa: no (0); yes (1).
255. Palatine-ectopterygoid exposure: more or less confined to tooth row (0); broad mesial exposure additional to tooth row (1).
256. Pterygoids flank parasphenoid: for most of length of cultriform process (0); not so (1).
257. Pterygoid junction with squamosal along cheek margin: unsutured (0); half and half (1); sutured entirely (2).
258. Parasphenoid wings: separate (0); joined by web of bone (1).
259. Parasphenoid sutures to vomers: yes (0); no (1).
260. Parasphenoid carotid grooves: curve round basipterygoid process (0); lie posteromedial to basipterygoid process (1).
261. Vomers separated by parasphenoid for more than half length: yes (0); no (1).
262. Vomers separated by pterygoids: for more than half length (0); for less than half length (1); not separated (2).
263. Ectopterygoid denticle row: present (0); absent (1).
264. Maxilla tooth number: more than 40 (0); 30–40 (1); less than 30 (2).
265. Maxillary caniniform teeth (about twice the size of neighboring teeth): absent (0); present (1).
266. Palatine row of smaller teeth: present (0); absent (1).
267. Palatine denticle row: present (0); absent (1).
268. Parasphenoid shagreen field: present (0); absent (1).
269. Parasphenoid shagreen field location: anterior and posterior to basal articulation (0); posterior to basal articulation only (1); anterior to basal articulation only (2).
270. Pterygoid shagreen: dense (0); a few discontinuous patches or absent (1).
271. Prearticular denticulated field: defined edges (0); scattered patches (1); absent (2).
272. Premaxillary teeth with conspicuous peak: absent (0); present (1).
273. Vomer fang pairs: present (0); absent (1).
274. Vomerine fang pairs noticeably smaller than other palatal fang pairs: no (0); yes (1).
275. Vomerine row of small teeth: present (0); absent (1).
276. Vomerine denticle row lateral to tooth row: present (0); absent (1).
277. Meckelian bone visible between prearticular and infradentaries: present (0); absent (1).
278. Naris position: ventral rim closer to jaw margin than height of naris (0); distance to jaw margin similar to or greater than height of naris (1).
279. Naris shape: slit-like (0); round or oval (1); upper margin ragged (2).

280. Naris orientation: ventrally facing (0); dorsolaterally facing (1).
281. Naris size relative to choana: less than 50% (0); same or larger (1).
282. Suspensorium proportions: distance from quadrate to temporal embayment anterior margin about equal to maximum orbit width (discounting any anterior extensions) (0); distance less than maximum orbit width (1); distance more than maximum orbit width (2).
283. Ornament character: fairly regular pit and ridge with starburst pattern at regions of growth (0); irregular but deep (1); irregular but shallow (2); absent or almost absent (3).
284. Centra: rhachitomous (0); gastrocentrous (1); holospondylous (2).
285. Centrum (sacral): distinguishable by size and shape from pre- and postsacrals (1); not so distinguishable (0).
286. Cleithrum dorsal end: smoothly broadening to spatulate dorsal end (0); distal expansion marked from narrow stem by notch or process or decrease in thickness (1); tapering (2).
287. Cleithrum stem cross section at midsection: flattened oval (0); complex (1); single concave face (2).
288. Femur adductor blade: distinguished distally from shaft by angle or notch (0); fades into shaft distally (1).
289. Humerus shape: ends more or less in line, little torsion apparent (0); ends offset by more than 60 degrees (1).
290. Humerus latissimus dorsi process: part of ridge (0); distinct but low process (1); spike (2).
291. Humerus anterior margin: smooth finished bone convex margin (0); anterior keel with finished margin (1); cartilage-finished (2); smooth concave margin (3).
292. Humerus radial and ulnar facets: confluent (0); separated by perichondral strip (1).
293. Neural arch ossification: paired in adult (0); single in adult (1).
294. Neural arch (sacral): distinguishable by spine morphology (1); not so distinguishable (0).
295. Pelvis: single ossification (0); at least two ossifications per side (1).
296. Pelvis obturator foramina: multiple (0); single or absent (1).
297. Ribs (trunk): no longer than height of neural arch plus centrum (0); less than two and a half times this height (1); more than two and a half times this height (2).
298. Ribs (trunk): tapered distally or parallel-sided (0); expanded distally into overlapping posterior flanges (1).
299. Ribs (trunk) bear proximodorsal (uncinate) processes: absent (0); present (1).
300. Ribs (trunk) differ strongly in morphology in "thoracic" region: absent (0); present (1).
301. Rib (sacral) distinguishable by size: shorter than trunk ribs, longer than presacrals (1); same length as presacrals (0).
302. Rib (sacral) distinguishable by shape: broader than immediate presacrals but not broader than midtrunk proximal shafts (0); broader than midtrunk proximal shafts (1).
303. Scapulocoracoid dorsal blade: absent (0); present (1).
304. Scutes: tapered and elongate, four times or greater than four times longer than broad (0); ovoid, no more than three times longer than broad (1).
305. Tibia and fibula width at narrowest point: 50% of length (0); less than 30% of length (1).
306. Tibia and fibula meeting along their length (0); separated by interepipodial space (1).
307. Number of pes digits: more than five (0); five (1); fewer than five (2).
308. Posterior process of ilium a slender, subhorizontal rod, with parallel dorsal and ventral margins, more than five times longer than deep: absent (0); present (1).
309. Process "2" of humerus: absent (0); present (1).
310. Basisphenoid: very narrow between basipterygoid processes, latter separated by about width of one process or less (1); basipterygoid processes set further apart than width of one process (0).
311. Basisphenoid in dorsal view: smooth concave retractor pit between basipterygoid processes (1); retractor pit paired or absent (0).
312. Basisphenoid in dorsal view: robust, broad bases for processi sellares, latter form backwall to retractor pit (1); processi sellares not forming stout buttresses (narrow wall or absent) (0).
313. Basipterygoid processes: processes rounded in ventral view, but not hemispherical (0); conspicuously bulbous, rounded posteriorly, nearly hemispherical (1); essentially simple triangular extensions from parasphenoid with little three dimensional morphology in ventral view (2).
314. Basipterygoid processes: faces of processes more or less concave throughout (0); faces reverse toroidal (i.e., convex centrally, concave laterally) (1).
315. Parasphenoid: forms narrow crest between basipterygoid processes (1); area between basipterygoid processes not a crest, but flat or depressed (0).
316. Parasphenoid cultriform process: flat, depressed, or rounded in section anteriorly (0); cultriform process a sharp keel, V-shaped in cross section from basiptergoid processes anteriorly (1).
317. Centra trunk: ossified portions of pleurocentra and intercentra differ in height by more than 25% (0); pleurocentra and intercentra about equal in height (1).
318. Ribs postsacral: elongate curved, at least three pairs (1); such pairs fewer or absent (0).
319. LAC 2 restated: lacrimal enters orbit margin (0); lacrimal excluded from orbit margin, with jugal/prefrontal contact (1).
320. Postorbital: with ventral component an acutely triangular extension forming posterior margin of orbit: absent (0); present (1).
321. Postorbital/intertemporal contact: interdigitating (0); or noninterdigitating (1).
322. Postorbital/squamosal contact: interdigitating (0); or smooth and noninterdigitating (1).
323. Postparietal margin: produced into posterior peak at midline ("widow's peak"): absent (0); present (1).
324. Supratemporal margin: contributes to posterior emargination of cheek (temporal notch): absent (0); present (1).
325. Supratemporal/squamosal contact: interdigitating (0); noninterdigitating butt joint (1).
326. TAB 2 restated: Tabular horn projection: absent (0); elongate blade-like unornamented (1); blade-like but ornamented (2).

327. Supratemporal/intertemporal margin: irregular (0); smoothly convex (1).
328. Preorbital region of skull longer than or equal in length as postorbital region (0). Postorbital region of skull longer than preorbital region (1).
329. No brassicate splenial boss in symphysis of the lower jaw present (0). Brassicate splenial boss in symphysis of the lower jaw present (1).
330. Supraorbital line on premaxilla runs parallel to jaw margin (0). Supraorbital line on premaxilla directed toward the jaw margin (1). No supraorbital line present of premaxilla (2). Character unordered.
331. Pterygoids not deeply wedged between vomers (0). The pterygoids are wedged deeply between the vomers (more than half the length of the vomers) (1).

Appendix II

Acanthostega

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110010011111010010100000000000000001000000001111000010001010000010000100001000? 1010000001? 0010
00010000200? 00001010000000001000000010?? 00000? 10? 0000100001

Adelogyrinus

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Anthracosaurus

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01? 11? 021122??????????????????????????? 1???????? 0000110100020

Archeria

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Ariekanerpeton

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Balanerpeton

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10101111? 0201001201100000000001000000001111?? 001100111?? 11? 31? 01101001112? 011210011010200? 111111
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Baphetes

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Bruktererpeton

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Caerorhachis

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Casineria

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Crassigyrinus

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Discosauriscus

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Eoherpeton

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Eusthenopteron

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Gephyrostegus

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Greererpeton

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Ichthyostega

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Loxomma

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Microbrachis

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Paleothyris

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Pederpes

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Saxonerpeton

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Seymouria

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Utegenia

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Westlothiana

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Whatcheeria

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St._Louis_tetrapod

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Chapter 4: The Roots of Amphibian Morphospace: A Geometric Morphometric Analysis of Paleozoic Temnospondyls

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Abstract

Temnospondyls—a major component of Permian and Carboniferous terrestrial ecosystems—display great diversity in skull shapes and proportions. To quantify and interpret this diversity, we conducted a geometric morphometric analysis using 45 landmarks on the dorsal skull surface of 90 species with well-represented cranial material. Results show a correlation between morphospace occupation and phylogenetic proximity of taxa for trees in which dvinosaurs and dissorophoids are sister groups and join an edopoid–eryopoid–basal archegosauriform clade. Most large groups of Carboniferous and Permian temnospondyls occupy specific areas of morphospace. Nearest-neighbor analyses reveal significantly greater taxon clustering than expected under either uniform or Gaussian null models. Size correlates strongly with shape across the whole data set, highlighting the association of some features (short, broad snout; large orbits) with small size. A significant relationship between size and shape is not observed in clades such as branchiosaurids, dvinosaurs, and olsoniforms (the clade encompassing trematopids plus dissorophids). This suggests that evolutionary allometry patterns vary across temnospondyls. In the case of branchiosaurids, this pattern may be explained by the similar sizes and relatively conservative morphologies of the constituent species. Distance-based disparity measures indicate that edopoids, eryopoids, and basal archegosauriforms make the largest contributions to total disparity (reflecting the peripheral locations of some of the constituent taxa in morphospace), whereas amphibamids, dissorophids, and trematopids make the smallest contributions. Disparity correlates strongly with diversity within groups, suggesting that skull shape was not subject to character state exhaustion (decrease or cessation in the acquisition of novel morphological conditions during clade evolution). The Kasimovian, Roadian, Wordian, and Changhsingian are time intervals of high disparity despite their low diversity. We hypothesize that this pattern stems from the fact that times of high diversity are characterized by larger areas of morphospace, which results in mean shapes being located relatively close to the grand mean; in contrast, mean shapes for low-diversity stages are based on incomplete morphospace samples. Many of these patterns are similar to those observed in previous analyses of stereospondyls, suggesting that similar controls on skull shape may have operated throughout the history of temnospondyls.

Introduction

Temnospondyl amphibians (ranging from the Viséan to the Albian; Milner, 1990; Holmes, 2000; Warren, 2000; Clack, 2002; Carroll, 2009; Steyer, 2012) are excellent model organisms for macroevolutionary analyses, given their remarkable diversity, their numerical dominance in numerous fossil vertebrate assemblages worldwide, and their extensive geographic and stratigraphic distributions. Although discoveries of new temnospondyl taxa continue to accrue in a steady fashion—a pattern that has remained almost unchanged for over five decades (Bernard et al., 2010)—researchers have recently begun to explore models of faunal turnover, rates of speciation, responses to mass extinctions, and dynamics of character acquisition and change either for the group as a whole or for constituent clades thereof (e.g., Ruta et al., 2006, 2007; Wagner et al., 2006; Ruta & Benton, 2008; Ruta, 2009).

The extraordinary variety of their body shapes, sizes, and proportions makes temnospondyls amenable to analyses of morphological evolution. However, very few papers have addressed patterns of shape diversity (= disparity) in these tetrapods. Witzmann and Pfretzschner (2003) examined ontogenetic changes in the skull of the dissorophoid *Micromelerpeton credneri* using a combination of Cartesian transformations and biometric analyses, whereas Witzmann and Scholz (2007) employed morphometric techniques to quantify allometric skull growth in the archegosauriform *Archegosaurus decheni*. Sengupta et al. (2005) used closed bilaterally symmetric Fourier curves to compare the outlines of dorsoventral skull projections in selected taxa from major temnospondyl groups. Stayton and Ruta's (2006) landmark-based geometric morphometrics analysis tackled skull roof variation in stereospondyls—the most species-rich and largely Mesozoic radiation of temnospondyls. Following this work, two additional papers applied landmark-based morphometrics to temnospondyls. Witzmann et al. (2009) compared ontogenetic trajectories in selected temnospondyl taxa in which growth series are fairly complete and well sampled, and Bourget and Anderson (2011) investigated skull roof variation in amphibamid dissorophoids in conjunction with the description and phylogenetic assessment of their new taxon, *Rubeostratilia texensis*, from the Early Permian of Texas.

Here, we provide a detailed treatment of cranial morphological variation in (mostly) Paleozoic species, using landmark-based geometric morphometrics and relative warps analysis. This study complements the treatment of skull shape diversity in temnospondyls that was initiated by Stayton and Ruta (2006). However, a comprehensive morphometric analysis of all adequately known temnospondyls, including stereospondyls, is beyond the scope of our investigation. Our taxonomic target includes the following: (1) basalmost groups (e.g., edopoids; Milner & Sequeira, 1998; Holmes, 2000; Sidor et al., 2005), (2) groups that are widely considered to be very derived and close to the origin of some or all of the crown-group lissamphibians (e.g., dissorophoids; Ruta & Coates, 2007; Anderson et al., 2008b), and (3) groups that are placed phylogenetically between edopoids and dissorophoids (e.g., dvinosaurs, eryopoids; Ruta & Bolt, 2006; Ruta, 2009; Schoch & Witzmann, 2009a,b). Although the stereospondyls are not covered in this study, we have included a variety of taxa that form the phylogenetic roots of this clade, i.e., the basal archegosauriforms (*sensu* Schoch & Milner, 2000; this term is co-extensive with the basal stereospondylomorphs *sensu* Yates & Warren, 2000). Four families represent the basal archegosauriforms in the present work, namely the actinodontids, intasuchids, archegosaurids, and melosaurids (Schoch & Milner, 2000). To sum up, our taxonomic exemplar encompasses all the plesions (*sensu* Craske & Jefferies, 1989; Smith, 1994; Ruta & Bartels, 1998; Ruta, 1999)—i.e., all extinct monophyla—that branch from the lissamphibian stem-group, although the phylogenetic proximity of temnospondyls to lissamphibians is by no means universally agreed upon. For the purpose of the present work, we subscribe to the hypothesis that monophyletic lissamphibians are rooted within one or more groups of dissorophoids (e.g., Ruta et al., 2003; Ruta & Coates, 2007, and references therein). Useful discussions of alternative hypotheses can be found in Schoch and Milner (2004), Anderson (2008), and Marjanovic and Laurin (2009).

Aims

The main aims of this work are as follows: (1) to quantify skull shape variation in (mostly) Paleozoic temnospondyls using landmark-based geometric morphometrics; (2) to examine the distribution of both species and groups within their skull shape morphospace; (3) to evaluate the amount of disparity contributed by each group; (4) to correlate disparity and taxonomic diversity; (5) to assess the concordance between proximity of species in morphospace and their phylogenetic relatedness; (6) to analyze changes in disparity through time; and (7) to test whether a significant relationship exists between skull shape and size across Paleozoic temnospondyls as a whole as well as within specific groups.

Rationale

Our work addresses complementary aspects of morphological diversification in Paleozoic temnospondyls. At a general level of inquiry, we seek to understand whether the relative placements of taxa in morphospace are concordant with currently recognized systematic groups, whether convergence resulting from overall phenetic similarity (e.g., long-snouted taxa; broad-skulled taxa) affects patterns of morphospace occupation, and whether size and shape correlate through phylogenetic relatedness. In addition, we want to establish the extent to which groups characterized by various types of heterochronic development—such as are revealed by the possession of short and wide snouts, large orbits, and broad skull tables (e.g., neotenous dvinosaurs and paedomorphic or progenetically dwarfed dissorophoids; Milner, 1988, 1990; Schoch & Fröbisch, 2006)—occur close to one another in morphospace. This study further addresses a number of problematic taxa (e.g., *Balanerpeton*; *Dendrerpeton*; *Peltobatrachus*; *Saharastega*) that display features observed in unrelated groups, and the affinities of which continue to be contentious (Panchen, 1959; Milner, 1980, 1988, 1990; Milner & Sequeira, 1994; Holmes et al., 1998; Steyer, 2000; Yates & Warren, 2000; Ruta et al., 2003; Sidor et al., 2005; Damiani et al., 2006; Laurin & Soler-Gijón, 2006; Ruta & Bolt, 2006; Steyer et al., 2006; Ruta & Coates, 2007; Ruta, 2009). Although resolution of the phylogenetic position of these taxa is outside the main aims of this work, we employ craniometric data to evaluate critically alternative hypotheses.

Material and Methods

A "Backbone Supertree" for Paleozoic Temnospondyls

A phylogenetic framework is a key component of several of our analyses. Cladistic studies have advanced considerably our understanding of the relationships of various temnospondyls. Although the majority of contributions in this area have targeted primarily the Mesozoic radiation—namely the stereospondyls (Yates & Warren, 2000; Maganuco et al., 2009; see Schoch & Milner, 2000 for a compendium of this group)—the relationships of Paleozoic temnospondyls have recently gained attention (for a succinct bibliography, see Ruta & Bolt, 2006; Anderson, 2008; Ruta, 2009). In particular, among Permian and Carboniferous groups, dissorophoids have been the focus of cladistic works spurred by recent discoveries (e.g., Huttenlocker et al., 2007; Anderson et al., 2008a,b; Fröbisch & Reisz, 2008; Reisz et al., 2009; Bourget & Anderson, 2011), assembly of new character matrices (e.g., Schoch & Milner, 2008), and new data on previously described taxa (e.g., Schoch & Rubidge, 2005; Clack & Milner, 2010; Sigurdsen & Bolt, 2009, 2010). In addition, recent studies have re-emphasized the role of dissorophoids in the debate on the origin and status of the extant lissamphibians (e.g., Ruta et al., 2003; Ruta & Coates, 2007; Anderson, 2008; Anderson et al., 2008b; Fröbisch & Schoch, 2009a). Despite the conflicting cladogram topologies for Paleozoic temnospondyls (e.g., Milner, 1990; Yates & Warren, 2000; Ruta & Bolt, 2006), it is currently generally accepted that they form a phylogenetic continuum, with the large stereospondyl radiation grafted onto a Carboniferous and Permian assemblage consisting of eryopoids and basal archegosauriforms (e.g., Schoch & Milner, 2000; Yates & Warren, 2000; Schoch et al., 2007; Ruta, 2009; Schoch & Witzmann, 2009a,b).

To evaluate the concordance between distributions of taxa in morphospace and in phylogeny, we opted for the construction of a "supertree." Despite the availability of a temnospondyl supertree (Ruta et al., 2007), new hypotheses of

Paleozoic temnospondyl relationships (e.g., Schoch & Milner, 2008; Berman et al., 2009; Ruta, 2009; Bourget & Anderson, 2011) published subsequently meant that an updated topology was required. In addition, as not all species were represented by adequate cranial material, it was necessary to prune numerous taxa from the supertree constructed by Ruta et al. (2007). Similarly, we excluded the stereospondyls, but we retained numerous basal archegosauriforms.

An outstanding issue is the incongruence between various recent cladograms. Resolution of the existing conflict must await the construction of a comprehensive taxon–character data matrix. For this reason, our supertree (Fig. 1) illustrates only a partial consensus for the different domains of Paleozoic temnospondyl phylogeny. To derive this topology, we did not use any of the currently implemented methods or algorithms (e.g., Bininda-Emonds, 2004). Instead, we used protocols akin to those used by Kammerer and Angielczyk (2009) and Tsuji and Müller (2009) in their "synthetic" supertrees of anomodont therapsids and parareptile amniotes, respectively. Thus, no formal computer-assisted analysis was performed, unlike in the work of Ruta et al. (2007). Instead, we collated different portions of phylogeny (one for each group of interest) and then grafted these onto a backbone topology showing the sequence in which major temnospondyl groups branch.

The shape of this backbone topology is also problematic, as highlighted by Ruta and Bolt (2006) and Ruta (2009). Most of the current controversy revolves around the placement of eryopoids and dvinosaurs as well as the internal relationships of the various dissorophoid families. For instance, dvinosaurs are the second most basal group (after edopoids) in certain schemes of temnospondyl interrelationships (e.g., Milner, 1990; Holmes, 2000), but appear as sister group to dissorophoids in others (e.g., Ruta & Bolt, 2006; Ruta, 2009). Concerning eryopoids, they are placed close to dissorophoids in some works (e.g., Milner, 1990; Holmes, 2000), but close to the large basal archegosauriform–stereospondyl radiation in others (e.g., Ruta, 2009; Schoch & Witzmann, 2009a,b). Edopoids form the sister group to the clade including eryopoids plus basal archegosauriforms–stereospondyls in Ruta and Bolt (2006) and Ruta (2009), but are treated as the most basal clade in other schemes of relationships (e.g., Milner, 1990; Milner & Sequeira, 1998; Holmes, 2000; Sidor et al., 2005; Damiani et al., 2006; Steyer et al., 2006).

With these potential uncertainties, our supertree (Fig. 1) consists of two major radiations: the first includes edopoids (clade Edopoidea) and basal archegosauriforms–stereospondyls (clades Eryopoidea and Archegosauriformes); the second includes dvinosaurs (clade Dvinosauria) and dissorophoids. The latter are divided into four groups based upon the constituent families: Dissorophidae/Trematopidae, i.e., Olsoniformes; "Amphibamidae"; Micromelerpetontidae; and Branchiosauridae as grouped by Anderson et al. (2008b).

The phylogeny of edopoids is more stable than that of other temnospondyl groups. In our study, we adopted well-established topological schemes from Milner (2000), Milner and Sequeira (1998), Holmes (2000), Sequeira (2004), Sidor et al. (2005), Damiani et al. (2006), Ruta and Bolt (2006), Steyer et al. (2006), and Ruta (2009) (see also comments in Milner and Sequeira, 2011).

For eryopoids, we combined results from partially overlapping topologies, using Laurin and Soler-Gijón (2006), Ruta (2009), and Schoch and Witzmann (2009a,b) as references. Following in part Ruta (2009), we treated *Capetus palustris* and *Iberospondylus schultzei* as successive sister taxa to the eryopoids plus basal archegosauriforms (but see Schoch & Milner, 2000, for alternative topologies). The interrelationships of eryopoids conform, in part, to results of Laurin and Soler-Gijón (2006) and Ruta (2009). The branching pattern for the basal archegosauriforms combines results of Schoch and Milner (2000) and Schoch and Witzmann (2009a,b). The peculiar, spiky-skulled zatracheids were placed close to eryopids, following the recent analysis by Ruta (2009; but see Schoch, 1997; Steyer, 2000; Witzmann and Schoch, 2006b; and Milner et al., 2007).

Dvinosaur interrelationships follow primarily studies by Milner (1990), Yates and Warren (2000), Ruta and Bolt (2006), Englehorn et al. (2008), and Ruta (2009). However, following Clack and Milner (2010; also, Andrew R. Milner, pers. comm. to M.R., 2008–2010, and research in progress by M.R.), the Early Permian *Perryella olsoni* is not considered to be a dvinosaur (as in Ruta & Bolt, 2006; Ruta, 2009), and is instead assigned to the amphibamid dissorophoids. Also, we conservatively placed the bizarre *Erpetosaurus radiatus* in a polytomy with a monophyletic *Trimerorhachis*. *Erpetosaurus* reveals a mosaic of features that are observed in trimerorhachids and dvinosauroids. A recent paper by Milner and Sequeira (2011) sheds new light on the position of *Erpetosaurus* among the dvinosaurs.

The interrelationships of dissorophoids have been the focus of renewed phylogenetic efforts (e.g., Schoch & Milner, 2008; Berman et al., 2009; Bourget & Anderson, 2011, and references therein), but incongruence affects the sister group relationships among these families. Therefore, we produced a partial summary of the current hypotheses as follows. First, we regarded trematopids and dissorophids as monophyletic sister groups, in agreement with Anderson et al. (2008a,b); for the internal relationships of these two families, we merged the results of Milner (2007), Ruta (2009), and Berman et al. (2009). This wider clade (olsoniforms) was placed as the sister group to remaining dissorophoids. We regarded "amphibamids" as a paraphyletic array (e.g., Ruta, 2009) relative to a clade including branchiosaurids and micromelerpetontids. Both of these families were treated as sister clades. The topology of the branchiosaurids conforms to Schoch and Milner (2008). Micromelerpetontid relationships are still poorly understood. We considered *Micromelerpeton* and *Eimerisaurus* as monophyletic sister genera, and *Branchierpeton* and *Limnogyrinus* as progressively more distal sister taxa to other branchiosaurids (e.g., Milner & Sequeira, 2003; Schoch & Milner, 2008).

Morphometric Data Collection and Relative Warps Analysis

Our data set consists of two-dimensional landmarks digitized on published drawings of the reconstructed dorsal surfaces of temnospondyl skulls. We focused on the dorsal surface of the skull both because its large number of sutural intersections provides a rich source of landmarks and because the individual bones and the overall shape of the skull show a high degree of variability within and between major groups. As in previous studies (e.g., Stayton & Ruta, 2006), we strove to achieve a trade-off between maximum representation of species in each group and adequate representation of cranial material. For each included species, it was possible to confirm the accuracy of published reconstructions either through inspection of photographed material or through first-hand

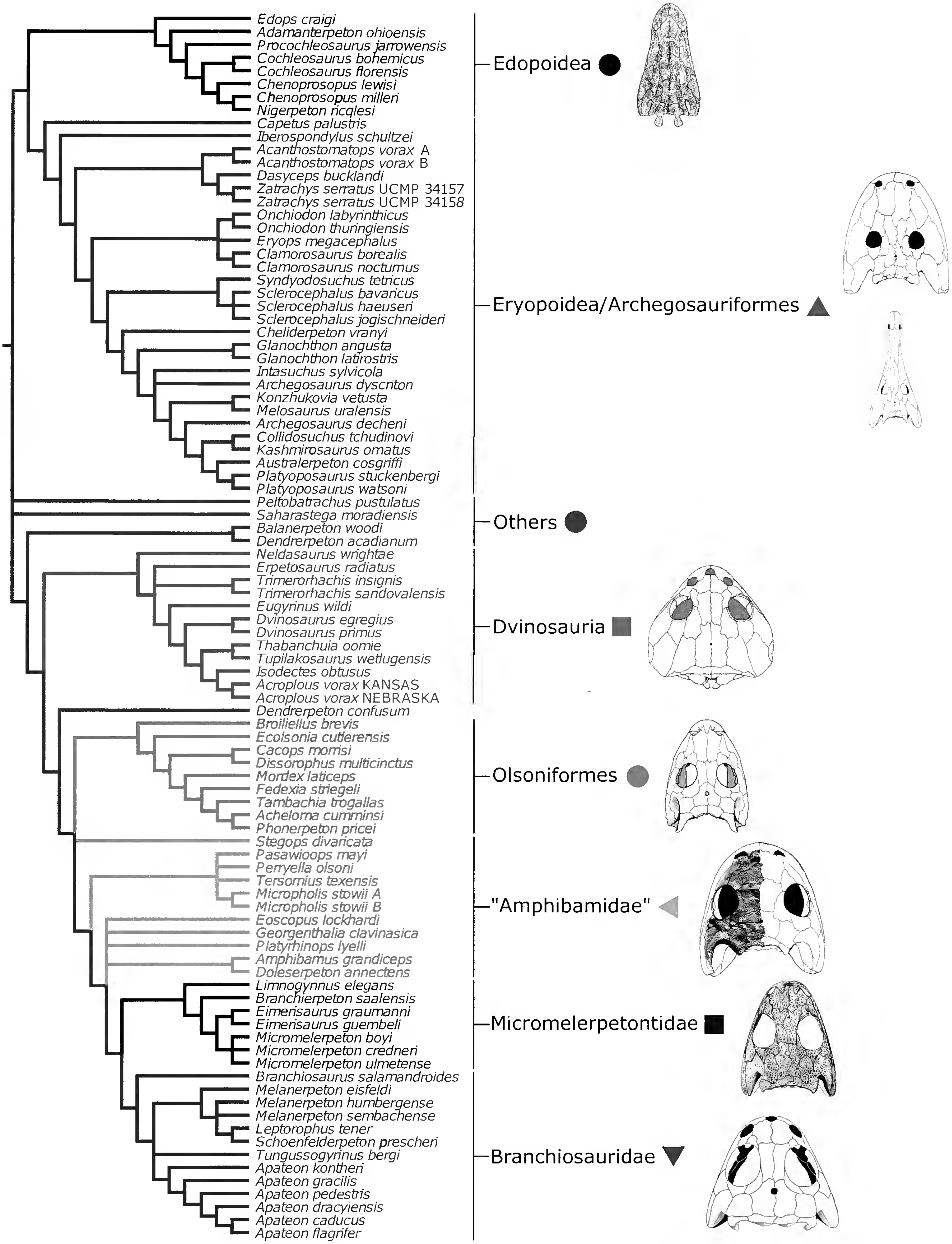

FIG. 1. A supertree of the (mostly) Carboniferous and Permian temnospondyl species included in the geometric morphometric analysis; the eight major groups discussed in the text are shown in different colors and with their representative symbols from the relative warps plots (others = taxa of uncertain affinities). From top to bottom, illustrated representative skulls include the following: the edopoid *Cochleosaurus bohemicus* (after Sequeira, 2004); the eryopid *Onchiodon labyrinthicus* (after Schoch & Milner, 2000); the basal archegosauriform *Archegosaurus decheni* (after Witzmann, 2006); the dvinosaur *Acroplous vorax* (after Foreman, 1990); the olsoniform *Cacops morrisi* (after Reisz et al., 2009); the amphibamid *Platyrhinops lyelli* (after Clack & Milner, 2010); the micromelerpetontid *Micromelerpeton credneri* (after Schoch, 2009); the branchiosaurid *Apateon pedestris* (Schoch, 1992).

specimen observations. Reconstructions that were thought to be inaccurate or based upon extremely fragmented and/or incomplete specimens were not considered. In some cases, entirely new skull reconstructions were kindly supplied by a number of colleagues, based upon their own ongoing or recently published revisions of various species. Our final data set consisted of 94 reconstructions representing a total of 90 species. Bourget & Anderson's (2011) recently described "amphibamid" *Rubeostratilia texensis* was published shortly after our analyses were completed; it therefore could not be included here.

Our use of reconstructions has advantages and disadvantages. Advantages include the fact that sutures are clearly visible and easy to digitize, potential problems such as tectonic deformation do not pose concerns, and it is possible to include taxa that are known only from disarticulated material. However, using reconstructions forces us to assume that they provide an accurate representation of the mean shape of each species, and that they are projected into two dimensions in a comparable way. We are unable to assess intraspecific variation in any detailed way, although in a small number of cases (e.g., *Acanthostomatops vorax*, *Zatrachys serratus*, *Acroplous vorax*, *Micropholis stowi*) we were able to include multiple reconstructions of a single species or reconstructions of multiple individuals of a species to gain some perspective on these issues. We consider the use of reconstructions to be adequate for an initial assessment of morphospace occupation and disparity among temnospondyls. We emphasize that the accuracy of our results is entirely contingent upon the accuracy of the reconstructions, and that the patterns we describe here should be tested in future analyses based upon original specimens, so far as possible (see also discussion in Bourget & Anderson, 2011).

We digitized a total of 45 landmarks using tpsDig 2.04 (Rohlf, 2005). Five landmarks are located along the midline of the skull, and 40 landmarks are bilaterally symmetric (Fig. 2). We selected landmarks to capture as much variation as possible on the dorsal surface of the skull, while taking into account the different reciprocal positions of some bones in certain species. For example, a landmark at the triple junction between parietal, postorbital, and supratemporal cannot be found consistently, due to an intervening intertemporal in some taxa (e.g., *Balanerpeton*, *Capetus*). Similarly, landmarks along the lateral margins of the skull are not always discernible in a dorsal view of the skull. Finally, the landmark along the midline at the premaxillary–nasal junction does not exist in some taxa (e.g., *Acanthostomatops*). Nearly all landmarks represent either triple junctions between sutures or endpoints of sutures (the four landmarks representing the extreme points along the orbital margin are notable exceptions). The selected landmarks emphasize the morphology of individual bones, the position and relative size of the orbits, and the relative proportions of the skull table, snout, and cheeks. To avoid inflating degrees of freedom in statistical analyses, among other problems (Klingenberg et al., 2002), we first reflected symmetric landmarks from one side of the skull onto the other side, and then calculated the mean position for each pair of landmarks. In those few cases where only one member of a symmetric pair of landmarks could be digitized on a reconstruction, we employed the coordinates of that landmark instead of a mean value. All analyses were carried out on the "half" specimens obtained from this reflection procedure. Finally, to quantify size we digitized two points representing a standard distance (10 mm) on the scale bars accompanying the reconstructions.

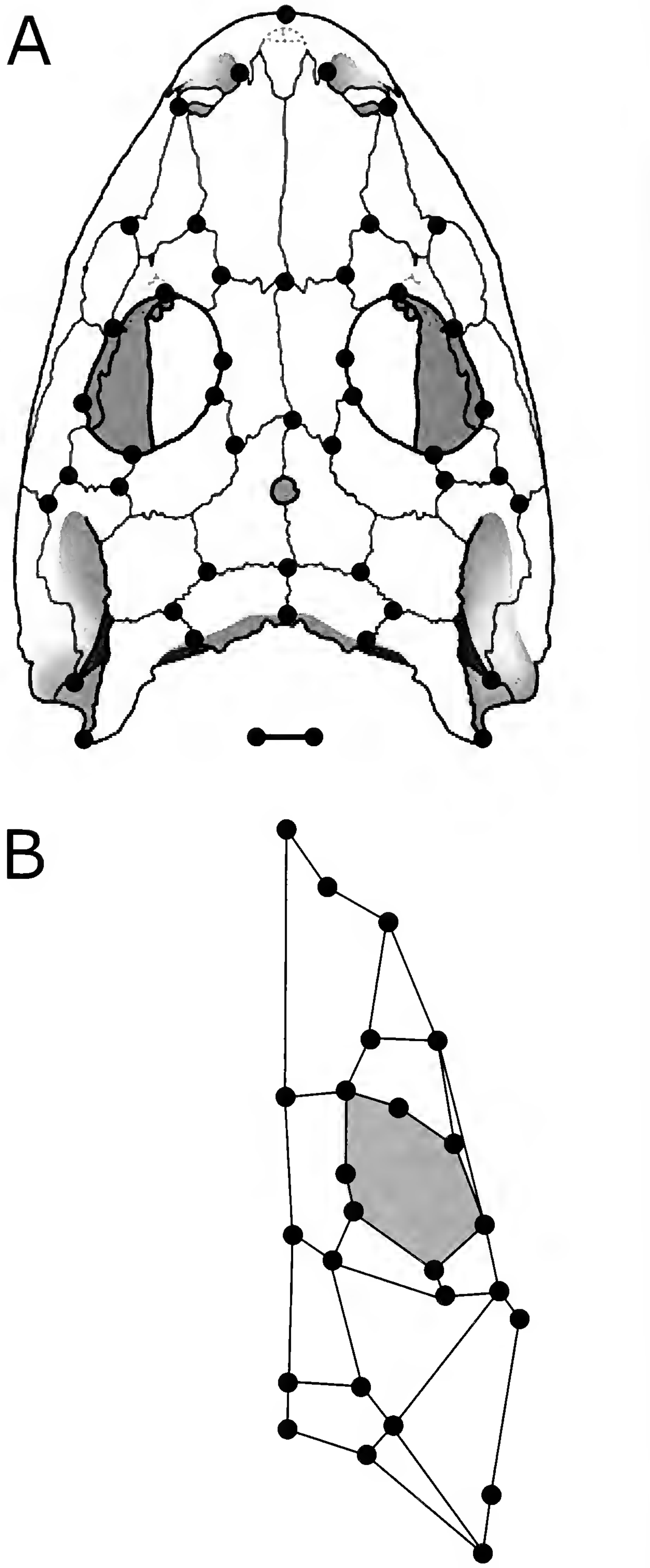

Fig. 2. Landmarks used in the geometric morphometric analysis. (**A**) Locations of the 45 morphological landmarks and two scale landmarks shown on the dorsal skull surface of the dissorophid *Cacops morrisi* (after Reisz et al., 2009); the scale bar equals 10 mm. (**B**) Configuration of 25 landmarks used in morphometric analyses after reflecting and averaging bilaterally symmetric landmarks. The overlain wireframe is included for visualizing relative shape differences in various parts of the skull, and does not strictly correspond to sutural boundaries.

Following data collection, we superimposed the configurations of landmarks for all skull reconstructions using generalized Procrustes analysis (Rohlf, 1990; Bookstein, 1991) in the program CoordGen 6d written by Professor David Sheets (http://www.canisius.edu/~sheets/morphsoft.html). The generalized Procrustes analysis removed the effects of position, orientation, and scale from the data set. We next derived partial warp and uniform component scores (e.g., see Bookstein, 1989, 1991, 1996, 1998; Rohlf, 1998; Zelditch et al., 2004) for all specimens. Partial warp and uniform component scores describe shape differences between each specimen and a reference shape, in this case the shape of the mean specimen in our data set. The two uniform components describe variation that represents uniform (or affine) transformations of shape, i.e., variation that affects all parts of a specimen equally. The partial warp scores describe progressively more localized, non-uniform (or non-affine) shape variation. To generate relative warp scores, we carried out a principal components analysis (PCA) on the covariance matrix of the partial warp and uniform component scores derived from the Procrustes superimposed configurations. We used Anderson's test (Anderson, 1958; see also Morrison, 1990; Zelditch et al., 2004) to determine which eigenvalues from PCA were significantly distinct from subsequent eigenvalues (i.e., which relative warps described significant components of shape variation in the data set).

The relative warps analysis provides an easy way to visualize the major patterns of shape variation and morphospace occupation among taxa of interest. The results of this analysis (see below) suggest that most of the temnospondyl groups occupy relatively distinct areas of morphospace (Figs. 3 and 4). To investigate this pattern further, we conducted a series of pair-wise comparisons using Goodall's *F* test (Goodall, 1991) to determine whether the mean shapes of our eight groups were significantly different given the shape variance within each group. To ensure we did not reject our null hypothesis of no difference between group means by chance, we Bonferroni-corrected our cut-off value for significance to 0.0018.

Comparisons Between Morphometric and Phylogenetic Distances

We used the Mantel test of matrix correlation (Mantel, 1967) to test whether taxa that are closely related are also in close proximity in morphospace. The morphometric data used in the test consisted of a matrix of pair-wise Procrustes distances between taxa, whereas the phylogenetic data consisted of a matrix of pair-wise distances between taxa on the supertree. We calculated these distances as the number of nodes (with internal branches assumed to be of equal length) separating any two taxa along the shortest path connecting them on the supertree. To assess the significance of matrix correlation, we carried out a permutation test using 5000 replicates in the program PAST 1.98 (Hammer et al., 2001; Hammer & Harper, 2006).

Disparity Analyses

To quantify the distribution of the eight temnospondyl groups in morphospace and to visualize how the pattern of morphospace occupation changed over time, we conducted two types of disparity analyses. In the first, we used a modified version of Foote's (1993) distance-based definition of disparity, adapted for use with geometric morphometrics data by Zelditch et al. (2003, 2004). This method calculates the partial disparity of each group of interest (that is, the group's contribution to the total amount of disparity entailed by the complete data set) by summing the squared Procrustes distances between the mean shape of each group and the grand mean shape of the complete data set. Thus, the total disparity equals the sum of the partial disparities associated with each group. We calculated partial disparities for two sets of taxon groups: (1) taxa belonging to each of the eight groups shown in Figure 1; (2) taxa belonging to each of the 14 stage-level time bins shown in Figure 5 (however, note that we excluded the oldest time bin—Viséan—from our calculations, because it includes only one species, *Balanerpeton woodi*). For both taxon-grouping schemes, we calculated Spearman's ρ to measure the correlation between the numbers of taxa in clades or time bins of interest and the partial disparities associated with those taxa. We carried out all partial disparity analyses in the program DisparityBox 6h by Professor David Sheets (http://www.canisius.edu/~sheets/morphsoft.html).

The second type of disparity analysis considers the modalities of taxon distribution in morphospace, that is, whether they are randomly distributed or closer together/farther apart than expected under a null model of spatial randomness. We used Foote's (1990) nearest-neighbor method for this analysis, modified and adapted for geometric morphometric data by Zelditch et al. (2004). First, we measured the nearest-neighbor distances (D_i for the *i*th specimen) for each of the 94 skull reconstructions using Procrustes distances. Subsequently, we generated four Monte Carlo simulations, each consisting of 500 individual data sets and each based upon a different null model (see below). Finally, we computed the nearest-neighbor distances between each observed specimen and its closest neighbor in each of the simulated data sets (R_i for the *i*th specimen), again using Procrustes distances. To calculate the fit of the simulated distances to the observed distances, we computed proportional distances for each specimen as

$$P_i = \frac{D_i - R_i}{R_i}$$

If the simulated data fit the real data well, then D_i and R_i should be equal on average, thus making the mean value of P (P_{mean}) equal to zero. However, if P_{mean} is strictly negative, then the observed specimens are more clustered in morphospace than predicted by the null model, whereas if P_{mean} is strictly positive, then the observed specimens are more dispersed in morphospace than predicted by the null model. To test the significance of these patterns, we calculated the P_{mean} value and 95% confidence interval for each of the 500 simulated data sets.

We used two underlying distributions for the Monte Carlo simulations, namely a uniform distribution and a Gaussian distribution. To generate the Monte Carlo data sets, we needed to estimate the mean and standard deviation for each landmark coordinate (Gaussian distribution), or the upper and lower bounds of the range for each landmark coordinate (uniform distribution). We estimated these parameters in two ways. First, we used the observed data without modification, which provides a conservative null model through which we aimed to test whether the skull reconstructions are more clustered in morphospace than expected by chance. Second, we followed Foote (1990) in using estimators developed by

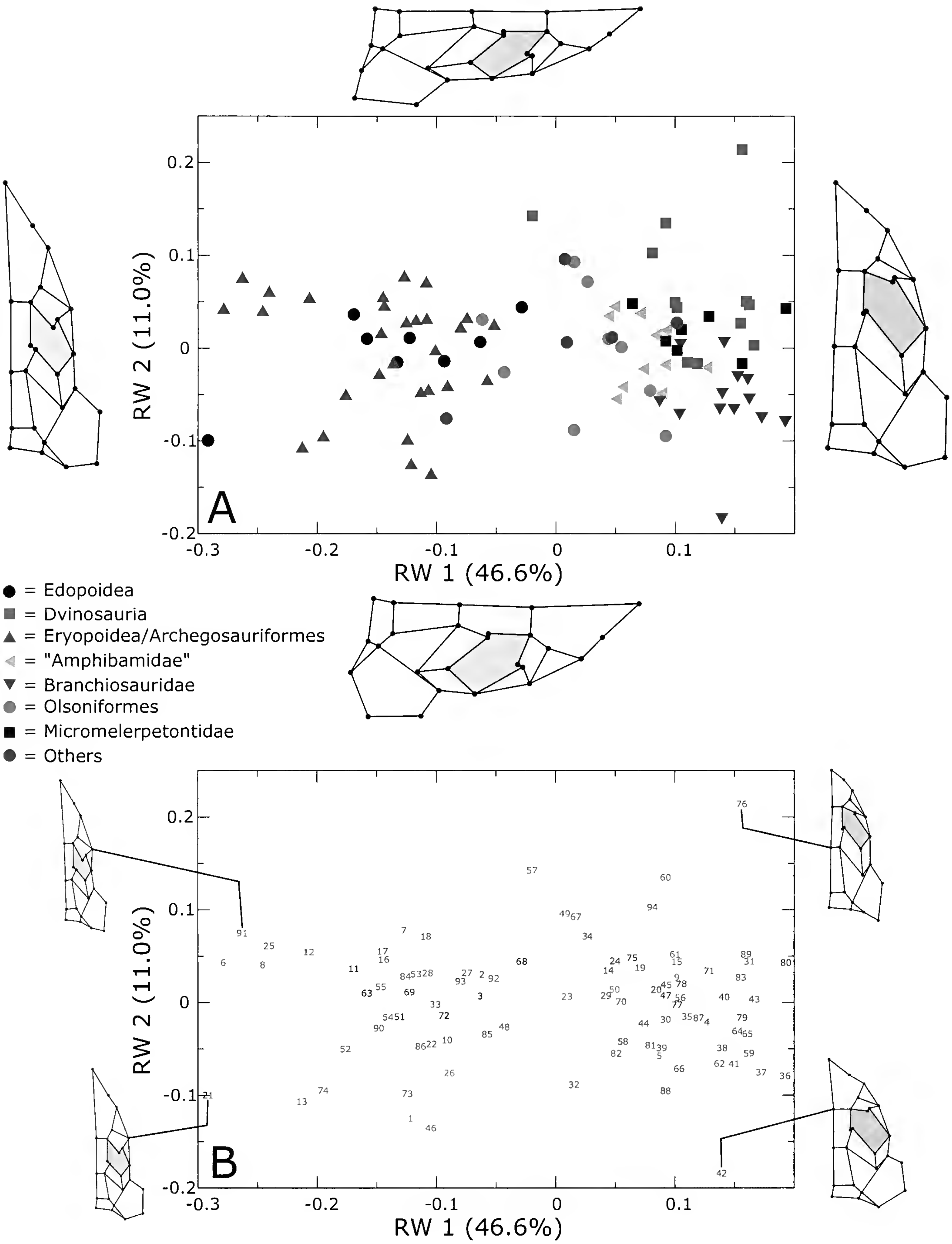

FIG. 3. Plot of the 94 reconstructions of temnospondyl skulls in the area of morphospace delimited by relative warp axes 1 and 2 (RW1 and RW2). (**A**) Color-coded symbols identify major groups to which reconstructions belong. Wireframes and landmark configurations show the shapes of hypothetical specimens located at the extremes of RW1 and RW2. (**B**) Numbers identify taxa as per the list in the Appendix, and are color-coded following the conventions in Figure 1. Extreme shapes of real taxa are visualized using landmark configurations and wireframes. At the lower left is the edopoid *Nigerpeton ricqlesi* (no. 21); at the lower right is the branchiosaurid *Apateon pedestris* (no. 42); at the upper left is the basal archegosauriform *Platyoposaurus watsoni* (no. 91); at the upper right is the dvinosaur *Erpetosaurus radiatus* (no. 76).

Strauss and Sadler (1989) to derive a predicted maximum and minimum for the ranges, given that the observed ranges may underestimate the true range due to sampling artifacts. The use of the estimated expanded ranges provides a conservative test of whether the taxa are more dispersed in morphospace than expected by chance (see Zelditch et al., 2004).

Thus, our four simulated data sets had the following parameters: (1) uniform distribution and observed range (testing clustering under a uniform distribution); (2) uniform distribution and estimated range (testing dispersion under a uniform distribution); (3) Gaussian distribution and observed range (testing clustering under a Gaussian distribution);

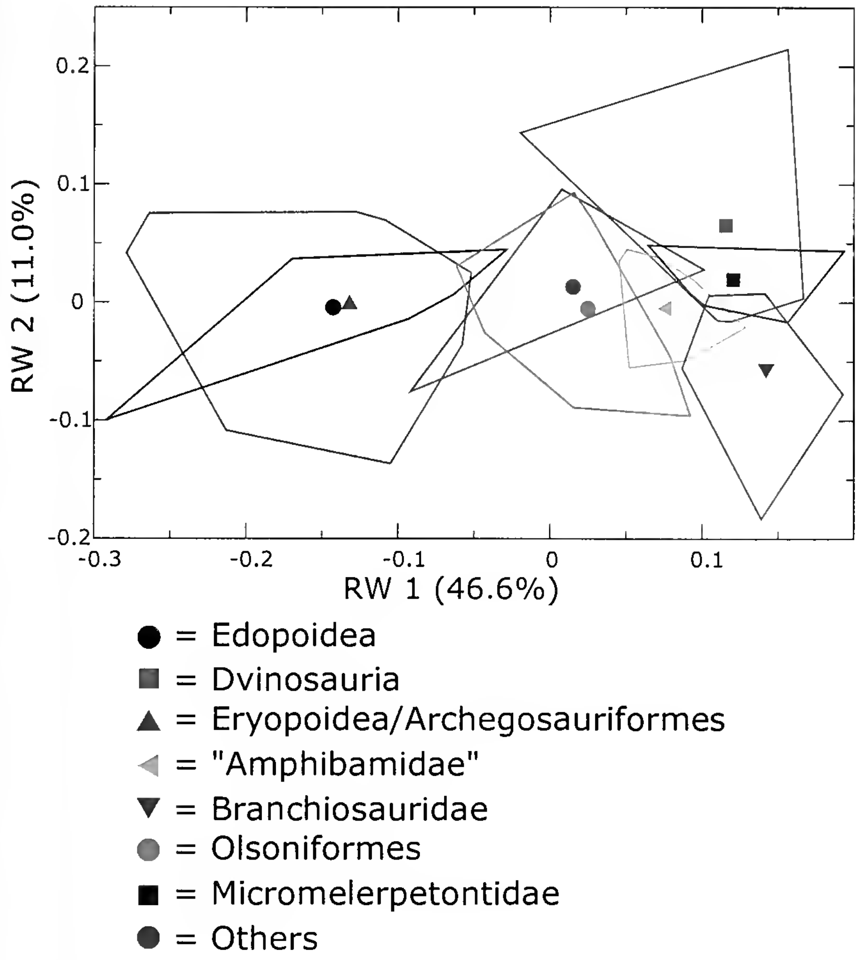

FIG. 4. Plot showing the positions of the mean shapes of the eight major temnospondyl groups in the area of morphospace delimited by relative warp axes 1 and 2 (RW1 and RW2). Convex hulls delimit the regions of morphospace occupied by members of each group (others = taxa of uncertain affinities).

(4) Gaussian distribution and estimated range (testing dispersion under a Gaussian distribution). We used DisparityBox 6h to carry out the nearest-neighbor analyses.

Interspecific Allometry

Recent quantitative studies of changes in temnospondyl skull shape during ontogeny (e.g., Steyer, 2000; Witzmann & Pfretzschner, 2003; Witzmann & Scholz, 2007; Witzmann et al., 2009) suggest that many species undergo fairly stereotyped changes in skull proportions (e.g., elongation of the snout; reduction in size of the orbits) as their size increases. Comparable differences are apparent among several species included in our data set. For example, branchiosaurids tend to be fairly small with relatively short snouts and large orbits, whereas eryopoids and archegosauriforms tend to be much larger with relatively longer snouts and smaller orbits. These observations raise the question of whether there is an underlying relationship between size and shape in temnospondyls that transcends species boundaries and characterizes deeper nodes of the phylogeny. To answer this question, we conducted a series of multivariate regressions of our shape data vs. the natural logarithm of centroid size (a measurement of scale). We first regressed partial warp and uniform component scores for the 94 skull reconstructions against the natural logarithm of centroid size to obtain a general picture of the relationship of size and shape across the whole data set. We also conducted comparable regressions within each of the major groups in Figure 1 to investigate whether the general pattern gleaned from the whole data set could also be observed in individual groups. We carried out all regression analyses in tpsRegr 1.23 (Rohlf, 2003).

Results

Relative Warps Analysis

MAJOR PATTERNS OF SHAPE VARIATION—Results from the relative warps analysis are illustrated in Figures 3 and 4. Anderson's test showed that the first two relative warp axes described significant components of shape variation (respectively, 46.6% and 11%). Therefore, our discussion focuses on these two axes. Relative warp 1 (RW1) primarily captures shape variation associated with snout length, snout width, orbit size, and skull table length. In moving from morphospace regions with high negative values on RW1 to regions with high positive values on RW1, the snout changes from very long and narrow to extremely abbreviated and broad; the orbits change from fairly small to very large; and the anterior portion of the skull table, between the posterior margins of the orbits and the pineal foramen, becomes increasingly elongate anteroposteriorly. Relative warp 2 (RW2) also captures variation associated with snout proportions, orbit size and position, and skull table proportions. In moving from morphospace regions with high negative values on RW2 to regions with high positive values on RW2, the snout becomes narrower and slightly shorter overall, but with marginal elongation of its immediately antorbital areas; the orbits become much smaller, shift slightly anteriorly, and tend to occur slightly closer to one another; and the skull table as a whole becomes narrower and longer (especially in its lateral portions).

The most outstanding pattern of taxon distribution is a clear separation between edopoids (black circles) plus eryopoids–basal archegosauriforms (blue triangles) on the negative side of RW1 and dvinosaurs (red squares) plus dissorophoids (other symbols) on the positive side of RW1. This separation corresponds to a major basal split on the supertree (Fig. 1). Below, we describe the patterns of distribution of major groups in morphospace.

EDOPOIDS—Except for the outlying position of the remarkably long-snouted *Nigerpeton ricqlesi*, edopoids closely overlap eryopoids–basal archegosauriforms, and the means of the two groups are very close to one another. Edopoids show a greater range along RW1 (*Cochleosaurus bohemicus* on the left to *Chenoprosopus lewisi* on the right; low to high negative scores on RW1), and a narrower range along RW2 (*Edops craigi* at the bottom to *Chenoprosopus lewisi* at the top; low negative to low positive scores on RW2). Despite their low taxonomic diversity, edopoids show remarkable skull variation. However, this clade is long-ranging and its fossil record and geographic distribution reveal conspicuous gaps (e.g., Milner & Sequeira, 1998; Sidor et al., 2005). These observations are consistent with the hypothesis that edopoid diversity still remains poorly documented. They further suggest the possible occurrence of mid- to late Permian "refugia" where edopoids continued to diversify and from which they spread geographically (see discussion in Steyer et al., 2006).

ERYOPOIDS AND BASAL ARCHEGOSAURIFORMS—The most outstanding feature of this clade's distribution is the clear separation between zatracheids (five lowermost blue triangles; mid- to high negative scores on RW2; e.g., *Acanthostomatops vorax*, *Dasyceps bucklandi*, *Zatrachys serratus*) and those archegosauriforms that display elongate and slender snouts (five leftmost blue triangles; high negative scores on RW1; e.g., *Archegosaurus decheni*, *Australerpeton cosgriffi*, *Collidosuchus*

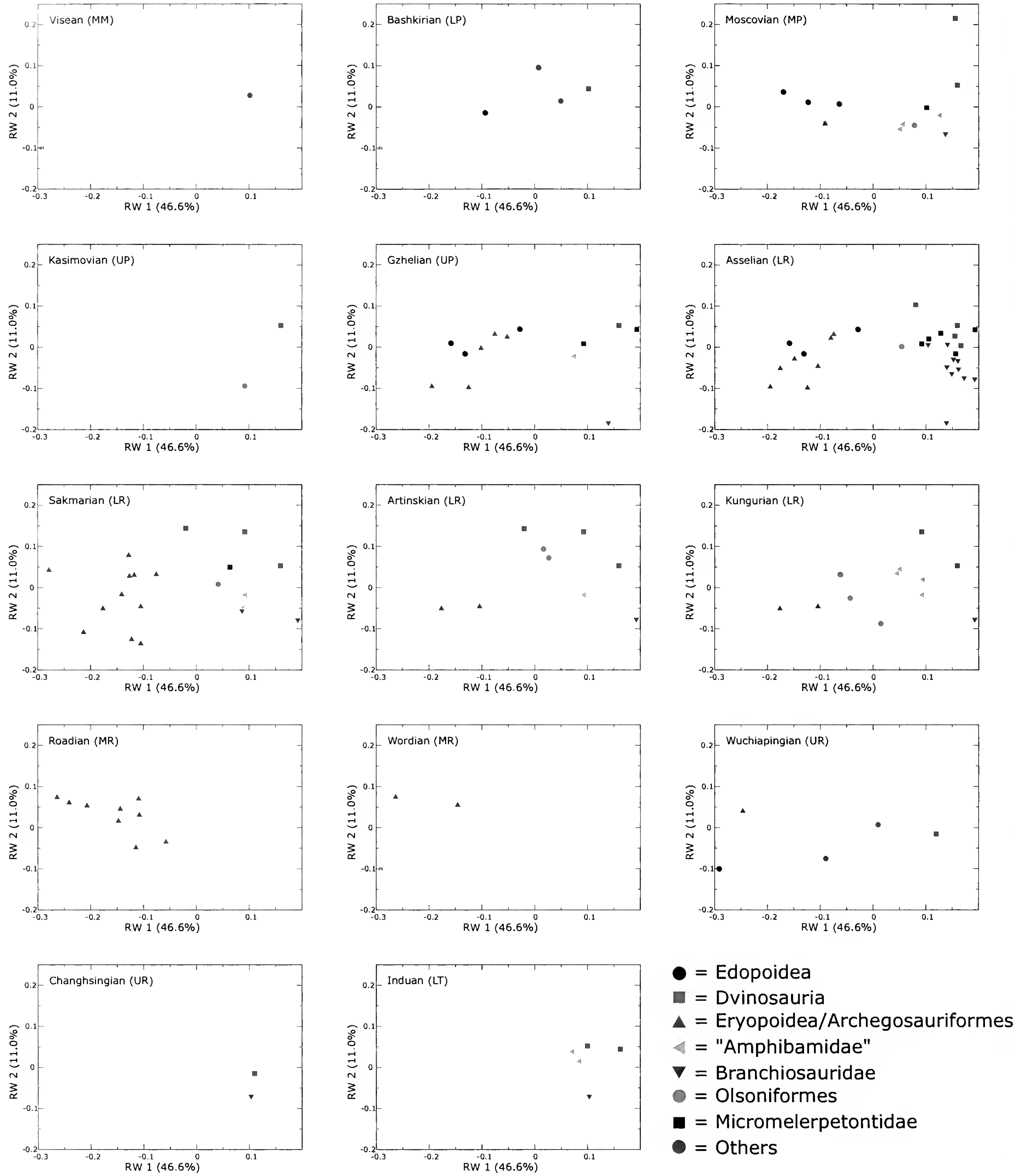

FIG. 5. Plots showing changes in the distribution of temnospondyls in the area of morphospace delimited by relative warp axes 1 and 2 (RW1 and RW2) across 14 stage-level time bins. The oldest time bin is at the upper left and the youngest is at the lowest right. MM = Middle Mississippian; LP = Lower Pennsylvanian; MP = Middle Pennsylvanian; UP = Upper Pennsylvanian; LR = Lower Permian; MR = Middle Permian; UR = Upper Permian; LT = Lower Triassic.

tchudinovi, *Platyoposaurus stuckenbergi*, *Platyoposaurus watsoni*). The remaining taxa in this clade mostly overlap edopoids. Eryopids are adjacent to a diverse array of broad-snouted archegosauriforms (low negative scores on RW2; e.g., *Clamorosaurus borealis*, *Clamorosaurus nocturnus*, *Eryops megacephalus*, *Capetus palustris*, *Onchiodon labyrinthicus*). In turn, these two groups are close to those archegosauriforms that show moderately to very elongate, broad-tipped, and spatulate snouts (low positive scores along RW2; e.g., *Archegosaurus dyscriton*, *Intasuchus sylvicola*, *Konzhukovia vetusta*, *Melosaurus uralensis*). Overall, the pattern of morphospace occupation of basal archegosauriforms shows a "gradient" that is in good agreement with current understanding of major branching events in the phylogeny of this group (e.g., see Schoch & Milner, 2000; Witzmann & Schoch, 2006a; Schoch & Witzmann, 2009a,b).

Dvinosaurs—This group has a heterogeneous distribution, mostly as a result of the wide trimerorhachid scatter (upper right-hand side of the plot; mid- to high positive scores on RW2; e.g., *Erpetosaurus radiatus*, *Neldasaurus wrightae*, *Trimerorhachis insignis*; *Trimerorhachis sandovalensis*). All remaining species (dvinosauroids = eobrachyopids plus dvinosaurids, e.g., Sequeira, 1998; Yates & Warren, 2000; Ruta & Bolt, 2006; Ruta, 2009) form a compact cluster in the right-hand side of the relative warp plot (high positive scores on RW1; low negative to low positive scores on RW2). In this cluster, the eobrachyopids *Isodectes obtusus* and *Acroplous vorax* (two morphs) plot out close to one another and to the tupilakosaurid *Thabanchuia oomie*, some distance from a second tupilakosaurid species, *Tupilakosaurus wetlugensis*. The latter, in turn, is close to *Eugyrinus wildi*—a basal dvinosaur (Milner, 1980) or dvinosauroid (Ruta, 2009).

Dissorophoids—The distribution in morphospace for dissorophoids is best understood with reference to the patterns that characterize individual families. Olsoniforms (i.e., dissorophids and trematopids; yellow circles) are among the most widely distributed of all dissorophoids, as their range stretches from low negative to low positive scores on RW1 (*Acheloma cumminsi* on the left to *Fedexia striegeli* on the right), and from mid-negative to low positive scores on RW2 (*Fedexia striegeli* at the bottom to *Broiliellus brevis* at the top). *Acheloma cumminsi* (a trematopid) and *Cacops morrisi* (a dissorophid) are close to, respectively, the basal archegosauriform *Sclerocephalus bavaricus* and the eryopid *Clamorosaurus borealis*.

Branchiosaurids (purple triangles) are also widely distributed and mostly occupy the bottom right-hand part of the relative warp plot (mid- to high positive scores on RW1; high negative to low positive scores on RW2). Large parts of this range are occupied only by species assigned to the genus *Apateon*: *Apateon pedestris* and *Apateon caducus* represent the extremes of the family's range along RW2, while *Apateon gracilis* and *Apateon flagrifer* bound its range along RW1. The remaining brachiosaurid species cluster in a small area at the far right-hand side of the relative warp plot.

"Amphibamids" (grey triangles) occur approximately in the middle of the area occupied by dissorophoids as a whole (low negative to low positive scores on RW2; low to mid-positive scores on RW1). *Stegops divaricata* and *Perryella olsoni* occupy the extremes of the family range along RW2, while *Doleserpeton annectens* and *Amphibamus grandiceps* delimit its range along RW1. The distribution of the amphibamids invites comparisons with Bourget and Anderson's (2011) morphometric analysis of the group.

Bourget and Anderson (2011) found that the distribution of amphibamids in morphospace agreed with their phylogenetic relationships. Specifically, they found that a monophyletic Amphibamidae consisted of a paraphyletic set of taxa showing longer and narrower skulls and with orbits placed some distance from the otic notches, and a clade with comparatively much wider and shorter skulls and in which the broader orbits occur closer to the otic notches. In addition, they found that the phylogenetic separation between the two morphotypes was mirrored by their presence in separate areas of morphospace. The first morphotype included *Micropholis*, *Pasawioops*, *Tersomius*, and *Rubeostratilia* (not included in our study; see above). *Perryella*, interpreted by Ruta and Bolt (2006) as a dvinosaur, is also a member of this group (e.g., Clack & Milner, 2010). The second morphotype included *Amphibamus*, *Doleserpeton*, *Eoscopus*, *Georgenthalia*, *Platyrhinops*, *Gerobatrachus* (not included due to the fact that its dorsal skull surface awaits further detailed preparation), and *Plemmyradytes* (not included due to its highly disrupted cranial material, and pending revision in the light of additional specimens; Bourget & Anderson, 2011).

Our results largely agree with Bourget and Anderson's (2011), but we note some differences, as follows: (1) near the top of the "amphibamid" range in Figure 3, we observe a small cluster of three species, namely (from left to right) *Doleserpeton annectens*, *Perryella olsoni*, and the more elongate of the two morphotypes of *Micropholis stowi*; (2) slightly below and to the right of the above-mentioned taxa are (left to right) the less elongate of the two morphotypes of *Micropholis stowi* and *Pasawioops mayi*; (3) farther below is a set of taxa arranged in an arc-like pattern and increasingly more widely spaced relative to one another from left to right: *Stegops divaricata*, *Platyrhinops lyelli*, *Eoscopus lockhardi*, *Tersomius texensis*, and *Amphibamus grandiceps*; and (4) finally, somewhat separate from the latter grouping is *Georgenthalia clavinasica*. From the above, it emerges that the separation between two "amphibamid" morphotypes is slightly less evident than in Bourget and Anderson's (2011) analysis, due chiefly to the proximity of *Doleserpeton* to species assigned to the first morphotype, and to the proximity of *Tersomius* to species assigned to the second morphotype. The selection of different landmarks in Bourget and Anderson's (2011) and our analysis, and the different taxonomic samples covered in the two studies, are likely to be responsible for the slightly different results.

Our analysis is further consistent with Milner and Scoch's (2006) preliminary re-assessment of *Stegops divaricata*, which they removed from zatracheids and placed within dissorophoids. In their study, Milner and Schoch (2006: 101A) concluded that "… *Stegops* shares conflicting similarities with Amphibamidae in some [phylogenetic] resolutions and with an *Ecolsonia* + Dissorophidae + Trematopidae clade in others." In our analysis, *Stegops* is close to *Platyrhinops*, although it occurs well within the area of morphospace where olsoniforms are present.

Micromelerpetontids occupy a fairly wide range on RW1 (low to high positive scores; *Micromelerpeton credneri* on the left to *Micromelerpeton ulmetense* on the right), but only a limited range along RW2 (mostly low positive scores; *Micromelerpeton boyi* at the bottom to *Micromelerpeton credneri* at the top). Also, their area of morphospace overlaps extensively that of dvinosauroid dvinosaurs, although the mean shape for all dvinosaurs is somewhat separated from that of micromelerpetontids. Micromelerpetontids are relatively poorly understood, especially as far as their ontogeny is concerned. Recently, additional information on adult (more precisely, metamorphosed) *Micromelerpeton credneri* became available (Lillich & Schoch, 2007; Schoch, 2009), providing a clearer picture of its lifestyle. Metamorphosed specimens of *Micromelerpeton credneri* were described and figured by Boy (1995) and Boy and Sues (2000). According to these authors, this species was facultatively neotenous, and both neotenous and metamorphosed forms lived in different lake horizons. For the purpose of this work, a metamorphosed skull reconstruction was used. We suspect that the wide morphological range of micromelerpetontids is due to the fact that our taxonomic sample includes a heterogeneous collection of larval, juvenile, and adult stages of different species. We also predict that future discoveries are likely to alter the morphometric pattern by showing the group to form a more "coherent" cluster.

OTHER TAXA—Five taxa—*Balanerpeton woodi*, *Dendrerpeton acadianum*, *Dendrerpeton confusum*, *Peltobatrachus pustulatus*, and *Saharastega moradiensis*—are included in an artificial group symbolized by green circles in the relative warp plot. Many of these taxa have very generalized skull morphologies (see discussion in Ruta, 2009), and their affinities with major temnospondyl groups are not unambiguously resolved (e.g., see Milner, 1990; Milner & Sequeira, 1994; Holmes et al., 1998; Holmes, 2000; Sidor et al., 2005; Damiani et al., 2006; Laurin & Soler-Gijón, 2006; Ruta & Bolt, 2006; Steyer et al., 2006; Ruta, 2009). Unsurprisingly, given their very disparate skull shapes, the five taxa in question occupy a wide region of morphospace, and plot out in close proximity to a variety of groups.

The two species of *Dendrerpeton* are quite distinct (Milner, 1980), although they resemble one another in snout proportions and orbit position relative to skull length. *Dendrerpeton acadianum* has comparatively smaller orbits, narrower skull table, and slightly more elongate posterolateral region of the cheek than does *Dendrerpeton confusum*. In the relative warp plot, *Dendrerpeton acadianum* is near the periphery of the olsoniforms, close to the dissorophid *Broiliellus brevis*. *Dendrerpeton confusum* plots near the boundary between olsoniforms (close to the trematopid *Tambachia trogallas* and to the dissorophid/trematopid intermediate *Ecolsonia cutlerensis*) and amphibamids (in particular, it is close to *Doleserpeton annectens* and *Perryella olsoni*). The ambiguous placement of the two *Dendrerpeton* species, even in slightly different versions of the same data matrix (Ruta & Bolt, 2006; Ruta, 2009), confirms the difficulty in identifying features that are uniquely shared by each with a single temnospondyl group (e.g., Milner, 1980, 1990; Holmes et al., 1998; Holmes, 2000).

Balanerpeton woodi occurs in a small area of morphospace where taxa from no fewer than three families are also present, including the amphibamid *Pasawioops mayi* (immediately to the left and slightly below), the micromelerpetontid *Eimerisaurus graumanni* (immediately to the right and slightly below), and the basal dvinosaur or dvinosauroid *Eugyrinus wildi* (immediately above). As with *Dendrerpeton*, *Balanerpeton* does not exhibit a set of derived characters uniquely shared with a particular group. Its age, fairly generalized morphology, and terrestrial adaptations suggest that if this taxon is indeed deeply nested within temnospondyl phylogeny, then most if not all major temnospondyl clades require a range extension minimally dating to the Early Carboniferous to fit current schemes of high-level relationship.

The bizarre *Saharastega moradiensis* possess a confusing combination of primitive and derived features. Ruta (2009) expressed reservations over the original interpretation of this animal as an edopoid, although he did not comment on alternative interpretations. Despite the fact that its skull shape and proportions are very similar to those of certain peltostegid rhytidostean stereospondyls (Schoch & Milner, 2000; Dias-da-Silva & Marsicano, 2011), its palate differs substantially from that of any known peltostegid. In the relative warp plot, *Saharastega* plots close to *Acanthostomatops vorax*, *Zatrachys serratus*, *Clamorosaurus nocturnus*, *Capetus palustris*, and *Onchiodon labyrinthicus*. As reconstructed, the palate of *Saharastega* reveals similar proportions to that of the zatracheids (e.g., strongly arcuate palatal rami of pterygoids, bordering broadly semi-elliptical interpterygoid vacuities; small, widely spaced, and round orbits; broad and elongate snout). However, *Saharastega* shares no obvious synapomorphies with zatracheids, and the similarities listed above appear to be superficial. *Saharastega* also falls out of the range of most edopoids along RW2 (though it still falls within their range on RW1), and we suspect that its position reflects merely its highly apomorphic skull construction.

A final comment concerns *Peltobatrachus pustulatus*, which was digitized from a composite photograph of reassembled skull pieces of the type material (M. Ruta, pers. obs., 2010). Curiously, the position of this taxon in the relative warp plot is very close to the intersection of the relative warp axes, well within the area of morphospace occupied by olsonifoms. This result agrees in part with Milner's (1990) hypothesis that *Peltobatrachus pustulatus* is phylogenetically proximal to the radiation of the dissorophoids. However, the affinities of *Peltobatrachus* remain enigmatic. A reassessment of its position in temnospondyl phylogeny is part of an ongoing study of the type material by one of us (M.R.) together with Drs. Rainer Schoch (Staatliches Museum für Naturkunde, Stuttgart) and Claudia Marsicano (Universidad de Buenos Aires, Argentina). However, recent analyses treated *Peltobatrachus* as a stereospondyl, either in a basal position within the stereospondyl clade or as a relative of the rhytidosteans (e.g., Yates & Warren, 2000; Piñeiro et al., 2007; Schoch et al., 2007; Dias-da-Silva & Marsicano, 2011).

Pair-wise Comparisons of Group Means

With two exceptions, all pair-wise comparisons between group means returned significant results (Table 1). The two exceptions were the comparison between edopoids and eryopoids–basal archegosauriforms, and that between dissorophoids and the five taxa of uncertain affinities. These results are logical when viewed in the context of the relative warps plot showing the positions of group means and convex hulls delimiting the boundaries of the various groups (Fig. 4). These exceptions are the only two cases where groups overlap each other extensively. Although there is overlap among other groups, this tends to be only at the periphery of their convex hulls, such that each group occupies a fairly distinct region of morphospace.

Comparisons Between Morphometric and Phylogenetic Distances

There is a significant concordance between closeness of taxa in morphospace and in the supertree (Mantel test; $R = 0.6562$; $p < 0.05$). As noted above, the phylogenetic separation between edopoids–eryopoids–basal archegosauriforms and dvinosaurs–dissorophoids is largely reflected in the relative positions of these groups in morphospace. Thus, the greatest morphological separation coincides with the deepest internal node of the supertree. These results suggest that skull shape may preserve a strong phylogenetic signal in Carboniferous and Permian temnospondyls. However, given the uncertain

TABLE 1. Results of pair-wise comparisons between mean shapes of the eight major temnospondyl groups in Figure 1. Significant p values (Bonferroni-corrected; $\alpha = 0.0018$) are in bold. The eight groups are numbered in the comparisons as follows: 1 = "Amphibamidae"; 2 = Branchiosauridae; 3 = Olsoniformes; 4 = Dvinosauria; 5 = Edopoidea; 6 = Eryopoidea/basal Archegosauriformes; 7 = Micromelerpetontidae; 8 = others (taxa of uncertain affinities).

Comparison	Goodall's F	Degrees of freedom	p
1 vs. 2	7.30	46, 1012	**<0.0001**
1 vs. 3	3.35	46, 828	**<0.0001**
1 vs. 4	7.07	46, 966	**<0.0001**
1 vs. 5	14.70	46, 782	**<0.0001**
1 vs. 6	21.93	46, 1748	**<0.0001**
1 vs. 7	2.88	46, 736	**<0.0001**
1 vs. 8	2.19	46, 644	**<0.0001**
2 vs. 3	7.37	46, 920	**<0.0001**
2 vs. 4	9.89	46, 1058	**<0.0001**
2 vs. 5	25.59	46, 874	**<0.0001**
2 vs. 6	39.19	46, 1840	**<0.0001**
2 vs. 7	3.03	46, 828	**<0.0001**
2 vs. 8	6.62	46, 736	**<0.0001**
3 vs. 4	5.57	46, 874	**<0.0001**
3 vs. 5	6.43	46, 690	**<0.0001**
3 vs. 6	10.53	46, 1656	**<0.0001**
3 vs. 7	3.24	46, 644	**<0.0001**
3 vs. 8	1.36	46, 552	0.064
4 vs. 5	17.93	46, 828	**<0.0001**
4 vs. 6	31.12	46, 1794	**<0.0001**
4 vs. 7	3.13	46, 782	**<0.0001**
4 vs. 8	3.63	46, 690	**<0.0001**
5 vs. 6	1.24	46, 1610	0.135
5 vs. 7	15.69	46, 598	**<0.0001**
5 vs. 8	4.33	46, 506	**<0.0001**
6 vs. 7	19.77	46, 1564	**<0.0001**
6 vs. 8	6.11	46, 1472	**<0.0001**
7 vs. 8	3.02	46, 460	**<0.0001**

relationships among the main groups, it is necessary to provide stringent tests of this underlying phylogeny, and to examine the strength of the phylogenetic signal using comparative methods (e.g., Klingenberg & Gidaszewski, 2010).

Disparity Analyses

The results of the partial disparity analyses are presented in Tables 2 and 3. For the taxonomic groups, the edopoids and eryopoids–basal archegosauriforms showed the highest partial disparity values, whereas the olsoniforms and the group of taxa with uncertain affinities showed the lowest. Again, such results are consistent with the relative warps plots (Figs. 3 and 4): groups with mean shapes located near the periphery of morphospace contribute larger amounts of disparity than do those with generalized skull shapes located near the grand mean shape of the entire data. Although the correlation between partial disparity and diversity was relatively high (Spearman's $\rho = 0.643$), it was not significant ($p = 0.083$).

Changes in morphospace occupation through time can be found in Figure 5. The Kasimovian, Roadian, and Wordian stages had the highest partial disparities, whereas the Gzhelian, Sakmarian, and Kungurian stages had the lowest partial disparities. Diversity and partial disparity per time bin were significantly *negatively* correlated (Spearman's $\rho = -0.766$, $p = 0.002$). At first glance, this relationship may seem surprising, but it is easily clarified with reference to the plots in Figure 5. Because stages showing high diversity tend to include representatives from many or all of the major taxonomic groups, and because those groups tend to occupy distinct areas of morphospace, the overall mean shapes for these stages are usually relatively close to the position of the overall mean shape for the entire data set. This translates into a low partial disparity using Foote's (1993) metric because the distance between the means is small. Conversely, low-diversity stages tend to include taxa from only one or a few of the major groups, and these taxa are often located toward the periphery of morphospace. In such cases, the mean specimens for the stages are also often located near the edges of morphospace, relatively far from the overall mean shape of the data set. This translates into higher partial disparities for such stages.

The results of the nearest-neighbor analyses are presented in Table 4, and indicate that Paleozoic species are not distributed randomly in morphospace. The first set of analyses, using estimated ranges for calculating the parameters of the null distributions for the Monte Carlo simulations, provides a robust test of whether the specimens are more dispersed in morphospace than expected by chance (as might be expected if factors such as competition actively prevented species from evolving similar shapes). For both the uniform and Gaussian distributions the mean P_{mean} value was negative, with a 95% confidence interval that was also less than zero. This result implies that taxa are closer together in morphospace than predicted by these null models, so it is unlikely that they "repel" one another in morphospace. The second set of analyses, using the observed ranges for calculating the parameters of the null distributions for the Monte Carlo simulations, provides a robust test of whether the taxa are more clustered in morphospace than expected by chance (as might be expected if the taxa tend to occupy more or less the same morphospace areas as their ancestors). Again, for both the uniform and Gaussian distributions, the P_{mean} value was

TABLE 2. Results of partial disparity analysis for the eight major groups of temnospondyls in Figure 1 (others = taxa of uncertain affinities). Standard errors were calculated by bootstrapping (2500 replicates).

Group	Partial disparity	Standard error	Percentage	Number of reconstructions
"Amphibamidae"	0.0011237	0.0013981	6.35	11
Branchiosauridae	0.0029760	0.0012757	16.82	13
Dvinosauria	0.0023457	0.0015182	13.26	12
Edopoidea	0.0040486	0.0012870	22.88	8
Eryopoidea–basal Archegosauriformes	0.0043518	0.0014159	24.59	29
Micromelerpetontidae	0.0015628	0.0014205	8.83	7
Olsoniformes	0.0006702	0.0012240	3.79	9
Others	0.0006172	0.0013163	3.49	5
All reconstructions	0.0176961	0.001914	100	94

TABLE 3. Results of partial disparity analyses of temnospondyls through time. Time bins are stages, and are listed from oldest to youngest. Standard errors were calculated by bootstrapping (2500 replicates).

Stage	Partial disparity	Standard error	Percentage	Number of reconstructions
Bashkirian	0.0003687	0.0012760	2.52	4
Moscovian	0.0002444	0.0019119	1.67	12
Kasimovian	0.0020633	0.0010640	14.09	2
Gzhelian	0.0001412	0.0008796	0.96	13
Asselian	0.0003605	0.0011515	2.46	30
Sakmarian	0.0002075	0.0012704	1.41	20
Artinskian	0.0002893	0.0012331	1.97	9
Kungurian	0.0002021	0.0012768	1.38	12
Roadian	0.0022803	0.0012423	15.57	9
Wordian	0.0045354	0.0019338	30.96	2
Wuchiapingian	0.0013028	0.0009286	8.89	5
Changhsingian	0.0015062	0.0012747	10.28	2
Induan	0.0011451	0.0019309	7.81	5
All stages	0.0146467	0.0023600	100	94

negative with a 95% confidence interval that was also less than zero. This result implies that the specimens are located more closely together than expected by chance. Taken together, these results suggest that there is significant clustering in the overall distribution of species in morphospace.

Interspecific Allometry

Results of the regression analyses are shown in Table 5. We found a strong and significant relationship between size and shape when the complete data set was analyzed. The regression explained slightly more than 30% of the variance in the data. Captured shape variation consists primarily of relative lengthening of the snout, reduction in size of the orbits, and minor skull table shortening as size increases. A significant relationship between size and shape was also evident in edopoids, eryopoids–basal archegosauriforms, "amphibamids," and taxa of uncertain affinities, with regressions capturing between about 10% and 54% of the variance in these data sets. The relationship between size and shape was only marginally nonsignificant in micromelerpetontids ($p = 0.053$), and not significant in dvinosaurs, olsoniforms, and branchiosaurids.

Discussion

During their evolutionary history, temnospondyls rapidly occupied large areas of morphospace, as shown by their spread on the plots of disparity through time (Fig. 5). They maintained high levels of morphospace occupation in the Moscovian, in the time interval from Gzhelian to Kungurian, and in the Wuchiapingian, with four to six different clades contributing to the range of morphological variation in each stage. The intervening stages are characterized by a much sparser occupation of morphospace, but also much lower phylogenetic diversity. Given that several representatives of the missing groups re-appear in later time periods, these sparsely occupied stages are likely to be artifacts of the fossil record. These observations agree well with phylogenetically corrected diversity estimates for temnospondyls (e.g., Milner, 1990; Ruta & Benton, 2008), which imply that numerous lineages must have been present during these stages, but that they have not been sampled. As members of higher taxa tend to occupy relatively consistent areas of morphospace, presumably the "missing" species would fill in many of the empty areas in the Kasimovian, Roadian, and Wordian. The limited morphospace occupation in the aftermath of the end-Permian mass extinction reflects the fact that only two tupilakosaurid dvinosauroids (Warren, 2000), one "amphibamid" (Schoch & Rubidge, 2005), and one branchiosaurid (Werneburg, 2009) represent Triassic temnospondyl diversity in our data set. However, stereospondyl diversity is already high during the Induan (e.g., Schoch & Milner, 2000; Ruta et al., 2007; Ruta & Benton, 2008); therefore, much of the remaining area of morphospace would likely be filled by members of that clade (Stayton & Ruta, 2006).

In their analysis of stereospondyls, Stayton and Ruta (2006) found that there is evidence of morphological conservatism within major groups in that clade, but morphological divergences between the major groups. Our results suggest similar patterns for their Paleozoic relatives. One of the main exceptions to this pattern in our data set is due solely to the artificially created assemblage of species with uncertain affinities (i.e., "others"; Figs. 1, 3, and 4). Therefore, regardless of uncertainty about the cladistic relationships for the major Paleozoic groups, the groups are morphologically quite distinct (see also Ruta, 2009).

Our results are also congruent with those of Stayton and Ruta (2006) in terms of the major axes of shape variation among temnospondyls and in the presence of a strong

TABLE 4. Results of the nearest-neighbor analyses. See main text for explanation of P_{mean}.

Model	Average P_{mean}	95% Range
Uniform distribution-observed range	−0.2943	−0.3582 to −0.2233
Gaussian distribution-observed range	−0.2877	−0.3432 to −0.2120
Uniform distribution-estimated range	−0.2700	−0.3379 to −0.1974
Gaussian distribution-estimated range	−0.2631	−0.3366 to −0.1892

TABLE 5. Results of the regression analyses (others = taxa of uncertain affinities). Significant p values are shown in bold.

Group	Goodall's F	Degrees of freedom	p	Percentage of variance explained
All reconstructions	40.3069	46, 4232	**<0.0001**	30.16
"Amphibamidae"	1.4527	46, 414	**0.0328**	13.83
Branchiosauridae	0.9862	46, 506	0.5012	8.13
Dvinosauria	0.8240	46, 460	0.7885	7.55
Edopoidea	3.9354	46, 276	**<0.0001**	39.12
Eryopoidea-basal Archegosauriformes	3.1134	46, 1242	**<0.0001**	10.26
Micromelerpetontidae	1.4120	46, 230	0.0531	21.97
Olsoniformes	0.9706	46, 322	0.5308	12.02
Others	3.5095	46, 138	**<0.0001**	53.8

relationship between shape and size. The fact that snout length, skull width, orbit size and position, and skull table length are the main aspects of shape variation in both Paleozoic temnospondyls and Mesozoic stereospondyls, and that in both groups increases in size are usually characterized by stereotyped changes in skull shape, suggest that developmental and/or functional constraints may have exerted consistent influence across most of temnospondyl history. Moreover, because each taxonomic group tends to occupy a distinct area of morphospace, the origins of new clades may have been accompanied by modifications of development that "locked" subsequent members of the group into a particular region of morphospace. The potential importance of developmental constraints on skull shape is well illustrated by the groups that differ from the temnospondyl-wide relationship between size and shape. These taxa, olsoniforms, dvinosaurs, and branchiosaurids, are all groups in which heterochronic modification of development is particularly evident, suggesting that such large-scale changes in ontogeny were necessary to escape the constraints working on the clade as a whole.

Despite the presence of such constraints, the fact that disparity correlates strongly with diversity within groups implies that skull shape was not subject to character state exhaustion (Wagner, 2000; that is, decrease or cessation in the acquisition of new morphological conditions during the evolutionary history of a group) and that clades could explore new areas of morphospace within limits. Even in the case of small clades, novel morphological features are accrued continuously during their evolution. A remarkable example of this is exhibited by long-ranging groups, such as edopoids (e.g., Milner & Sequeira, 1998), with extremes in the range of cranial variation extending from small species resembling juvenile alligators (*Adamanterpeton ohioensis*) to extremely large predators with very elongate and robust snouts (e.g., *Nigerpeton ricqlesi*). Likewise, within the dvinosaurs, some taxa display elongate, parabolic, or triangular skulls with small circular orbits situated in the middle of the skull or displaced slightly anteriorly; other taxa resemble gigantic salamanders with very broad and spade-like skulls.

It also seems that major episodes of morphospace exploration coincided with significant increases in net speciation rates (see Ruta et al., 2007). For instance, a Moscovian increase in diversification underpinned the separation between olsoniforms and other dissorophoids, and a Sakmarian increase in diversification marked the beginning of the basal archegosauriform radiation. When the Mesozoic stereospondyl radiation is taken into account, the picture of temnospondyl evolution emerging from comparisons between speciation models and morphospace occupation shows that "pulses" of temnospondyl diversification bracketed narrowly the end-Permian mass extinction. However, there are also some differences in these evolutionary events in that in the Paleozoic, changes in lineage diversification rates mostly occurred along branches connecting major clades, whereas in the Mesozoic, such changes were most common within major clades (Ruta et al., 2007).

Finally, changes in speciation rate and exploration of morphospace were presumably correlated with significant modifications in lifestyle and ecology. Dissorophoids represent a particularly interesting example of this relationship because they experienced a relatively rapid diversification, accompanied by an equally rapid morphological separation between the more terrestrial olsoniform radiation (e.g., Milner, 1990; Reisz et al., 2009) and the largely aquatic "amphibamid"–branchiosaurid–micromelerpetontid radiation (Schoch, 2009; but see Fröbisch & Schoch, 2009a, for a discussion of lifestyle in branchiosaurids). A particularly interesting spin-off of these results is that, if some or all of the extant lissamphibian orders originated from separate dissorophoid families (e.g., Schoch & Milner, 2004; Ruta & Coates, 2007; Anderson et al., 2008b), then the base of the lissamphibian crown-group divergence was presumably more diverse morphologically and ecologically than formerly thought, and the roots of this morphological variety can be traced back to the Carboniferous (cf. San Mauro, 2010). Another example of the correlation between shape and novel ecological shifts can be found among basal archegosauriforms, with long-snouted taxa converging increasingly toward alligator- and gharial-like lifestyles within a predominantly aquatic radiation (e.g., Schoch & Milner, 2000).

We hope that the present research will initiate novel quantitative treatments of the crown-group tetrapod emergence, using old and new comparative anatomical data in a combined phylogenetic and morphometric synthesis.

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We dedicate this paper to our esteemed colleague and friend, John Bolt, in recognition of his numerous outstanding contributions to vertebrate paleontology. John's research has shed light on the apical part of the tetrapod stem-group and on the base of the tetrapod crown radiation, and continues to bear fruit in the form of remarkable fossil discoveries. Although primarily a taxonomist and comparative anatomist with a refined eye for subtle morphological features, John has

embraced and followed enthusiastically several other areas of paleontological research, with interests spanning from phylogeny and macroevolutionary analysis to taphonomy and functional morphology. Therefore, we hope that the present contribution will appeal to him.

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Appendix

List of taxa included in the morphometric analysis; the number accompanying each taxon refers to the order in which the taxon was digitized; these numbers identify the position of taxa in the morphospace in Figure 3B. In the case of four taxa, an additional specimen was digitized: *Micropholis stowi* (two skull morphotypes: Schoch & Rubidge, 2005); *Acanthostomatops vorax* (two of the largest known specimens: Witzmann & Schoch, 2006b); *Zatrachys serratus* (two of the largest known specimens: Schoch, 1997); *Acroplous vorax* (collection from Kansas: Foreman, 1990; collection from Nebraska: Englehorn et al., 2008). UCMP = University of California Museum of Paleontology, Berkeley, USA; LFUG = Landesamt für Umwelt und Geologie, Freiberg, Germany.

List of Taxa in the Order in which They Were Digitized

Acanthostomatops vorax (LFUG 13232) = 1; *Acheloma cumminsi* = 2; *Adamanterpeton ohioensis* = 3; *Amphibamus grandiceps* = 4; *Apateon gracilis* = 5; *Archegosaurus decheni* = 6; *Archegosaurus dyscriton* = 7; *Australerpeton cosgriffi* = 8; *Balanerpeton woodi* = 9; *Capetus palustris* = 10; *Cochleosaurus bohemicus* = 11; *Collidosuchus tchudinovi* = 12; *Dasyceps bucklandi* = 13; *Doleserpeton annectens* = 14; *Eugyrinus wildi* = 15; *Intasuchus sylvicola* = 16; *Konzhukovia vetusta* = 17; *Melosaurus uralensis* = 18; *Micropholis stowi* (more elongate morphotype) = 19; *Micropholis stowi* (less elongate morphotype) = 20; *Nigerpeton ricqlesi* = 21; *Onchiodon labyrinthicus* = 22; *Peltobatrachus pustulatus* = 23; *Perryella olsoni* = 24; *Platyoposaurus stuckenbergi* = 25; *Saharastega moradiensis* = 26; *Sclerocephalus haeuseri* = 27; *Syndyodosuchus tetricus* = 28; *Tambachia trogallas* = 29; *Tersomius texensis* = 30; *Thabanchuia oomie* = 31; *Dissorophus multicinctus* = 32; *Iberospondylus schultzei* = 33; *Phonerpeton pricei* = 34; *Dvinosaurus egregius* = 35; *Apateon flagrifer* = 36; *Apateon kontheri* = 37; *Melanerpeton eisfeldi* = 38; *Georgenthalia clavinasica* = 39; *Apateon caducus* = 40; *Apateon dracyiensis* = 41; *Apateon pedestris* = 42; *Acroplous vorax* (Nebraska) = 43; *Eoscopus lockhardi* = 44; *Pasawioops mayi* = 45; *Acanthostomatops vorax* (LFUG 13245) = 46; *Branchierpeton saalensis* = 47; *Cacops morrisi* = 48; *Dendrerpeton acadianum* = 49; *Dendrerpeton confusum* = 50; *Edops craigi* = 51; *Eryops megacephalus* = 52; *Glanochthon angusta* = 53; *Glanochthon latirostre* = 54; *Kashmirosaurus ornatus* = 55; *Leptorophus tener* = 56; *Neldasaurus wrightae* = 57; *Platyrhinops lyelli* = 58; *Schoenfelderpeton prescheri* = 59; *Trimerorhachis insignis* = 60; *Tupilakosaurus wetlugensis* = 61; *Branchiosaurus salamandroides* = 62; *Chenoprosopus milleri* = 63; *Melanerpeton humbergense* = 64; *Melanerpeton sembachense* = 65; *Tungussogyrinus bergi* = 66; *Broiliellus brevis* = 67; *Chenoprosaurus* *lewisi* = 68; *Cochleosaurus florensis* = 69; *Ecolsonia cutlerensis* = 70; *Eimerisaurus guembeli* = 71; *Procochleosaurus jarrowensis* = 72; *Zatrachys serratus* (UCMP 34158) = 73; *Zatrachys serratus* (UCMP 34157) = 74; *Micromelerpeton credneri* = 75; *Erpetosaurus radiatus* = 76; *Limnogyrinus elegans* = 77; *Eimerisaurus graumanni* = 78; *Micromelerpeton boyi* = 79; *Micromelerpeton ulmetense* = 80; *Mordex laticeps* = 81; *Stegops divaricata* = 82; *Acroplous vorax* (Kansas) = 83; *Cheliderpeton vranyi* = 84; *Clamorosaurus borealis* = 85; *Clamorosaurus nocturnus* = 86; *Dvinosaurus primus* = 87; *Fedexia striegeli* = 88; *Isodectes obtusus* = 89; *Onchiodon thuringiensis* = 90; *Platyoposaurus watsoni* = 91; *Sclerocephalus bavaricus* = 92; *Sclerocephalus jogischneideri* = 93; *Trimerorhachis sandovalensis* = 94.

List of Taxa in Alphabetical Order; References Include Skull Images Used for Landmark Selection

Acanthostomatops vorax (LFUG 13232) = 1 (Witzmann & Schoch, 2006b); *Acanthostomatops vorax* (LFUG 13245) = 46 (Witzmann & Schoch, 2006b); *Acheloma cumminsi* = 2 (Dilkes & Reisz, 1987); *Acroplous vorax* (Kansas) = 83 (Foreman, 1990); *Acroplous vorax* (Nebraska) = 43 (Englehorn et al., 2008); *Adamanterpeton ohioensis* = 3 (Milner & Sequeira, 1998); *Amphibamus grandiceps* = 4 (Bolt, 1979); *Apateon caducus* = 40 (Fröbisch & Schoch, 2009b); *Apateon dracyiensis* = 41 (Werneburg, 2001); *Apateon flagrifer* = 36 (Boy, 1987); *Apateon gracilis* = 5 (Werneburg, 1991; Schoch & Fröbisch, 2006); *Apateon kontheri* = 37 (Werneburg, 1988a); *Apateon pedestris* = 42 (Schoch, 1992); *Archegosaurus decheni* = 6 (Witzmann, 2006; new skull reconstruction kindly supplied by Dr Florian Witzmann); *Archegosaurus dyscriton* = 7 (Milner, 1978); *Australerpeton cosgriffi* = 8 (Barberena, 1998); *Balanerpeton woodi* = 9 (Milner & Sequeira, 1994); *Branchierpeton saalensis* = 47 (Werneburg, 1988b); *Branchiosaurus salamandroides* = 62 (Schoch & Milner, 2008); *Broiliellus brevis* = 67 (Carroll, 1964); *Cacops morrisi* = 48 (Reisz et al., 2009); *Capetus palustris* = 10 (Sequeira & Milner, 1993); *Cheliderpeton vranyi* = 84 (Schoch & Milner, 2000); *Chenoprosaurus lewisi* = 68 (Hook, 1993); *Chenoprosopus milleri* = 63 (Langston, 1953); *Clamorosaurus borealis* = 85 (Gubin, 1983); *Clamorosaurus nocturnus* = 86 (Gubin, 1983); *Cochleosaurus bohemicus* = 11 (Sequeira, 2004); *Cochleosaurus florensis* = 69 (Godfrey & Holmes, 1995); *Collidosuchus tchudinovi* = 12 (Gubin, 1986); *Dasyceps bucklandi* = 13 (Paton, 1975); *Dendrerpeton acadianum* = 49 (Holmes et al., 1998); *Dendrerpeton confusum* = 50 (Milner, 1980); *Dissorophus multicinctus* = 32 (DeMar, 1968); *Doleserpeton annectens* = 14 (Sigurdsen & Bolt, 2010); *Dvinosaurus egregius* = 35 (Shishkin, 1973); *Dvinosaurus primus* = 87 (Shishkin, 1973); *Ecolsonia cutlerensis* = 70 (Berman et al., 1985); *Edops craigi* = 51 (Romer & Witter, 1942); *Eimerisaurus graumanni* = 78 (Boy, 2002b); *Eimerisaurus guembeli* = 71 (Boy, 2002b); *Eoscopus lockhardi* = 44 (Daly, 1994); *Erpetosaurus radiatus* = 76 (Milner & Sequeira, 2011; new skull reconstruction kindly supplied by Dr Andrew Milner); *Eryops megacephalus* = 52 (Sawin, 1941); *Eugyrinus wildi* = 15 (Milner, 1980); *Fedexia striegeli* = 88 (Berman et al., 2009); *Georgenthalia clavinasica* = 39 (Anderson et al., 2008a); *Glanochthon angusta* = 53 (Schoch & Witzmann, 2009a); *Glanochthon latirostre* = 54 (Schoch & Witzmann, 2009a); *Iberospondylus schultzei* = 33 (Laurin & Soler-Gijón, 2006); *Intasuchus sylvicola* = 16 (Gubin, 1984); *Isodectes obtusus* = 89 (new skull reconstruction kindly supplied by Dr Andrew Milner); *Kashmirosaurus ornatus* = 55 (Werneburg & Schneider, 1996); *Konzhukovia vetusta* = 17 (Gubin, 1991); *Leptorophus tener* = 56 (Boy, 1986); *Limnogyrinus elegans* = 77 (new skull reconstruction kindly supplied by Dr Andrew Milner); *Melanerpeton eisfeldi* = 38 (Werneburg, 1988a); *Melanerpeton humbergense* = 64 (Boy, 1978); *Melanerpeton sembachense* = 65 (Werneburg, 1989); *Melosaurus uralensis* = 18 (Gubin, 1993); *Micromelerpeton boyi* = 79 (Boy, 2002a); *Micromelerpeton credneri* = 75 (Schoch, 2009; new skull reconstruction kindly supplied by Dr Rainer Schoch); *Micromelerpeton ulmetense* = 80 (Boy, 2002a); *Micropholis stowi* (more elongate skull morphotype) = 19 (Schoch & Rubidge, 2005); *Micropholis stowi* (less elongate skull morphotype) = 20 (Schoch & Rubidge, 2005); *Mordex laticeps* = 81 (new skull reconstruction kindly supplied by Dr Andrew Milner); *Neldasaurus wrightae* = 57 (Chase, 1965); *Nigerpeton ricqlesi* = 21 (Steyer et al., 2006); *Onchiodon labyrinthicus* = 22 (Schoch & Milner, 2000); *Onchiodon thuringiensis* = 90 (Werneburg, 2008); *Pasawioops mayi* = 45 (Fröbisch & Reisz, 2008); *Peltobatrachus pustulatus* = 23 (Panchen, 1959; M.R., pers. obs.); *Perryella olsoni* = 24 (Ruta & Bolt, 2006); *Phonerpeton pricei* = 34 (Dilkes, 1990); *Platyoposaurus stuckenbergi* = 25 (Gubin,1991); *Platyoposaurus watsoni* = 91 (Ivakhnenko, 1987); *Platyrhinops lyelli* = 58 (Clack & Milner, 2010); *Procochleosaurus jarrowensis* = 72 (Sequeira, 1996); *Saharastega moradiensis* = 26 (Damiani et al., 2006); *Schoenfelderpeton prescheri* = 59 (Boy, 1986); *Sclerocephalus bavaricus* = 92 (Schoch & Milner, 2000); *Sclerocephalus haeuseri* = 27 (Schoch & Witzmann, 2009b); *Sclerocephalus jogischneideri* = 93 (Schoch & Witzmann, 2009b); *Stegops divaricata* = 82 (new skull reconstruction kindly supplied by Dr Andrew Milner); *Syndyodosuchus tetricus* = 28 (Gubin, 1984); *Tambachia trogallas* = 29 (Sumida et al., 1998); *Tersomius texensis* = 30 (Carroll, 1964); *Thabanchuia oomie* = 31 (Warren, 1999); *Trimerorhachis insignis* = 60 (Case, 1935); *Trimerorhachis sandovalensis* = 94 (Berman & Reisz, 1980); *Tungussogyrinus bergi* = 66 (Werneburg, 2009); *Tupilakosaurus wetlugensis* = 61 (Shishkin, 1973); *Zatrachys serratus* (UCMP 34157) = 74 (Schoch, 1997); *Zatrachys serratus* (UCMP 34158) = 73 (Schoch, 1997).

Chapter 5: Evolution of the Amphibian Ear with Implications for Lissamphibian Phylogeny: Insight Gained from the Caecilian Inner Ear

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Abstract

The inner ear is a complex structure consisting of the vestibular and auditory systems. Across vertebrates, morphological variation in the inner ear provides a source of homologous features (characters) that may aid in resolving phylogenetic relationships. The morphology of the inner ear in extant frogs and salamanders is well known, and has been extensively studied from functional perspectives. However, the ability of its form and features to shed light on the broader question of lissamphibian origins and relationships has not been as thoroughly explored. Herein we review the morphology of the inner ear of the least well-known lissamphibian group, the caecilians, and present three-dimensional reconstructions of otic capsule endocasts and of soft-tissue labyrinths. We use these data to explore previous statements about the structure of the caecilian inner ear and its evolutionary significance. The postulate that the periotic canal has a posterior path is corroborated, and the periotic sacs of each ear are observed to extend into the brain cavity, where they are applied to a fluid-filled compartment that is located ventral to the brain. These features are shared with frogs and salamanders. Additionally, it is hypothesized that the regression of two endorgans in caecilians is correlated with the secondary loss of the two middle ear auditory pathways, the tympanum–stapes and opercularis hearing pathway, suggesting that the lissamphibian-type ear is present, but in a derived state in caecilians. Identification of osteological correlates of this lissamphibian-type ear permits the interpretation of the evolution of this distinct ear type in the context of the three competing hypotheses of lissamphibian phylogeny. The distribution of traits is shown to be most parsimoniously explained when optimized onto the phylogenetic pattern that incorporates a monophyletic temnospondyl-derived Lissamphibia. This interpretation is consistent with a single origin of a lissamphibian-type tympanic ear. Therefore, characters of the ear seemingly provide synapomorphies that unite lissamphibians with amphibamid temnospondyls, potentially improving the resolution of concepts about the affinities of frogs, salamanders, and caecilians and clarifying issues of tetrapod ear evolution.

Introduction

The inner ear is a complex structure that is contained within the otic capsules, and consists of the vestibular apparatus (the membranous semicircular canals and utricle), which perceives angular and linear acceleration, and the auditory apparatus (saccule, lagena, and various derived organs) that perceives sound. The inner ear has attracted much attention with regard to its morphology (e.g., Retzius, 1881, 1884; de Burlet, 1934; Baird, 1974; Lombard, 1977; Wever 1978, 1985), function (e.g., Lewis et al., 1982; Hetherington, 1985), and evolution (e.g., Lombard & Bolt, 1979; Bolt & Lombard, 1985; Fritzsch, 1987, 1992; Clack, 2002; Fay & Popper, 2000). In its simplest form, represented by the condition seen in extant non-gnathostome craniates, the ear contains one (hagfish) or two (lamprey) semicircular canals, their associated ampullae and cristae (sensory epithelia), and a ventrally located, central sensory epithelium termed the macula communis (Fig. 1A,B). Along the stem of gnathostomes the pattern of the inner ear evident in basal craniates became modified. The morphology of the inner ear in chondrichthyans, osteichthyans, and subsequently in tetrapods is considered to be derived and structurally more complex than that of basal craniates. The appearance of three semicircular canals (including the horizontal canal) and the differentiation of the ventral region of the inner ear, containing the macula communis, into discrete organs, each with its own sensory epithelium (saccular, lagenar, and utricular maculae), occurred in the stem gnathostome lineages (Fig. 1C). These represent key events in the evolution of the craniate ear and in the elaboration of audition.

The inner ear of gnathostomes (chondrichthyans, osteichthyans, and tetrapods) remains relatively consistent throughout their evolutionary history, and homologous structures and their derivatives are recognizable in most taxa (Fritzsch, 1992; Platt et al., 2004). This is especially true of the vestibular apparatus, wherein three orthogonally oriented semicircular canals, their ampullae, and the utricle are ubiquitously present (Fig. 1C–F; Platt & Popper, 1981; Platt, 1983).

The auditory apparatus, on the other hand, has undergone a number of changes throughout its evolution, many of which are functionally related to the water-to-land transition and the subsequent radiations of terrestrial vertebrates, and are

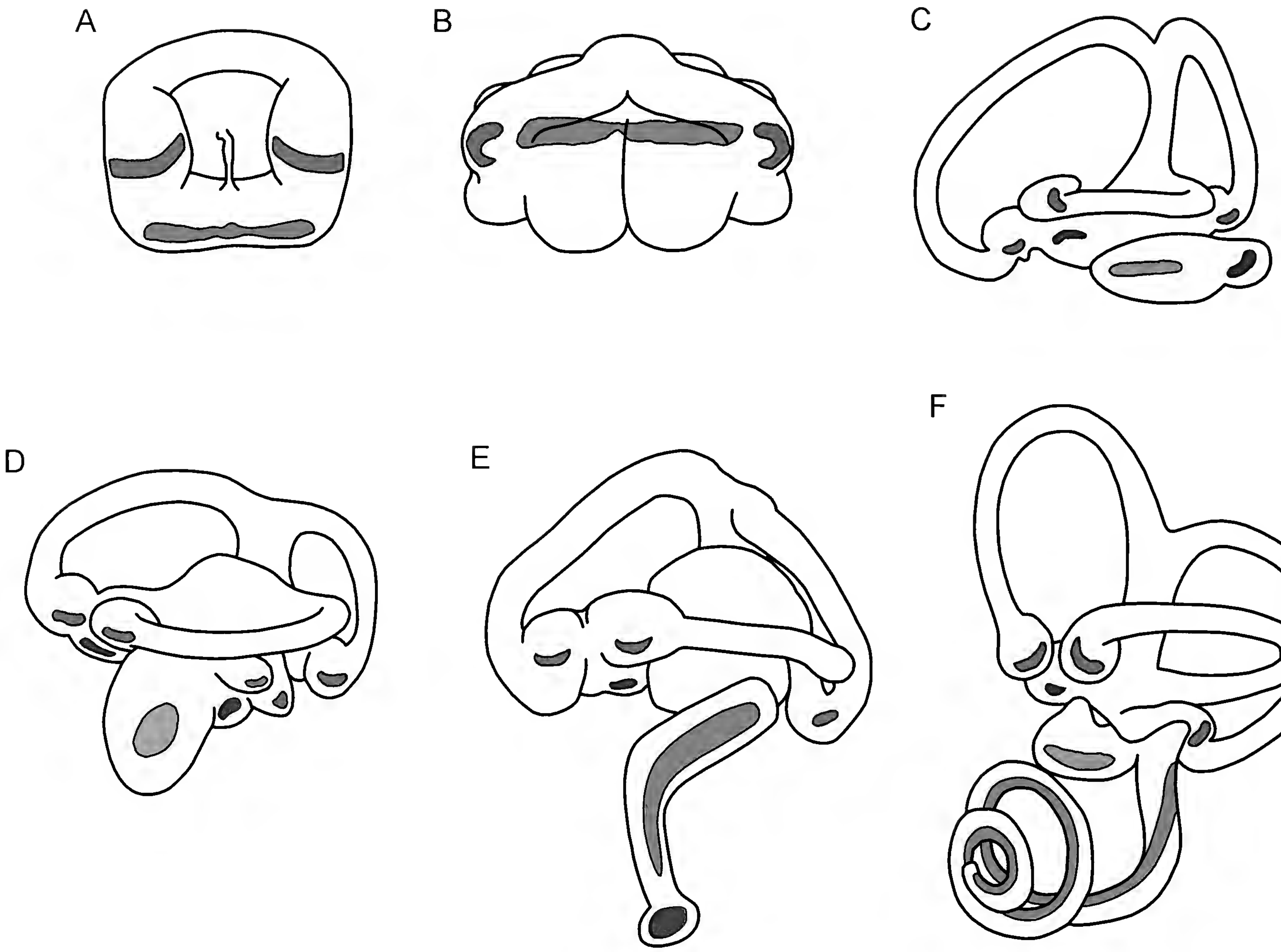

FIG. 1. Schematic illustrations of the left inner ear of various vertebrates in lateral view. (**A**) and (**B**), hagfish (myxinoid) and lamprey (petromyzontoid), respectively, with their one and two semicircular canals, respectively and associated cristae (red). The relatively simple morphology of the inner ear, with its undifferentiated macula (orange), is modified in gnathostome vertebrates (**C–F**). (**C**) A teleost fish with discrete utricular (purple), saccular (pink), and lagenar (blue) maculae; (**D**) a frog showing the presence the unique amphibian papilla (green); (**E**) a crocodile showing the modified basilar papilla (yellow); (**F**) a mammal showing the further modification to the basilar papilla, the coiled cochlear organ. Images not to scale (**A** and **B** modified from Horodysky et al., 2008; **C**, **D**, and **F** modified from Romer, 1962; **E**, modified from Khorevin, 2008).

correlated with concerted evolution of the outer and middle ear (Fritzsch, 1992; Clack, 2002; Christensen-Dalsgaard & Carr, 2008). At the forefront of these changes are those associated with the detection of airborne sounds that are correlated with certain modifications to the inner ear, and ultimately the evolution of the tympanic ear, a tetrapod novelty. The tympanic ear, comprised of outer (tympanum) and middle ear (middle ear cavity and ossicle[s]) components, permits the impedance mismatch between air and the fluid of the inner ear to be overcome, enabling airborne sound to reach the auditory epithelia.

The ears of groups of tetrapods that possess a tympanic system are distinguished from one another by a number of unique features, and this has led researchers to hypothesize that the tympanic ears are evolutionarily unrelated (Olson, 1966; Lombard & Bolt, 1979; Clack, 2002; Mason, 2007). For example, in mammalian amniotes the basilar papilla has been dramatically modified into the primary auditory organ, the cochlea (Fig. 1E, F; Fritzsch & Beisel, 2001). Lengthening of the basilar papilla increases the auditory range through mechanical tuning, resulting in high-frequency sound perception (Evans, 1936; Manley, 2000), and this property likely is correlated with the coiling of the structure (Fig. 1F). This ear type is correlated with the independent acquisition of a tympanum and a unique complement of middle ear ossicles (stapes, incus, and malleus).

In contrast, the basilar papilla of anuran tetrapods (frogs) is small. This may be because the frog ear is neurologically tuned to ranges of frequencies (Lewis, 1988), rather than predominantly mechanically as it is in amniotes (Manley, 2000), thereby allowing a broad range of frequency sensitivity within a small sensory structure. Additionally, the non-amniote ear is correlated with the independent acquisition of a tympanum and another unique complement of middle ear ossicles (stapes, and sometimes an operculum).

One question that structural variation in the inner ear may contribute to is resolution of the continuing debate about the relationships between frogs, salamanders, and caecilians, and the identity of their closest fossil relatives. Recent analyses continue to challenge the conventional hypothesis that the three groups of lissamphibians comprise a monophyletic cluster that is derived from within Temnospondyli (the temnospondyl hypothesis [TH]; Bolt, 1969; Trueb & Cloutier, 1991; Milner, 1988, 1993; Ruta et al., 2003; Ruta & Coates, 2007). Alternative hypotheses advocate either a polyphyletic

TABLE 1. Histologically prepared specimens examined in the current study. All histological specimens are curated in the lab of M. H. Wake (S-book numbers; University of California, Berkeley).

Species	Total length of specimen (mm)	S-book number (MHW)	Specimen number
Boulengerula boulengeri	171	239	MHW* 9004
Chthonerpeton indistinctum	unavailable	275	R. de Sá 108
Dermophis mexicanus	415	255A/B	MVZ 178976
	305	254	MVZ 178906
Epicrionops bicolor	161	425	LSUMZ 27254
Geotrypetes seraphini	180	143	MHW 548
Gymnopis multiplicata	200	166	CRE 2783
Hypogeophis rostratus	218	183	MHW 428
Ichthyophis glutinosus	334	222	MHW 1002
Oscaecilia ochrocephala	434	242	MHW O-2
Scolecomorphus kirkii	275	230	MCZ 27115
Typhlonectes natans	321	171	MVZ 179713

* Abbreviations: MHW, M. H. Wake collection, University of California, Berkeley, CA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, CA; LSUMZ, Louisiana State University Museum of Natural Science, Louisiana State University, Baton Rouge, LA; CRE, Costa Rican Expedition, J. M. Savage collection, University of Miami, FL (uncatalogued material curated in the laboratory of M. H. Wake, University of California, Berkeley, CA); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA.

"Lissamphibia", wherein frogs and salamanders cluster with temnospondyls, and caecilians with Lepospondyli (the polyphyly hypothesis [PH]; Carroll, 2007; Anderson et al., 2008), or a monophyletic Lissamphibia derived from within Lepospondyli (the lepospondyl hypothesis [LH]; Laurin & Reisz, 1997; Vallin & Laurin, 2004; Marjanovic & Laurin, 2008).

The presence of osteological correlates of inner ear morphology and function permit the incorporation of fossil taxa into discussions relating to ear evolution (Lombard & Bolt, 1979; Bolt & Lombard, 1985; Clack, 1997). These correlates include morphology of the otic region (e.g., temporal embayment or otic notch), the middle ear ossicles (e.g., stapes), as well as the general morphology of the otic capsule, including the foramina pertaining to relevant inner ear structures and organs (e.g., perilymphatic foramen versus an open medial wall).

One of the greatest impediments to the resolution of this debate has been the relatively poor understanding of basic anatomy and morphology, and subsequently variation, including that of the inner ear, within Gymnophiona. This has led to problems in interpreting plesiomorphic states for Lissamphibia, making inferences of phylogeny on the basis of morphology more difficult.

The inner ear of caecilians has been examined in several species (Wever, 1975, 1985; Wever & Gans, 1976; Fritzsch & Wake, 1988), but its contribution to broad-scale phylogenetic problems has not been fully explored. The middle and outer ear auditory pathways are limited in caecilians, rendering these regions anatomically much simpler than they are in frogs (tympanic and opercularis pathways) and salamanders (opercularis pathway). The stapes, which fills the entire fenestra vestibuli, is the only middle ear ossicle of caecilians, and it articulates with the quadrate distally; therefore, a tympanic ear is absent (Wever, 1985). An operculum is unknown among extant caecilians.

The focus of the current investigation is to re-examine the anatomy and morphology of the inner ear in caecilians to assess its utility in shedding light on the relationships between caecilians and the other lissamphibians, and between extant lissamphibians and their putative extinct relatives. The observations are discussed within the context of the three competing hypotheses of lissamphibian phylogeny, through the synthesis of data pertaining to the ear of both extinct and extant vertebrates.

Materials and Methods

Histologically Prepared Specimens

Previously prepared histological specimens of 11 species of caecilians were available for examination (Table 1). Specimens were prepared in frontal, parasagittal, or transverse orientations, and thicknesses range from 7 to 12 μm. Slides were stained with hematoxylin and eosin, picroponceau, or Mallory's trichrome (Table 1; S-book numbers pertain to the catalogue in the laboratory of M. H. Wake, University of California, Berkeley).

Three of the species, *Gymnopis multiplicata, Dermophis mexicanus,* and *Geotrypetes seraphini*, were sufficiently well preserved to permit the generation of three-dimensional reconstructions from the histological sections (Table 1). Each histological section in a series was digitized using a Nikon Coolpix digital camera. Photographs (eight-bit, grayscale jpegs) were imported into the Amira v.5® software package (Visage Imaging, San Diego, CA), aligned using the AlignSlices module, and the different structures of the inner ear were isolated by applying the LabelField module to the aligned data set. The SurfaceGen and SurfaceView modules were applied to the labeled data tab to visualize the isolated structures.

High-Resolution Microcomputed Tomography

High-resolution microcomputed tomography (hrμCT) was performed on representative specimens of each species for which complementary histological data were available. Scans were conducted using either a Scanco μCT35 scanner (55 kVp, 72 μA) or SkyScan 1173 scanner, at voxel resolutions ranging between 12 μm^3 and 20 μm^3 depending on the size of the specimen (Table 2). The reconstructed data were analyzed in Amira v.5® (Visage Imaging, San Diego, CA). Endocasts of the otic capsules were extracted using the LabelField module by selecting the void space. The locations of the various

TABLE 2. Specimens analyzed using a Scanco µCT35 (55kVp, 70 µA) or SkyScan 1173, and the voxel resolutions.

Species	Total length (mm)	Specimen number	Resolution (µm^3)	Scanner
Boulengerula boulengeri	176	FMNH* 189157	12	Scanco
Chthonerpeton indistinctum	229	FMNH 206622	12	Scanco
Dermophis mexicanus	skull only	UMMZ 219030	20	Scanco
Epicrionops bicolor	185	FMNH 152310	12	Scanco
Geotrypetes seraphini	292	FMNH 189099	12.1	SkyScan
Gymnopis multiplicata	390	KU 79951	20	SkyScan
Hypogeophis rostratus	210	FMNH 187128	12	Scanco
Ichthyophis beddomei	242	FMNH 189230	15.6	SkyScan
Oscaecilia ochrocephala	264	FMNH 153627	12	Scanco
Scolecomorphus kirkii	339	FMNH 233340	12	Scanco
Typhlonectes natans	unknown	FMNH 98887	12	Scanco

* Abbreviations: FMNH, Field Museum of Natural History, Chicago, IL; UMMZ, University of Michigan Museum of Zoology, University of Michigan, Ann Arbor, MI; KU, Natural History Museum, University of Kansas, Lawrence, KS.

foramina were also selected to reveal their relative positions on the endocast. The endocast models were visualized using the SurfaceGen and SurfaceView modules.

Results

Description of the Inner Ear of Caecilians

Detailed anatomical descriptions of the inner ear in caecilians have been provided previously, largely on the basis of histological series of a few species (see Sarasin & Sarasin, 1887–1890; Retzius, 1891; Wever, 1975, 1985; Lombard, 1977; Wever & Gans, 1976; Fritzsch & Wake, 1988). However, the gross morphology is less well understood for many species, and will be described here on the basis of endocasts generated from hrµCT (Fig. 2) and three-dimensional models constructed from histological sections (Figs. 3 and 4).

The caecilian inner ear is composed of an endolymphatic labyrinth (Fig. 3E, F) and a perilymphatic labyrinth (Fig. 3G, H). The endolymphatic labyrinth is divisible into the dorsally located vestibular apparatus (pars superior; Fig. 3A, B) and the ventrally located auditory chamber (pars inferior; Fig. 3A, B). The vestibular apparatus contains the three semicircular canals and the utricle. The semicircular canals are oriented

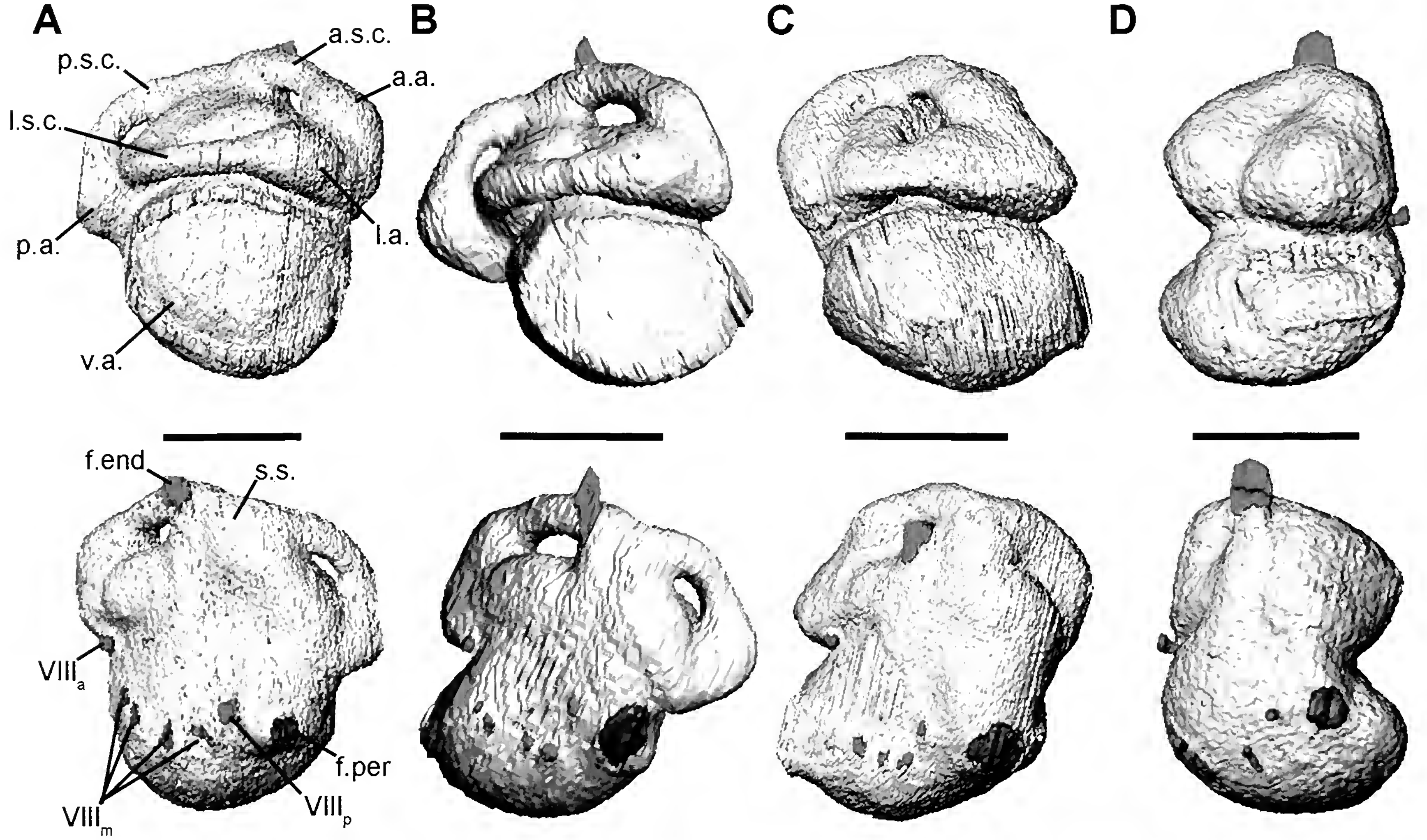

FIG. 2. Endocasts of the right otic capsule from species sampled widely across caecilian phylogeny, showing the great diversity of form, and the relative positions of the endolymphatic foramen (f.end; yellow), perilymphatic foramen (f.per; brown), and branches of the vestibulocochlear nerve (VIII$_{a,m,p}$: orange). (**A**) *Epicrionops bicolor* in lateral (top) and medial (bottom) view. (**B**) *Ichthyophis beddomei* in lateral and medial view. (**C**) *Gymnopis multiplicata* in lateral and medial view. (**D**) *Oscaecilia ochrocephala* in lateral and medial view. Abbreviations: a.a., anterior ampulla; a.s.c., anterior semicircular canal; l.a., lateral ampulla; l.s.c., lateral semicircular canal; p.a., posterior ampulla; p.s.c., posterior semicircular canal; s.s., superior sinus; v.a., ventral auditory region. Scale bars equal 1 mm.

roughly orthogonally to one another, and the entire apparatus is oriented within the head such that the anterior and posterior semicircular canals occur at 45° angles to the midline of the head when viewed dorsally. The proportions of the canals vary widely across the group (Fig. 2). In general, a vestibular region that is long anteroposteriorly appears to be the plesiomorphic state (Fig. 2A, B) and a more anteroposteriorly compact condition, the derived state (Fig. 2C, D).

An expanded ampullar region is located at one end of each semicircular canal (Figs. 3 and 4). Each ampulla contains a sensory epithelium comprised of a patch of hair cells, referred to as the ampullar crista (Fig. 3A). Fibers from the anterior branch of the vestibulocochlear nerve ($VIII_a$) serve the cristae of the anterior and horizontal semicircular canals, and a single foramen near the anterior margin of the medial wall of the otic capsule transmits the entire anterior branch of VIII to these epithelia (Fig. 2, $VIII_a$). Fibers of the posterior branch of the vestibulocochlear nerve ($VIII_p$) serve the cristae of the posterior canal, and a posteroventrally located foramen transmits this entire branch (Fig. 2, $VIII_p$). The anterior and posterior canals meet dorsomedially at a junction termed the superior sinus (or common crus; Baird, 1974; Wever, 1978).

All three canals are confluent with the centrally located, endolymph-filled utricle (Figs. 2 and 3B). A large, expanded sensory epithelium, the utricular macula, is located in the floor of the anterior portion of the utricle (Fig. 3A). The majority of $VIII_a$, which is a very thick nerve branch in the species examined, serves this sensory epithelium. Posterior to this, in the proximity of the utriculosaccular foramen, which connects the vestibular apparatus to the saccule of the auditory chamber, is an additional sensory epithelium, considered to be homologous with the papilla neglecta of fish and amniotes (Fritzsch & Wake, 1988). It has been variably referred to as such, or as the utricular papilla or macular neglecta (Platt et al., 2004). Fibers of $VIII_p$ serve this epithelium (Fritzsch & Wake, 1988), which is absent from frogs and salamanders (Baird, 1974).

The ventral portion of the inner ear endocast is very large and bulbous in all the caecilians examined (Fig. 2), although it is relatively small in the aquatic taxon *Typhlonectes natans*. Histology reveals that the medial half of this space is occupied by a large saccule and the amphibian, lagenar, and basilar recesses of the endolymphatic labyrinth (Fig. 3A, B). The saccule is situated ventral to the utriculosaccular foramen, and has the form of a large, hemispherical sac. The long, tubular endolymphatic duct exits the saccule at its dorsomedial border (Fig. 3B) and courses dorsally along the medial wall of the otic capsule to enter the brain cavity through the endolymphatic foramen, which is located in proximity to the superior sinus (Fig. 2). The duct terminates in the blind endolymphatic sac. An extensive sensory epithelium, the saccular macula, is situated along the ventromedial margin of the saccule (Fig. 2B). The hair cells of the macula are embedded within a mass containing otolithic structures (Wever, 1985; Fritzsch & Wake, 1988). Branches of the medial branch of the vestibulocochlear nerve ($VIII_m$) traverse the medial wall of the otic capsule to serve this epithelium. Two to four foramina pertaining to $VIII_m$, indicating two to four branches of $VIII_m$, are present in the species examined (Fig. 2, $VIII_m$).

The amphibian recess is present in all caecilians, and is an outpocketing of the medial wall of the saccule (Figs. 5A and 4B, D), lying just ventral to the utriculosaccular foramen. Within this recess is a sensory epithelium, the amphibian papilla, that is unique to lissamphibians. Previous work has postulated, on the basis of development and innervation, that the amphibian papilla is derived from the papilla neglecta (Fritzsch & Wake, 1988).

The lagenar recess is another outpocketing of the posterior wall of the saccule (Fig. 5B). It also carries within it a sensory epithelium, the lagenar macula. The presence of a lagenar recess is plesiomorphic for caecilians, but it is reduced in size and in the number of sensory hair cells comprising the epithelium in several species, representing the derived condition. It is completely devoid of hair cells in at least one species, *T. natans* (Fritzsch & Wake, 1988).

The third recess, the basilar recess, is intimately related to the lagenar recess, and also occurs as an outpocketing of the saccule at the base of the lagenar recess. It, too, contains a sensory epithelium, the basilar papilla. The presence of the basilar recess and papilla is plesiomorphic for caecilians, but both are lost multiple times within the group, representing the derived condition. No basilar papilla is present in the ear structure of the species modeled in three dimensions here.

The endolymphatic labyrinth is surrounded by periotic tissue inside the otic capsule. Spaces and canals within the periotic tissue occur around the ventral portion of the endolymphatic labyrinth in caecilians, as they do in other extant tetrapods, and contribute to the bulbous nature of the ventral portion of the endocasts (Fig. 2). The spaces and canals are filled with perilymph, and the network of structures comprises the perilymphatic labyrinth. The perilymphatic labyrinth includes the periotic cistern, the periotic duct or canal, and the periotic sac (Fig. 3G, H). The periotic cistern is a large, hemispherical chamber that lies lateral to the saccule and medial to the footplate of the stapes (Figs. 3C and 4A, C). It is particularly large in caecilians in comparison with that of frogs and salamanders (Baird, 1974). Extending from the anterodorsal region of the cistern is the periotic canal, which, in the specimens we examined, courses dorsally through the space surrounded by the semicircular canals before turning sharply ventrally (Fig. 3G). It then passes medially along the posterior margin of the saccule toward the medial wall of the otic capsule. It is evident from the three-dimensional model derived from the histological data that a recess off the periotic canal makes contact, across a thin membrane, with the amphibian recess of *Gymnopis multiplicata* (Fig. 3B, D, H). The periotic canal terminates at the periotic sac, which protrudes into the brain cavity through a discrete foramen located posteroventrally, the perilymphatic foramen (Fig. 2). Also, in all three species for which the histological structure was modeled in three dimensions, a recess off the periotic sac makes contact with the lagenar recess (Fig. 3B, D, H). In two species with well-preserved ears examined here (*G. multiplicata* and *Chthonerpeton indistinctum*), the periotic sac extends into the brain cavity and is applied to a fluid-filled chamber ventral to the brain (Fig. 5C). The periotic sacs of either side are therefore indirectly connected via this fluid-filled chamber spanning the brain cavity (Fig. 5D).

Discussion

Reduction of the Lagenar Macula

As described above, the lagena in lissamphibians is a small, posteromedial outpocketing of the saccule. A sensory epithelium,

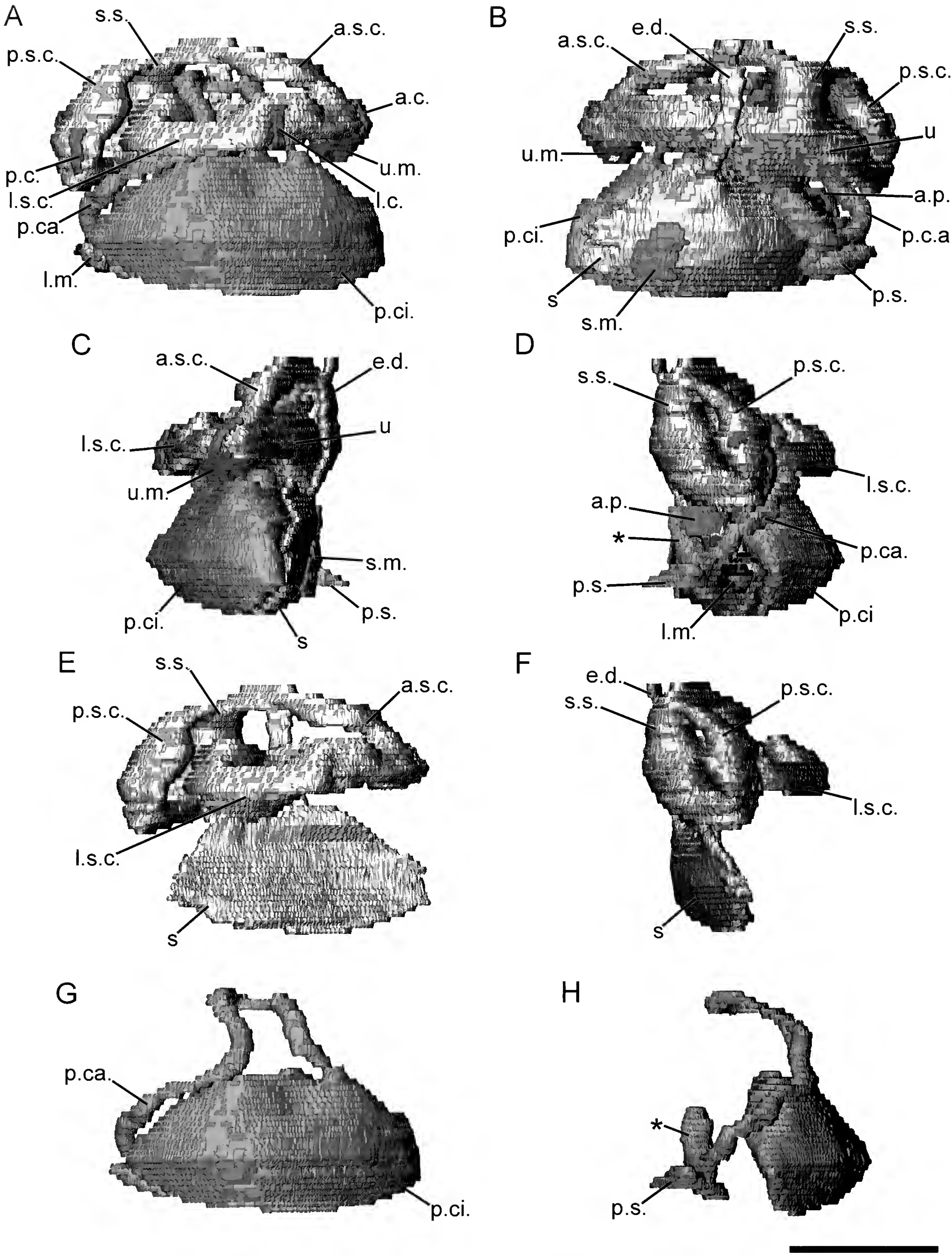

FIG. 3. Three-dimensional reconstruction of the right inner ear of *Gymnopis multiplicata* (CRE 2783). Lateral view with anterior to the left (**A**), medial view (**B**), anterior view (**C**), and posterior view (**D**), showing the division of the inner ear into the dorsal vestibular apparatus composed of the anterior, lateral, and posterior semicircular canals (a.s.c., l.s.c., p.s.c.) and utricle (u) and its macula (u.m., purple), and the ventral auditory apparatus composed of the perilymphatic labyrinth (perilymphatic cistern, periotic canal, and perilymphatic sac; p.ci., p.ca., p.s.), saccule (s) and the various sensory epithelia, including the saccular macula (s.m., pink), lagenar macula (l.m., blue), and amphibian papilla (a.p., green). (**E**) and (**F**), isolated endolymphatic labyrinth of *G. multiplicata* (CRE 2783) in lateral and posterior views, respectively, showing the shape and location of the saccule. (**G**) and (**H**), isolated perilymphatic labyrinth of *G. multiplicata* (CRE 2783) in lateral and posterior views,

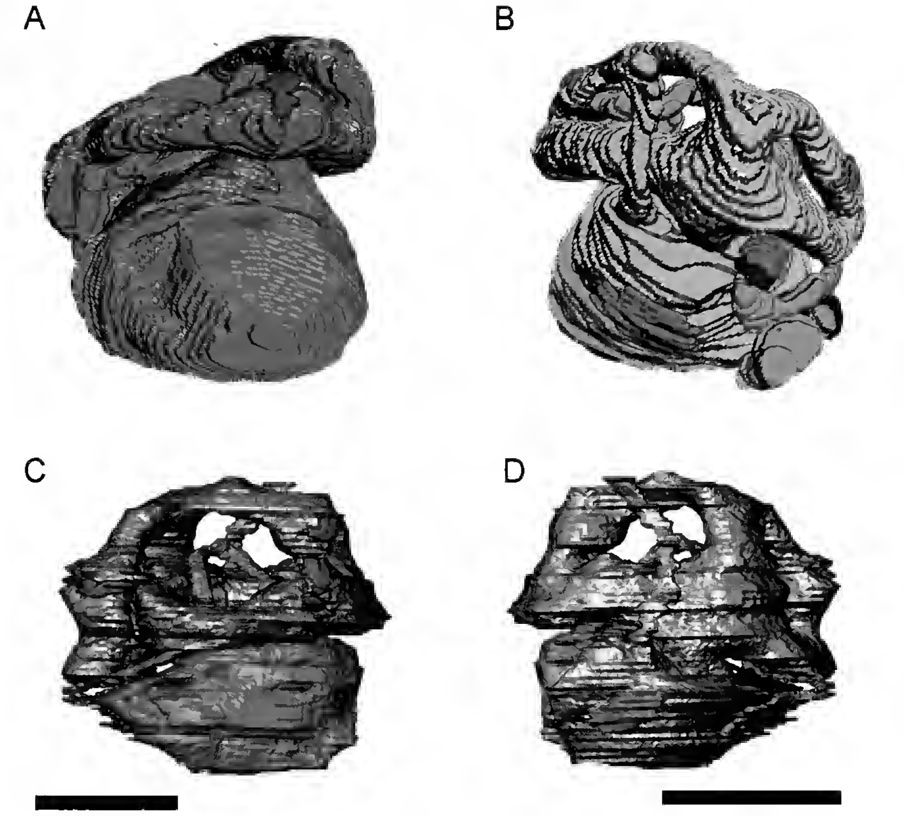

FIG. 4. Three-dimensional reconstructions of the right inner ear of *Geotrypetes seraphini* (MHW 548; **A, B**) and *Dermophis mexicanus* (MCZ 178976; **C, D**), in lateral (**A, C**) and medial (**B, D**) views, respectively. The overall morphology of the various components and their relationships to one another are remarkably similar in the species shown here, including the posterior path of the periotic canal. Structures are color-coded as in Figure 3: Gray, endolymphatic labyrinth; yellow, perilymphatic labyrinth; red, cristae of the semicircular canals; pink, saccular macula; purple, utricular macula; blue, lagenar macula; green, amphibian papilla. MHW, M. H. Wake collection, University of California, Berkeley, CA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA. Scale bars equal 0.5 mm.

the lagenar macula, is contained within it. A lagena with its macula is present in most tetrapods (lost in non-montreme mammals; Fritzsch et al., 2006), as well as in most gnathostome fish (Baird, 1974). In fish and amniotes excluding non-montreme mammals the lagenar macula functions primarily in the perception of sound (von Frisch, 1938; Wever, 1978; Popper & Fay, 1993, 1999; Fritzsch et al., 2006; Khorevin, 2008). In lissamphibians, on the other hand, this does not appear to be the case. Detection of substrate-borne (not airborne) vibrations has been hypothesized and observed to be the primary function of the lagenar macula in some salamanders and frogs (Koyama et al., 1982; Lewis et al., 1982; Hetherington et al., 1986); however, the saccule, utricle, and the amphibian papilla are also sensitive to substrate-borne vibrations (Ross & Smith, 1979; Jørgensen & Christensen-Dalsgaard, 1991).

Several functions of the opercularis system (operculum ossicle plus muscular slip connected to the shoulder girdle) have been proposed. These were recently reviewed by Mason (2007), and include the detection of body movement (put forth by Eiselt [1941]), the protection of the inner ear against intense sounds (put forth by Wever [1979, 1985]), enhancement of airborne sound perception (put forth by Lombard & Straughan [1974]), and, perhaps the most widely accepted function, detection of substrate-borne vibrations (put forth by Kingsbury & Reed [1909], and corroborated by experiments conducted by Hetherington [1985, 1987, 1988]). Under the latter hypothesis, the muscular slip that connects the suprascapular cartilage of the shoulder girdle to the operculum of the middle ear transmits vibrations collected by the forelimbs to the ear. The vibrations oscillate the operculum, which is coupled to the stapes within the fenestra vestibuli, thereby setting the perilymph in motion and stimulating the inner ear. The frequency sensitivity of the lagenar macula has been shown to correspond to that that is typical of vibratory stimuli (Hetherington et al., 1986).

An operculum is absent from extant caecilians, and it is unclear whether its absence represents a primary absence or a secondary loss. Fritzsch and Wake (1988), in an exhaustive survey of caecilian inner ear anatomy, documented the presence of a well-developed lagena and lagenar macula in caecilians considered to be representative of the plesiomorphic condition, and multiple instances of progressive reduction of sensory cells within the lagenar macula (and one instance of their complete loss, in *T. natans*) in species representative of the derived condition. If the lagenar macula is associated with the perception of vibration, as is potentially the case in frogs and salamanders, then the presence of this macula and its gradual reduction in caecilians supports the hypothesis that the opercularis pathway was present in stem caecilians or more basal taxa. Limblessness and the loss of girdles and associated musculature may be correlated with the loss of the operculum and, therefore, loss of the primary source of stimulation of the lagenar macula. This hypothesis, then, posits that an operculum and opercularis pathway were secondarily lost in the evolution of caecilians.

This correlation between the opercularis pathway and the lagenar macula assumes that the lagenar macula of caecilians functions to perceive substrate-borne vibrations, similar to that of some salamanders and frogs, but the function of this macula has never been empirically tested in caecilians. Additionally, the role of the operculum and opercularis pathway is still debated (Mason, 2007). A vibration perception role for the lagenar macula is supported by the apparent loss of the lagena in the aquatic form *T. natans* (Fritzsch & Wake, 1988). It is conceivable that detection of substrate vibrations is minimal and likely poorly transmitted due to the buoyancy of animals, and therefore lack of a good connection between the animal and the substrate in the aquatic environment (Mason, 2007). This is consistent with the observation of the condition of a reduced or absent opercularis pathway in strictly aquatic frogs (e.g., Pipidae; Mason, 2007) and salamanders (e.g., sirenids, proteids, and amphiumids; Lombard, 1977). Although the lagenar macula is not described as being reduced in these frog and salamander taxa, the consequences of the loss of the opercularis pathway may not be as profound due to its more recent loss in those frogs and salamanders relative to caecilians (i.e., the presence of the opercularis pathway is plesiomorphic for both frogs and salamanders). The saccule

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respectively, showing the posterior path of the periotic canal (p.ca.) relative to the perilymphatic sac (p.s.). CRE, Costa Rican Expedition, J. M. Savage collection, University of Miami, FL (uncatalogued material curated in the laboratory of M. H. Wake, University of California, Berkeley, CA). Additional abbreviations: a.c., anterior crista; l.c., lateral crista; p.c., posterior crista; e.d., endolymphatic duct; s.s., superior sinus; asterisk, recess off the periotic duct that contacts the amphibian papilla. Scale bars equal 0.5 mm.

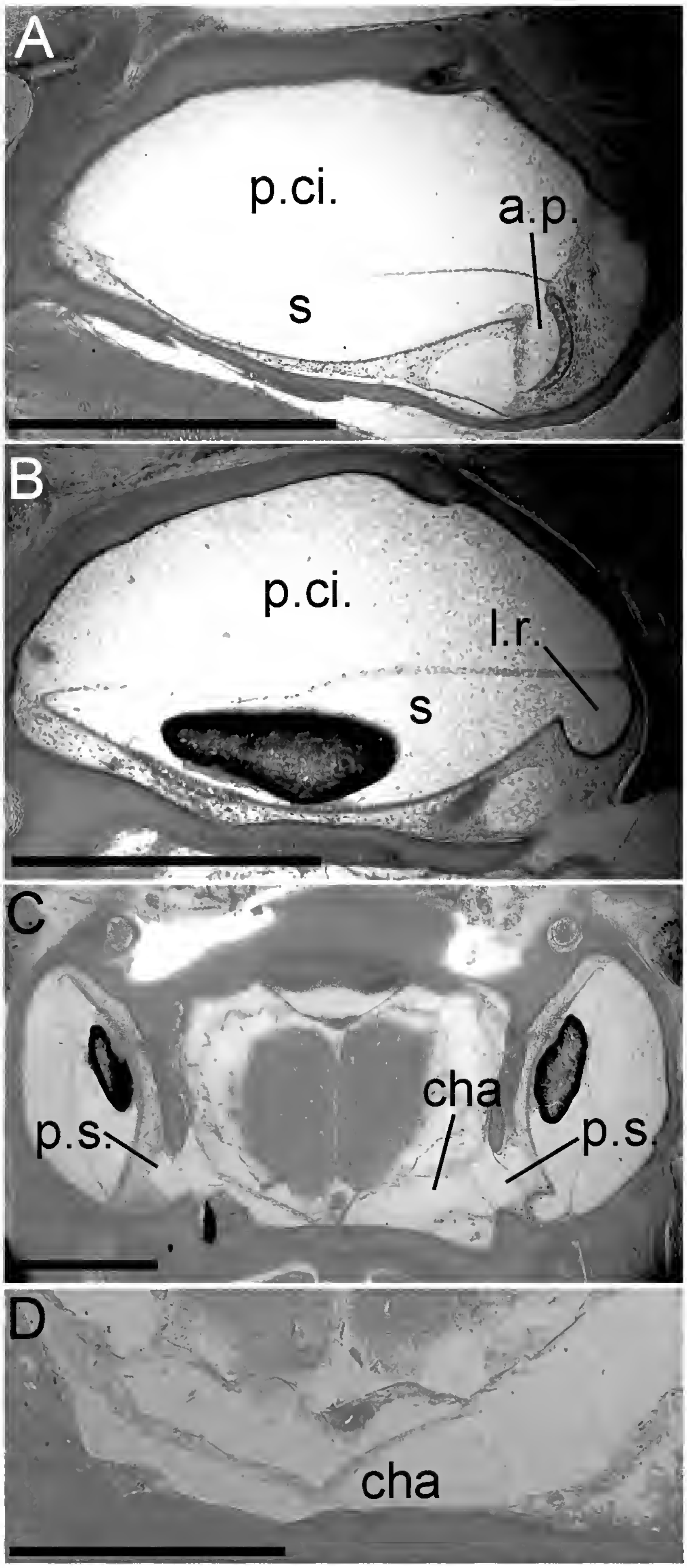

FIG. 5. Histological sections of the otic capsule of *Gymnopis multiplicata* (CRE 2783) in frontal view. (**A**) Otic capsule of *G. multiplicata* at the level of the amphibian papilla (a.p.); the structure is seen as an outpocketing of the saccule (s). (**B**) Otic capsule in *G. multiplicata* at the level of the lagenar recess (l.r.); the structure is also seen as an outpocketing of the saccule (s). (**C**) Otic capsule of G. *multiplicata* at the level of the perilymphatic sac (p.s.), showing its extension into the brain cavity and how it is applied to a fluid-filled chamber (cha) beneath the brain. (**D**) Close-up of the fluid filled chamber of *G. multiplicata* in a more ventral position, showing the fluid-filled chamber as a continuous space spanning the brain cavity. CRE, Costa Rican Expedition, J. M. Savage collection, University of Miami, FL (uncatalogued material curated in the laboratory of M. H. Wake, University of California, Berkeley, CA). Scale bars equal 0.5 mm.

has been demonstrated to be important in the perception of vibration in frogs and salamanders (Jørgensen & Christensen-Dalsgaard, 1991), and this may include routes that are independent of the opercularis pathway (as demonstrated when the animals are placed on their back; Ross & Smith, 1979). The saccule of caecilians is also likely sensitive to vibrations received directly through the head. The limbless nature of caecilians means that their heads contact the substrate most of the time, and the saccule and saccular macula are particularly large in caecilians (Fig. 2). This does not preclude the lagenar macula from also having a role in vibration perception associated with the opercularis pathway.

The secondary loss of the opercularis pathway in caecilians is also seemingly supported by the identification of a putative operculum in the fossil stem caecilian *Eocaecilia micropodia* (Jenkins et al., 2007); however, several features are in conflict with this identification. First, the operculum of frogs and salamanders is typically cartilaginous (Mason, 2007), minimizing its potential for preservation in the fossil record. Second, the putative operculum of *Eocaecilia* is located medial to the element identified as the fused stapes and quadrate (i.e., the "stapes-quadrate" of Jenkins et al. [2007]). Among extant frogs and salamanders the operculum is located in the same plane as the stapes, within the fenestra vestibuli, and never lies medial to the stapes. The close juxtaposition of the stapes-quadrate to the operculum would prevent the insertion of the muscular slip connecting the latter to the shoulder girdle. Finally, there is a strong morphological resemblance between the putative operculum of *Eocaecilia* and the footplate of the stapes of caecilians and some salamanders. These features support the identification of the element in *Eocaecilia* as a stapes rather than an operculum, and the stapes-quadrate as the quadrate alone. The feature cited as evidence against this hypothesis is the presence of a foramen, considered to be the stapedial foramen, in the stapes-quadrate element, which would support the hypothesis that the stapes is incorporated into this element (Jenkins et al., 2007). However, foramina are known to vary in position, and caution should be taken when using the presence or absence of foramina in making assessments of bone homology (Jamniczky & Russell, 2008). Despite this, the data concerning the lagenar macula suggest that an opercularis pathway was already reduced in the caecilian lineage before the divergence of *Eocaecilia*.

Reduction of the Basilar Papilla

The basilar papilla is a sensory epithelium found in most tetrapods. It is located at the base of the lagena. Its primary function is in the perception of sound, and, in particular, it is capable of perceiving high-frequency sound (Smotherman & Narins, 2000). Among terrestrial vertebrates, a tympanum and stapes are associated with the transmission of high-frequency sound to the inner ear. High-frequency sound waves are more negatively affected by the impedance mismatch between air and the fluid of the inner ear than are low-frequency sounds. Without a tympanum, the majority of high-frequency sounds would be reflected from the surface of the inner ear, limiting perception of sound to the low frequencies. A tympanum coupled with a stapes work together to focus and amplify high-frequency sound waves, thereby permitting them to overcome the impedance at the fluid boundary and enabling the successful transmission to the fluid of the inner ear.

The presence of a basilar papilla appears to be plesiomorphic for caecilians. Similar to the distribution documented for the lagenar macula, the basilar papilla is reduced and lost in species representing the derived condition (Fritzsch & Wake, 1988). This suggests, just as the modification of the lagenar macula did, that the source of stimulation of this epithelium has been lost. Given its known function in frogs (Lewis et al., 1982), this source of stimulation may have been a tympanum–stapes pathway. The tympanum–stapes pathway is absent from all caecilians. However, the regression and loss of the basilar papilla suggests that a tympanum–stapes pathway may have been present in stem caecilians or more basal taxa, and was subsequently secondarily lost.

The morphology of the stapes and its association with the otic capsule provide additional support for the secondary loss of the tympanum–stapes pathway. Most caecilians possess a tight articulation between the anteroventral margin of the fenestra vestibuli and the footplate of the stapes. The joint has been described as a synchondrosis or as a synovial joint between the margin of the fenestra vestibuli and the footplate of the stapes (de Jager, 1939, 1947; Wever, 1975; Mason, 2007), or at least as a connection involving dense connective tissue seen in the histological material examined in this study. In frogs the footplate of the stapes is also connected to the anteroventral margin of the fenestra vestibuli (Mason, 2007). This joint is associated with a pump-handle or hingelike motion of the stapes in response to airborne sound (Bolt & Lombard, 1985; Mason & Narins, 2002), rather than the pistonlike motion that characterizes amniotes. The presence of this hingelike morphology in the caecilian ear is suggestive of stapedial motion like that associated with a tympanum–stapes pathway in frogs. In the latter this morphology is considered to be adapted for transmitting airborne sounds through the amplification of sound waves via a rocking lever mechanism (Jørgensen & Kanneworff, 1998). This morphology, therefore, supports the presence of functional tympanum–stapes early in caecilian evolution and points to its secondary loss in the common ancestor of extant caecilians.

The tympanum–stapes pathway has been lost multiple times in frogs. Interestingly, however, there does not appear to be reduced sensitivity in these "earless" frog species, because the basilar papilla is not reduced or lost (Lindquist & Hetherington, 1996; Jaslow et al., 1988). In these cases extratympanic pathways, such as that from the lungs to mouth to Eustachian tubes (Narins et al., 1988; Hetherington, 1992; Lindquist et al., 1998), collect and transmit sound to the ears. Therefore, unlike caecilians, these earless frogs have evolved efficient alternate mechanisms of maintaining stimulation of the basilar papilla. One possible exception is the aquatic frog *Xenopus laevis*, in which the basilar papilla is described and figured as being extremely small (Bever et al., 2003). This may be a consequence of the loss of a traditional tympanum–stapes pathway (the tympanum is a cartilaginous disc beneath normal skin; Wever, 1985; Mason, 2007), possibly correlated with living in an aquatic environment.

Path of the Periotic Canal

In vertebrates that possess a mobile, vibratory stapes, the periotic canal (scala tympani, helicotrema, scala vestibuli of amniotes; Lombard, 1977; Lombard & Bolt, 1979) transmits translated sound waves received by the periotic cistern to the auditory epithelia within the endolymphatic system and terminates at the periotic sac. Among extant tetrapods there are two patterns of relationship of the periotic canal to the vestibular apparatus of the inner ear. One pathway is characteristic of lissamphibians, having been documented in detail for frogs and salamanders, as well as for some caecilians (Sarasin & Sarasin, 1887–1890; Retzius, 1891; Fritzsch & Wake, 1988; Lombard, 1977). The other is characteristic of amniotes (de Burlet, 1934; Lombard & Bolt, 1979). In lissamphibians the periotic canal emerges from the posterior margin of the periotic cistern and courses toward the perilymphatic foramen along the posterodorsal margin of the endolymphatic labyrinth (Fig. 6A; Lombard, 1977; Lombard & Bolt, 1979). In contrast, the periotic canal of amniotes emerges from the anterior margin of the periotic cistern (Wever, 1978), and courses toward the medial wall of the otic capsule along the anterior margin of the endolymphatic labyrinth (Fig. 6B; Lombard, 1977).

Our observations corroborate previous descriptions provided for *Caecilia occidentalis* (Lombard, 1977). The periotic canal of the caecilians examined here emerges from the anterodorsal margin of the periotic cistern, similar to the condition seen in amniotes, but, after following a convoluted path dorsally into the vestibular region, passes medially toward the perilymphatic foramen along the posterior margin of the endolymphatic labyrinth. In this regard the course of the periotic canal is more similar to that of frogs and salamanders than it is to that of amniotes. In addition, no other vertebrate taxa possess this distinctive path of this canal exhibited by frogs, salamanders, and caecilians.

Re-entrant Fluid Circuit and the Path of Pressure Relief

We observed that in caecilians the periotic sacs of both sides of the head are indirectly (separated by a thin membrane) in contact with a fluid-filled chamber beneath the brain, in a similar fashion to that described for salamanders (Wever, 1978). This observation has implications for the reported re-entrant fluid circuit previously hypothesized to be operating in the caecilian ear (Wever, 1975; Wever & Gans, 1976). In Wever's (1975) model, pressure from the perilymphatic labyrinth is dissipated into the brain cavity via the perilymphatic foramen, similar to the pathway evident in frogs and salamanders. However, unlike the situation in frogs and salamanders, the path of the pressure waves is described as continuing anteriorly, where it exits the brain cavity through a foramen located anterior to the otic capsule. The pressure waves then re-encounter the stapes. This pathway was termed the re-entrant fluid circuit, because pressure could restimulate the footplate of the stapes. This pathway was interpreted by Wever (1975) to be similar to the fluid circuit seen in amniotes, wherein the round window located in the middle ear cavity transmitted the pressure waves back to the lateral surface of the stapes.

However, recent observations made here and elsewhere (Maddin, 2011) provide evidence that largely refutes the re-entrant fluid circuit model in caecilians. Pressure waves entering the periotic sac are likely transmitted medially and not anteriorly because the periotic sac contacts the fluid-filled chamber that extends medially into the brain cavity. An anterior path would involve traveling through unconstrained fluids within the brain cavity toward a target foramen. The accuracy required does not seem likely enough in this scenario to support the re-entrant fluid circuit model. Additionally, the

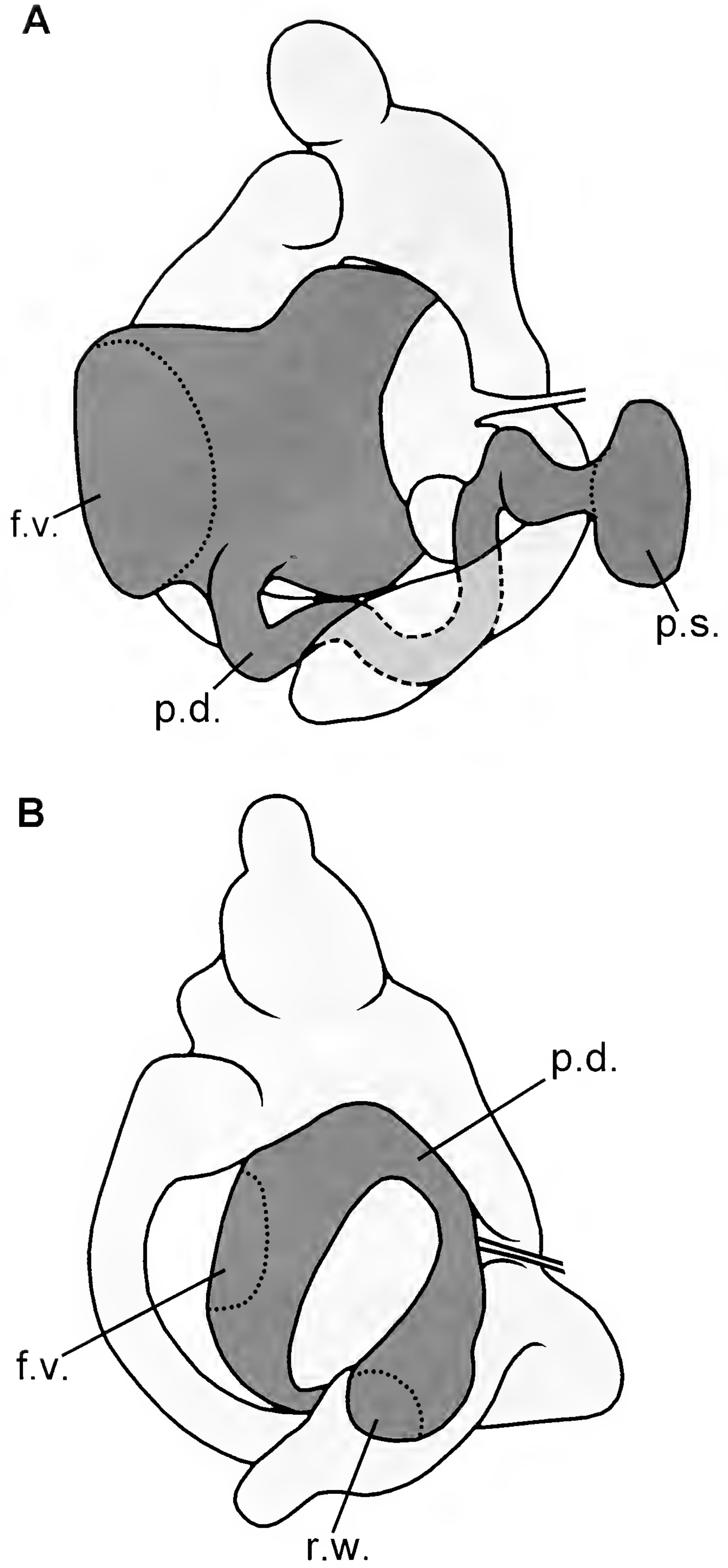

Fig. 6. Schematic illustrations of the inner ear in amphibians (**A**) and amniotes (**B**), in ventral view with anterior to the top and lateral to the left. (**A**) In amphibians the periotic canal (p.ca.) courses toward the perilymphatic sac (p.s.), along the posterior margin of the inner ear toward the medial wall of the otic capsule. (**B**) In amniotes the periotic canal (p.ca.) courses along the anterior margin of the inner ear, toward the medial wall of the otic capsule, and terminates at the round window (r.w.). Additional abbreviations: f.v., location of fenestra vestibuli. Not to scale (modified from Lombard, 1977).

foramen proposed by Wever to be the exit for the pressure waves from the brain cavity has recently been identified as that for the exit of the entire trigeminal nerve (Maddin, 2011). This is a large nerve in caecilians comprised of two large trunks (V_{op} and $V_{mx,md}$) and their ganglia (ophthalmic and Gasserian ganglia, respectively), which often fill the entire foramen (H.C.M., pers. obs.). It seems unlikely that pressure waves could be accurately directed through the brain cavity fluid toward this foramen, and then transmitted successfully through the tissues traversing the foramen to the external surface of the braincase. It is therefore unlikely that an amniote-like re-entrant fluid circuit operates in caecilians.

The morphology of the tissues associated with the perilymphatic foramen in caecilians is remarkably similar to that of salamanders and some frogs, wherein pressure is released into the brain cavity rather than the middle ear, as it is in amniotes. Additionally Wever (1978) demonstrated that sound traveling through one ear could be transmitted to the contralateral ear in the salamander *Taricha granulosa*, through the transmission of pressure waves across the brain cavity and into the perilymph of the contralateral ear. It was hypothesized that this would lead to pressure relief as well as functioning in directional hearing (Wever, 1978; Mason, 2007) by setting the perilymph and stapes of the opposite ear in motion, similar to the process observed in other extratympanic auditory pathways. In this regard, the association of the perilymphatic sacs with the fluid-filled volume in the brain cavity of caecilians may be even more similar to the condition seen in salamanders. Additionally it has been shown that in some frogs pressure changes within the fluids of the brain cavity can incite responses in the auditory endorgans (Seaman, 2002). Directional hearing may be operating in the ears of caecilians, in remarkably similar ways to those operating in frogs and salamanders; however, this has yet to be tested empirically. Minimally, these observations support a similar configuration of the caecilian pressure relief pathway to that of salamanders and some frogs (many other frogs relieve pressure via a membrane-covered foramen in the roof of the mouth; Baird, 1974).

Implications for the Phylogeny of Lissamphibia

Previously the anatomy of the caecilian ear has been placed in an evolutionary context (Fritzsch & Wake, 1988). However, this was from the perspective of evolutionary trends within the group, as well as being forwarded with the implicit assumption that lissamphibians form a monophyletic group. The relationship between the three living orders of lissamphibians remains a contentious issue among vertebrate paleontologists, as discussed above. We hereby combine the new observations made here with a reconsideration of previously described trends pertaining to the inner ear of caecilians and discuss these within a broader phylogenetic context. Our arguments are strongly functionally influenced, based upon a consideration of evolutionary morphology of intact integrated organisms. As such, we use integrative rather than reductionistic reasoning in an attempt to understand anatomical evolution as opposed to atomized character evolution. Our goal is to determine whether examination of this integrative anatomy can provide insight into the relationship between caecilians and frogs and salamanders, and to assist in identifying the closest fossil relatives of caecilians and thus clarify the evolutionary history of the group.

The evolution of the tetrapod ear is a topic that has been extensively studied by many researchers (e.g., Olson, 1966; Baird, 1974; Wever, 1974, 1985; Lombard & Bolt, 1979, 1988; Bolt & Lombard, 1985, 1992; Clack, 1992, 1993, 1997, 2002; Fritzsch, 1992; Popper & Fay, 1997; Fay & Popper, 2000; Fritzsch & Beisel, 2001). There is now a general consensus that a tympanic ear evolved independently multiple times within tetrapods (Clack, 2002). Among lissamphibians, only frogs possess a tympanic ear, and, as a result, only frogs are often considered as exemplars of non-amniotes in discussions of the evolution of the tympanic ear (Christensen-Dalsgaard & Carr, 2008). However, there is now substantial evidence from the fossil record that a tympanic ear was present in the crownward members of the Permian temnospondyls (members of Dissorophoidea, including amphibamids; DeMar, 1968; Bolt, 1969; Sigurdsen, 2008). This observation is taken into consideration in the discussion below.

Caecilians uniquely share the posterior pathway of the periotic canal with frogs and salamanders. Additionally, caecilians share with salamanders and frogs the configuration of the pressure relief system. Furthermore, the morphology of the periotic sac with its associated fluid-filled chamber is shared with salamanders. To understand the influence these traits have on hypotheses of lissamphibian phylogeny, it is first necessary to determine whether these similarities are synapomorphies, convergences, or symplesiomorphies. Early fossil tetrapods must be considered in assessments of potential homology of inner ear structures among extant lissamphibians and their fossil relatives (Lombard & Bolt, 1979; Bolt & Lombard, 1985; Clack, 1987, 1992, 1993; Clack et al., 2003). The presence of a periotic canal and its morphology is difficult to determine in fossil taxa due to the lack of preservation of the delicate soft tissues involved. Inferences can be made, however, on the basis of the presence/absence of potential osteological correlates of the periotic canal, and the perilymphatic labyrinth in general.

The evolution of a system that permits the detection of the pressure component of sound increases the range of frequencies to which the ear is sensitive (Fay & Popper, 1975; Horodysky et al., 2008). A mechanism to detect the pressure component of sound is present in extant members of both non-tetrapod and tetrapod taxa. However, fundamental differences exist that are of significance in the interpretation of the plesiomorphic condition of tetrapods. For example, some groups of osteichthyan fish are capable of perceiving the pressure component of sound. One way that this is achieved is via a chain of special ossifications, the Weberian ossicles, that connect the swim bladder (the primary collector of sound waves) to a canal within periotic tissue (referred to as a periotic canal; Fritzsch, 1992) that is applied to the auditory receptors of the inner ear (Baird, 1974; Fay & Popper, 1974, 1975; Popper & Fay, 1993; Casper & Mann, 2006). A periotic canal is therefore present in these fish, with the primary direction of transduction being medial (the swim bladder) to lateral (the inner ear).

In extant terrestrial tetrapods a tympanum coupled to a vibratory stapes is used to transmit the pressure component of airborne sound to the inner ear. The periotic canal carries the waves collected on the lateral surface of the inner ear across the auditory epithelia, and eventually terminates at the pressure relief structure in the medial wall of the otic capsule. Thus, in contrast to the condition in some fish, the primary direction of transduction is lateral to medial. The orientation of the perilymphatic labyrinth relative to the head is exactly opposite in tetrapods to the situation encountered in these fish, and this has been used as evidence to argue (e.g., Baird, 1974; Lombard & Bolt, 1979) that the perilymphatic labyrinths of fish and tetrapods are not homologous.

A tympanic ear, complete with vibratory stapes, may therefore be an osteological correlate of a perilymphatic labyrinth in tetrapods. Early tetrapods have been extensively surveyed for evidence of a tympanic ear (Table 3). We conclude, as have others before us, that a mobile stapes, like that seen in extant forms that transmits pressure waves to the inner ear, was absent from taxa at the base of Tetrapoda (Lombard & Bolt, 1979; Clack, 1992, 1997). The sarcopterygian fish *Panderichthys,* considered to be the sister taxon to tetrapods, bears a stapes that is affixed midshaft to the opercular bone (a cranial bone not related to the opercular ear ossicle) of the skull (Brazeau & Ahlberg, 2006). In basal tetrapods, such as *Acanthostega*, the footplate of the stapes is partially affixed to the lateral wall of the otic capsule (Clack, 1992). In other basal tetrapods, such as *Greererpeton* and *Baphetes*, the stapes is broad and winglike distally, and it forms an extensive contact with elements of the palatoquadrate, which presumably would have limited any substantial motion (Clack, 2002). These taxa also lack an otic notch, and the medial wall of the otic capsule is poorly ossified (Clack, 1993), similar to the condition seen in many fish (de Burlet, 1934). In fact, it has been hypothesized that a condition similar to that seen in *Latimeria* and lungfish was likely present in early tetrapods (Fritzsch, 1992; Platt et al., 2004; Christensen-Dalsgaard et al., 2011). Therefore, on the basis of the functional association between a vibratory stapes (and operculum when present) and the perilymphatic labyrinth in extant tetrapods, data from early fossil tetrapods suggest that the presence of a periotic cistern, canal, and sac is not plesiomorphic for tetrapods.

The implications of this hypothesis have a significant impact on the interpretation of the pattern of evolution of the tympanic ear and associated structures under the three competing hypotheses of lissamphibian phylogeny. Because the last common ancestor of temnospondyls and lepospondyls lacks evidence of a tympanic ear (as outlined above), under the PH the similarities between the ears in caecilians and batrachians (frogs plus salamanders) must be interpreted as being the result of evolutionary convergence (Fig. 7A). This includes the common path of the periotic canal shared among caecilians, frogs, and salamanders; the morphology of the pressure relief mechanism shared among caecilians, salamanders, and some frogs; and the association of the perilymphatic sacs with the fluid-filled chamber in the brain cavity. Similarities also include additional features such as the presence of the amphibian papilla, an epithelium considered to have evolved through the division of the papilla neglecta (Fritzsch & Wake, 1988). The PH is even more tenuous because it is not clearly evident why a taxon would independently evolve traits associated with a tympanic hearing pathway (and potentially the opercularis hearing pathway), a perilymphatic labyrinth and the various target epithelia, within a clade that is otherwise devoid of taxa possessing these hearing pathways (Lepospondyli; Table 3). Recent examination of the otic region in the microsaur *Carrolla craddocki* reveals a well-developed vestibular region but a poorly differentiated and medially unconfined ventral auditory region (Maddin et al., 2011). Additionally, the stapes is robust in *Carrolla* and, when fully articulated, would have contacted the quadrate distally at a broad articular surface. Addition of the lissamphibian-type ear as a character to a slightly modified version (see Tables 4 and 5) of Anderson et al. (2008) that incorporates new information from *Eocaecilia* (Jenkins et al., 2007) and includes caecilians (previously not included) results in a monophyletic Lissamphibia derived from

TABLE 3. Tabulation of stapes morphology and presence or absence of tympanic ear in relevant tetrapod taxa. "Ear" denotes whether a tympanic ear was likely present (yes or no).

Taxon	Higher taxon	Stapedial morphology	Ear	Reference
Acanthostega	Tetrapoda	robust, contacts palate	no	Clack, 1992
Greererpeton	Colosteidae	robust, contacts palate	no	Smithson, 1982
Baphetes	Baphetidae	broad, flaring stapes	no	Clack, 2002
Eryops	Temnospondyli	robust stapes, toward notch	n/y	Sawin, 1941
Dendrerpeton	Temnospondyli	robust stapes, toward notch	yes	Robinson et al., 2005
Acheloma	Dissorophoidea	attenuate stapes, toward notch	yes	Polley & Reisz, 2011
Doleserpeton	Amphibamidae	attenuate stapes, toward notch	yes	Bolt & Lombard, 1985
Pasawioops	Amphibamidae	attenuate stapes, toward notch	yes	Fröbisch & Reisz, 2008
Limnoscelis	Diadectomorpha	stapes toward quadrate, no notch	no	Berman & Sumida, 1990
Pholiderpeton	Embolomeri	robust stapes, toward quadrate	no	Clack, 1983
Archeria	Embolomeri	stapes unknown, no notch	no	Clack & Holmes, 1988
Seymouria	Seymouriamorpha	robust stapes, toward quadrate	no	White 1939
Gephyrostegus	Gephyrostegidae	poorly known, weak notch	no	Carroll et al., 1972
Tuditanus	Microsauria	platelike stapes, no rod, close to quadrate, no notch	no	Carroll & Gaskill, 1978
Hapsidoparieon	Microsauria	platelike stapes, no rod, no notch	no	Carroll & Gaskill, 1978
Pantylus	Microsauria	platelike stapes, short rod, no notch, toward quadrate ramus of pterygoid	no	Carroll & Gaskill, 1978
Cardiocephalus	Microsauria	platelike stapes, short rod, toward quadrate, no notch	no	Carroll & Gaskill, 1978
Euryodus	Microsauria	latelike stapes, short rod, toward quadrate, no notch	no	Carroll & Gaskill, 1978
Pelodosotis	Microsauria	latelike stapes, multiprocesses, toward quadrate	no	Carroll & Gaskill, 1978
Micraroter	Microsauria	platelike stapes, long rod, toward quadrate, no notch	no	Carroll & Gaskill, 1978
Rhynchonchos	Microsauria	platelike stapes, short rod, toward quadrate and quadrate ramus of pterygoid, no notch	no	Carroll & Gaskill, 1978
Microbrachis	Microsauria	platelike stapes, stout rod, toward quadrate and quadrate ramus of pterygoid, no notch	no	Carroll & Gaskill, 1978
Hyoplesion	Microsauria	platelike stapes, short rod, toward quadrate ramus of pterygoid, no notch	no	Carroll & Gaskill, 1978
Phlegethontia	Aïstopoda	platelike stapes, no rod, no notch	no	Anderson, 2002
Captorhinus	Eureptilia	rodlike stapes, distally expanded, toward quadrate, no notch	no	Heaton, 1979
Ennatosaurus	Synapsida	no notch	no	Maddin et al., 2008

within dissorophoid temnospondyls (Fig. 8). This result posits *Eocaecilia* as the sister taxon to extant caecilians and, therefore, both taxa as temnospondyls. However, Gymnophiona (caecilians plus *Eocaecilia*) forms the sister taxon to salamanders, rather than the sister taxon to Batrachia (frogs plus salamanders), as is the pattern found in the other monophyletic temnospondyl-derived hypotheses (Trueb & Cloutier, 1991; Milner, 1993; Ruta et al., 2003; Ruta and Coates, 2007).

The LH is also problematic, but in different ways. Since it is unlikely that traits associated with a tympanic ear are plesiomorphic for tetrapods, as outlined above and in Table 3, the LH invokes a separate evolution of a tympanic ear in tetrapods (Fig. 7B). This has already been pointed out to be a problem with the PH of tetrapod relationships, because the last common ancestor of temnospondyls and lepospondyls likely lacked a tympanic ear (Clack, 2002). The LH implies that the tympanic ears of amphibamid temnospondyls and lissamphibians (exemplified by frogs) evolved convergently. This in itself is not particularly problematic, but rather it is the vast number of similarities shared between the tympanic ear of amphibamids and frogs that makes this hypothesis difficult to accept. Similarities between the frog ear and that of crownward temnospondyls include, and may not be limited to, the morphology and orientation of the stapes; the hingelike articulation between the stapes and otic capsule; and the presence and morphology of the otic notch (and therefore tympanum; Bolt & Lombard, 1985). More recent work on the amphibamid *Doleserpeton* has revealed additional similarities. Those related to the inner ear include the presence of a pressure relief mechanism in the form of a perilymphatic foramen closely associated with the jugular foramen, as seen in many extant frogs (Duellman & Trueb, 1994; Sigurdsen, 2008). This is less closely associated with, but lies near, the jugular foramen in salamanders and caecilians. This may also constitute indirect evidence of a posterior path of the periotic canal, like that seen exclusively in frogs, salamanders, and caecilians; however, the distribution of this trait, and its soft tissue correlates, among other taxa has yet to be fully documented. Incorporation of a lissamphibian-type ear character into the matrix of Vallin and Laurin (2004) does not change the topology presented therein, and lissamphibians are retrieved as being a monophyletic clade within Lepospondyli. However, this matrix has been criticized for being limited in the taxa included (Ruta & Coates, 2003; Schoch & Milner, 2004), especially in the omission of those taxa relevant to potentially critical transitions leading to lissamphibians found in the other hypotheses (7 temnospondyls included by Vallin & Laurin [2004; LH] in comparison with 17 included by Anderson et al. [2008; PH] and 24 included by Ruta et al.

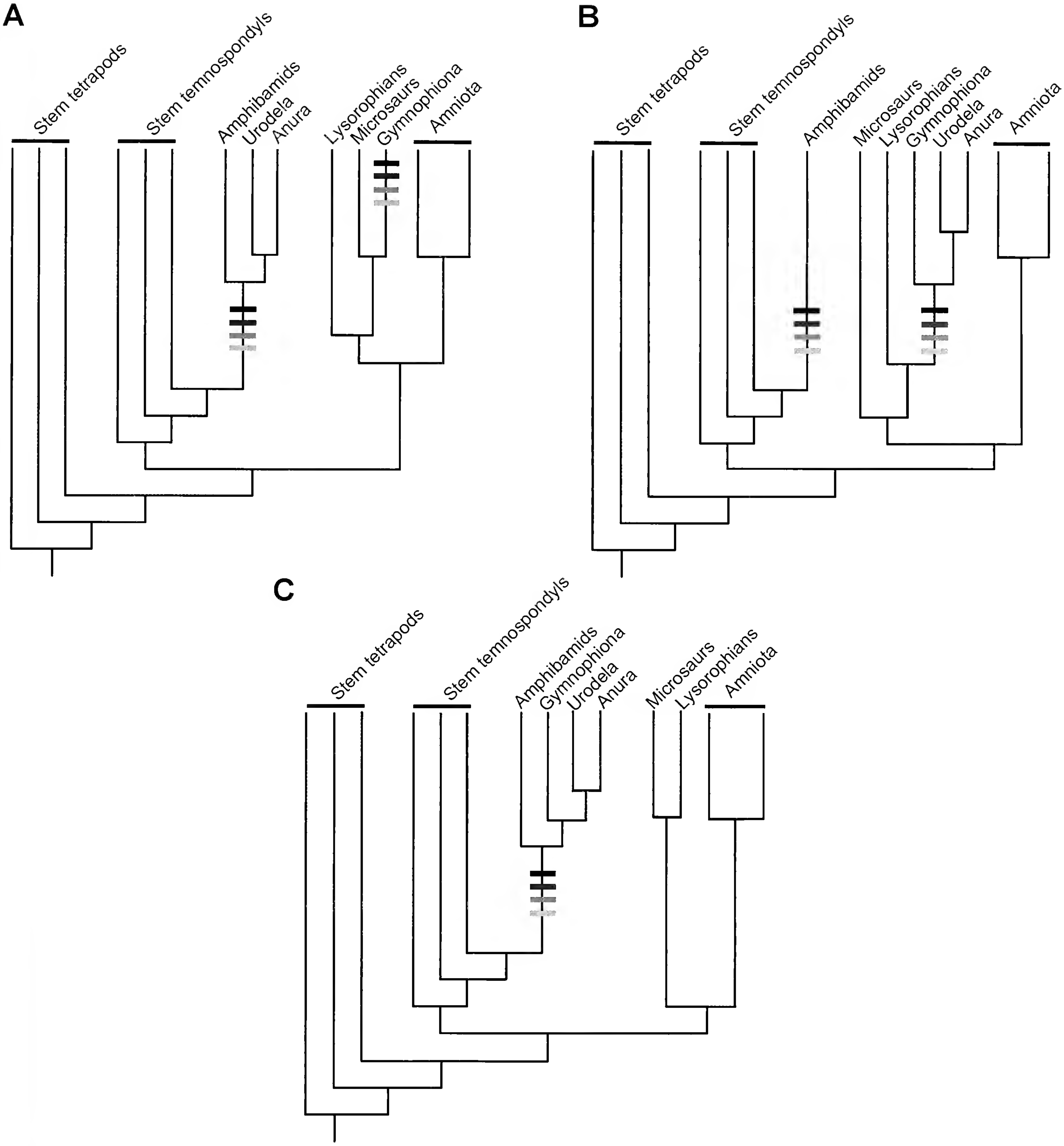

FIG. 7. Optimization of the lissamphibian-type ear on tetrapod phylogeny on the basis of interpretations of both fossil and extant forms. Black bars represent the lissamphibian-type ear, which is characterized here as being comprised of the posterior periotic canal and pressure relief into the brain cavity (dark gray bar), the tympanum–basilar papilla pathway (medium gray bar), and the operculum–lagenar macula pathway (light gray bar). (**A**) and (**B**), the polyphyletic hypothesis (PH) and lepospondyl hypothesis (LH), respectively, require an additional evolution (and loss) of the lissamphibian-type ear. Even though caecilians do not possess all of the traits, they possess correlates of them. (**C**) The temnospondyl hypothesis (TH) invokes a single appearance of the lissamphibian-type ear at some point in crownward temnospondyls. The opercular pathway may be restricted to the last common ancestor of frogs, salamanders, and caecilians, rather than having been present in amphibamids, as depicted.

[2003; TH]). This may, therefore, have an impact on the outcome, and bias results toward a LH topology.

Interpretation of the evolution of the tetrapod ear is most parsimonious under the TH (Fig. 7C). Ear structure in a variety of temnospondyls has been well documented, and features support a tympanic ear arising early in the evolutionary history of the group (Table 3; Bolt & Lombard, 1985, and references cited therein). Osteological features of the

TABLE 4. Summary of the modifications made to the matrix of Anderson et al. (2008), reanalyzed here incorporating caecilians and the new "lissamphibian-type" ear.

Character	Modification	Comment
8	*Eocaecilia* 0→?	a definitive tabular is not known in *Eocaecilia*
10	*Eocaecilia* 0→?	same as for character 8
17	salamanders 1→-	the jugal is absent in salamanders, and other characters concerning the jugal are scored as '-'
19	salamanders 1→-	same as for character 17
26	*Eocaecilia* ? →0	alary process of the premaxilla absent in *Eocaecilia*
28	*Eocaecilia* 1→0	internarial fontanelle absent in *Eocaecilia*
29	*Eocaecilia* 2→1	the prefrontal does not appear to contribute to the external naris in *Eocaecilia*; however, the prefrontal is near the naris
34	*Eocaecilia* 2→1	posterior margin of the skull is somewhat more straight than convex in *Eocaecilia*
44	*Eocaecilia* 1→0	raised orbital rim absent in *Eocaecilia*
52	*Eocaecilia* 1→?	same as character 8
59	*Eocaecilia* 1→?	same as character 8
60	*Eocaecilia* 1→?	same as character 8
70	frogs -→0 salamanders -→0	palatines are present; the maxilla is longer than those in frogs and salamanders
86	character redefined Albanerpetontidae -→1 *Dendrerpeton* ?→0 *Diplocaulus* ?→0 *Eryops* ?→0 salamanders ?→1	position of the jugular foramen is an artifact of fusion between opisthotic and exoccipitals, or not. Opisthotic and exoccipital not fused (0), fused (1).
104	*Eocaecilia* 1→0	parasphenoid falls medial to the footplate of the stapes in *Eocaecilia*
105	*Eocaecilia* 0→1	outline of the basal plate portion of the parasphenoid of *Eocaecilia* rectangular laterally
109	salamanders -→0	plesiomorphic condition of the columellar process in salamanders is directed toward the quadrate
112	*Eocaecilia* ?→0	accessory ossicle in the middle ear absent in *Eocaecilia*
113	*Eocaecilia* ?→1 frogs ?→0 salamanders ?→0	well-developed pleurosphenoid region present in *Eocaecilia*; absent in frogs and salamanders
114	salamanders 1→0	sphenethmoid (or orbitosphenoid) is ossified in salamanders
118	salamanders -→0	no contact between pterygoid and palatine in salamanders, when the latter element is present
123	*Eocaecilia* 0→?	presence of pharyngeobranchial pouches unclear in *Eocaecilia*
125	*Eocaecilia* -→?	status of splenial as a separate bone in *Eocaecilia* unclear, not visible in lateral view
135	*Eocaecilia* 1→-	angular absent in *Eocaecilia* (pseudoangular)
139	*Eocaecilia* 1→?	status of splenial as a separate bone and its contribution to the symphysis in *Eocaecilia* unclear
141	*Eocaecilia* 1→?	presence of ossified hyoids uncertain in *Eocaecilia*

tympanic ears of crownward temnospondyls (such as amphibamids) and frogs are interpreted as being synapomorphies under the TH. This in turn suggests that the common pattern of the periotic canal represents a synapomorphy of lissamphibians, and is interpreted here as also likely to have been present in the tympanic ear of amphibamid temnospondyls. The morphology of the pressure relief mechanism seen in caecilians, salamanders, and some frogs also represents a synapomorphy of these taxa and is also interpreted here as likely having been present in amphibamids. The appearance of the amphibian papilla associated with low-frequency sound perception, a basilar papilla capable of perceiving high-frequency sound, and a lagenar macula adapted to perceiving substrate-borne vibration (in addition to the saccule) are all interpreted as synapomorphies under the TH.

Additional relevant observations include the reduction of two sensory epithelia, the lagenar macula and the basilar papilla, with the eventual loss of the latter in caecilians. Those epithelia are interpreted as associated with the opercularis (lagenar macula) and tympanum–stapes (basilar papilla) pathways in frogs and salamanders, and the latter in frogs only (salamanders lack a tympanum). Optimization of a lissamphibian-type ear onto the TH tree corroborates the hypothesis of the secondary loss of the tympanic hearing pathways in caecilians and salamanders. Evidence of an operculum has yet to be definitively identified in any fossil. However, under the TH the presence of soft-tissue correlates of the opercularis pathway in extant caecilians suggests its presence in the last common ancestor of lissamphibians, and its secondary, progressive, loss in caecilians. In combination, all of these data support the evolution of a unique and distinctive ear type, the lissamphibian-type ear, with all its associated anatomy and functions, from within temnospondyls on one occasion only.

Perhaps most significantly, these data support the hypothesis that the ear represents an integrated complex comprised of multiple correlated and potentially codependent features. It is evident that a tympanic ear has evolved multiple times within tetrapods; however, each evolutionary appearance is characterized by a distinct set of features and morphological consequences in the inner ear (e.g., epithelia and organ morphology, perilymphatic labyrinth; Lombard & Bolt, 1979). Additionally, the features outlined here contribute to the identification of the specific lissamphibian-type ear (Table 6), the evolution of which is most parsimoniously interpreted under the temnospondyl hypothesis of tetrapod relationships (Fig. 7). It is understood that the fossil record, and the anatomy it preserves, dramatically limits interpretation of the inner ear in critical taxa. However, potential osteological correlates, and data from extant forms, indicate

TABLE 5. Caecilian scores (based on *Rhinatrema bivittatum*) for the 220 characters in the matrix of Anderson et al. (2008). Slashes denote polymorphic characters: forward slash—states 0 and 1; back slash—states 1 and 2.

	Character scores				
Taxon	**1**	**10**	**20**	**30**	**40**
Caecilians	33011----	-1-1----1-	-0000?000-	102111001-	--0001---0
	50	**60**	**70**	**80**	**90**
	-0-21----1	-0--12011-	-000/20010	0100111100	1000100101
	100	**110**	**120**	**130**	**140**
	1011011000	1001001001	1\-000--11	2-101-3--?	1000?2?012
	150	**160**	**170**	**180**	**190**
	0000021---	-111??011?	????1???02	0---------	----------
	200	**210**	**220**		
	----------	----------	1		

that the lissamphibian-type ear appeared only once during the evolution of crownward temnospondyls, thereby contributing to the resolution of hypotheses of lissamphibian phylogeny.

Summary

It is apparent from the considerations presented that the morphology of the inner ear of lissamphibians is most consistent with the TH with regard to the constitution of and phylogeny of Lissamphibia. The distribution of the characters of the ear of lissamphibians is most parsimoniously explained under the TH. The TH does not necessitate the interpretation of the numerous similarities between the caecilian and frog plus salamander ear as being the result of convergence, as required by the PH. Nor does the TH necessitate the argument of an additional, novel evolution of a tympanic ear in tetrapods (once in frogs and additionally, nearly identically, in temnospondyls), in contrast to the LH. Therefore, under the TH the condition of the ear in caecilians represents a derived, secondary loss of the outer and middle ear components of both the tympanic and opercularis hearing pathways. This has previously been suggested (Schmalhausen, 1968; Ruta et al., 2003), and is supported here by new data and the reconsideration of previously published data. Empirical studies of the ears of caecilians will continue to provide new insights into auditory capabilities, functions of the various epithelia, and ultimately the evolutionary history of hearing in tetrapods. We trust that the integrative nature of

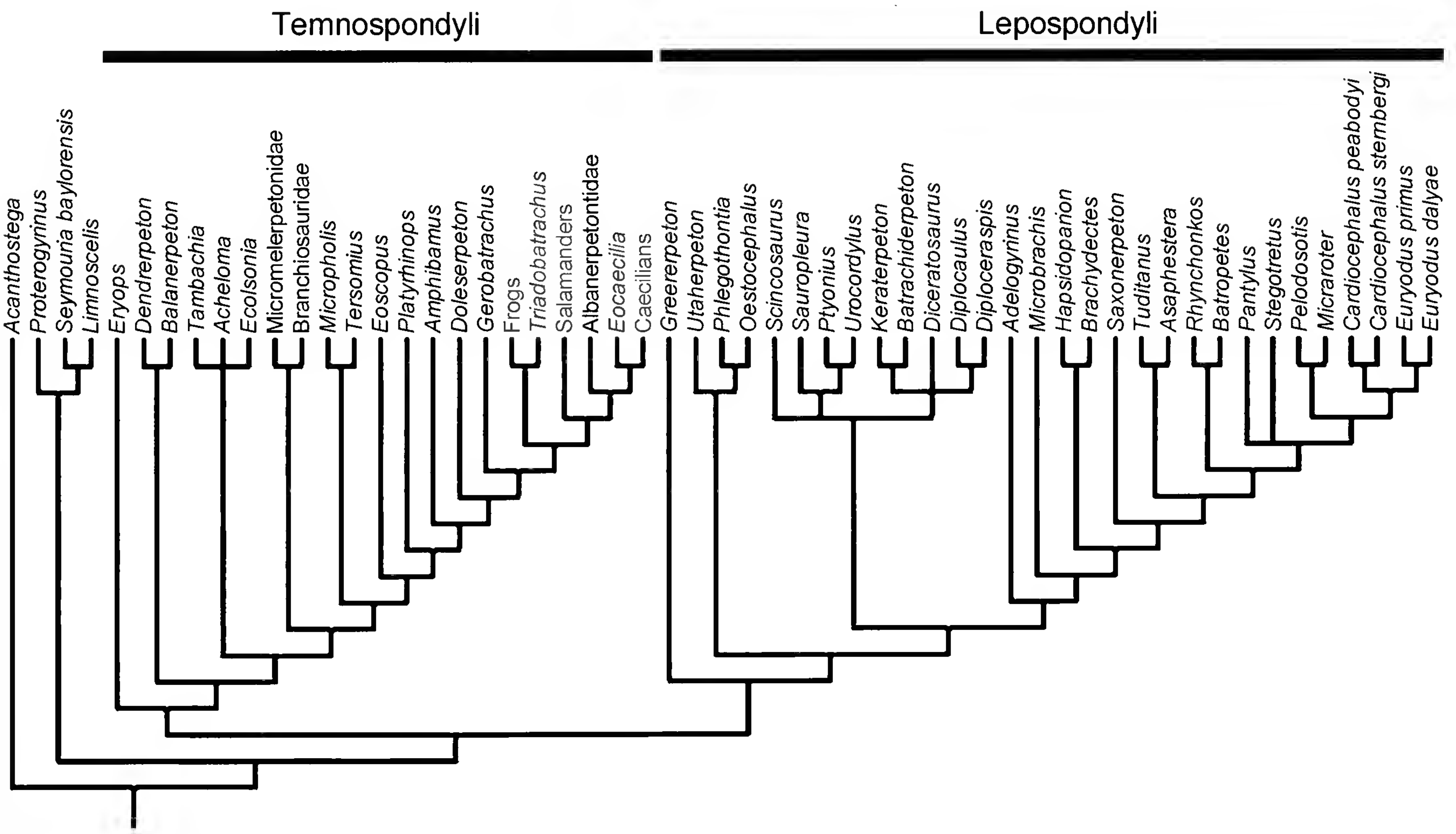

FIG. 8. The 50% majority rule consensus tree of 8 MPTs obtained when lissamphibian-type ear (character 220) is added to a modified matrix (see Tables 4 and 5) of Anderson et al. (2008). Lissamphibians (in red) are monophyletic (including Albanerpetontidae) and derived from within Temnospondyli. Heuristic search run in PAUP*4.0b10, *Acanthostega* set as the outgroup, characters unordered and equally weighted. Based on the osteological correlates identified here, a score of 1 (lissamphibian-type ear) is given to: *Eocaecilia*, Micromelerpetontidae, *Tersomius*, *Ecolsonia*, *Acheloma*, *Doleserpeton*, Albanerpetontidae, *Micropholis*, *Eoscopus*, *Tambachia*, *Triadobatrachus*, *Gerobatrachus*, *Platyrhinops*, *Amphibamus*, salamanders, frogs, and caecilians; question mark given to: Albanerpetontidae, Branchiosauridae, and *Eryops*; the remainder get a score of 0 (lissamphibian-type ear absent).

TABLE 6. Traits that characterize the lissamphibian-type ear, and its occurrence among frog, salamanders, and caecilians. All traits diagnose the plesiomorphic condition for Lissamphibia.

Trait	Trait occurrence
Tympanic hearing pathway	frogs, secondarily lost in salamanders and caecilians
Opercularis hearing pathway	frogs and salamanders, secondarily lost in caecilians
Periotic canal with posterior pathway	frogs, salamanders, and caecilians
Pressure relief into the brain cavity	salamanders and caecilians, some frogs (pressure relief into mouth is derived for some frogs)
Directional hearing via brain cavity	frogs, salamanders, and caecilians
Amphibian papilla (low frequency)	frogs, salamanders, and caecilians
Basilar papilla (high frequency)	frogs, salamanders, and caecilians

the tetrapod ear has been demonstrated, and that this feature is taken into consideration during the construction of characters when assessing the utility of the ear in informing interpretations of tetrapod relationships, and during the interpretation of the evolution of the ear across hypothesized patterns of relationship of taxa.

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Chapter 6: Did *Triadobatrachus* Jump? Morphology and Evolution of the Anuran Forelimb in Relation to Locomotion in Early Salientians

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Abstract

The Lower Triassic amphibians *Triadobatrachus massinoti* and *Czatkobatrachus polonicus* are universally regarded as stem anurans. However, there is still uncertainty about whether or not they were capable of jumping like true anurans as their postcranial features have so far provided only equivocal evidence. Although previous work has concentrated on the anatomy of the hind limb, here we examine the anatomy of the forelimb, comparing stem and crown-group anurans to other amphibians. The forelimb and pectoral girdle of *Triadobatrachus* share several features with modern frogs, including a frog-like deltoid attachment of the scapula. Though the radius and ulna are unfused, the humerus is similar to those of modern anurans. The deltopectoral crest is slightly elongated and a lateral deflection of the ventral edge of the crest creates a concavity on the lateral face of the humerus. These features are uncommon in most tetrapod groups characterized by a sprawling stance but are typical of modern anurans, in which the anterior chest musculature is enlarged. Our findings indicate that the importance of the deltoid had increased relative to that of the pectoralis muscle in *Triadobatrachus*. *Czatkobatrachus* is somewhat less similar to modern jumping anurans in its deltopectoral crest and pectoral girdle. Most anurans extend the forelimbs forward during a jump and land on their forefeet, perhaps accounting for the enlargement of the deltoid and the orientation of the deltopectoral crest. This type of behavior during landing is not seen in *Ascaphus* and *Leiopelma* but several features of these two genera, such as the fusion of the radio-ulna, the forearm musculature, and the degree of medial rotation of the manus, indicate that their landing behavior may be derived rather than primitive. Overall, *Triadobatrachus* was certainly not as capable of long jumps as some modern anurans, yet its anatomy does suggest that jumping or hopping was part of its locomotor repertoire.

Introduction

The anatomy of the hind limbs and pelvic region has justifiably received much attention in studies of the evolution of jumping in anurans (e.g., Shubin & Jenkins, 1995; Jenkins & Shubin, 1998; Wang et al., 2007; Přikryl et al., 2009; Reilly & Jorgensen, 2011). Though the evolution of anuran saltation seems to have been fully realized by the Lower Jurassic (Jenkins & Shubin, 1998), it remains uncertain whether the earliest known proanuran salientians from the Lower Triassic, *Triadobatrachus* and *Czatkobatrachus*, could jump too (Rage & Roček, 1989; Evans & Borsuk-Białynicka, 1998). These forms do show some features that may be associated with saltation, but their relatively short hind limbs and the lack of fusion of their limb bones have left the manner of their locomotion equivocal (Roček & Rage, 2000). The frog-like specializations seen in the pelvic structure of *Triadobatrachus massinoti* might conceivably be interpreted as a preadaptation originally serving a function unrelated to the jumping locomotion seen in modern frogs (Rage & Roček, 1989; Roček & Rage, 2000). If so, then other parts of the anatomy are unlikely to show clear trends toward saltatory adaptations. Furthermore, the evolution of saltation in anurans is now thought to be independent from that of swimming (Abourachid & Green, 1999; Přikryl et al., 2009), although it may have been linked to escaping predators by jumping toward water (Gans & Parsons, 1966).

Modern anurans show a range of locomotory behaviors. Emerson (1978) and Wells (2007) divided anurans roughly into strong jumpers (e.g., *Rana*), hoppers (e.g., *Bufo*, and most Pelobatidae), walkers and runners (e.g., *Kaloula* and *Kassina*), and fully aquatic swimmers (e.g., *Pipa* and *Xenopus*). These modes of locomotion are overlapping, and combined with various degrees of aquatic habits and/or arboreality and terrestriality. However, most modern anurans are capable of some form of saltation, and many features of their anatomy suggest that this highly specialized behavior is primitive for the whole group.

There can be little doubt that the forelimbs play a vital part in anuran saltation. Not only are they employed during takeoff, but they serve also an important role as shock absorbers during landing (Zug, 1972; Borsuk-Białynicka & Evans, 2002; Liem et al., 2001; Nauwelaerts & Aerts, 2006). The forces of impact absorbed by the forelimbs and pectoral girdle have been measured to be three times higher than the takeoff forces, due to the relative abruptness of deceleration when landing (Nauwelaerts & Aerts, 2006). Anurans also use their forelimbs actively during amplexus and sometimes when feeding (Duellman & Trueb, 1994), in signaling behavior (head-bobbing), or even during territorial fights (Peters & Aulner, 2000).

Yet apart from amplexus, which often results in a marked sexual dimorphism in forelimb morphology, the way other

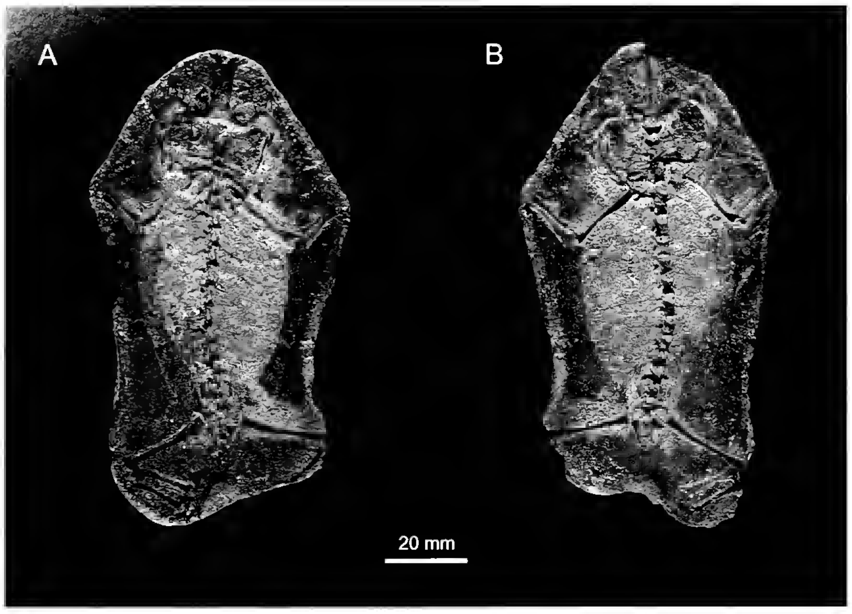

FIG. 1. The Lower Triassic salientian *Triadobatrachus massinoti* from Madagascar, natural mold (MNHN, No. MAE 126). (**A**) Dorsal part. (**B**) Ventral part.

factors relate to the anatomy of the forelimbs has scarcely been mentioned in the literature. Emerson (1984, 1988) discussed the importance of the morphology of the pectoral girdle but, even so, hardly mentioned the anatomy of the forelimbs. In recent anatomical descriptions of anurans by Banbury and Maglia (2006) and Pugener and Maglia (1997), the forelimbs were only partially examined.

In this study, we focus on some previously overlooked features of the forelimb and compare the features found in *Triadobatrachus* and *Czatkobatrachus* to both the presumed ancestral state as seen in salamanders, amphibamids, or lepospondyls, and to the derived condition in modern anurans to assess the most likely mode of locomotion in the Triassic taxa.

Institutional Abbreviations

FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNA, Museum of Northern Arizona, Flagstaff, Arizona; MNHN, Muséum National d'Histoire Naturelle, Paris; RM, Redpath Museum, Montreal, Quebec, Canada.

Materials and Methods

High-definition casts of *Triadobatrachus massinoti* (MNHN, No. MAE 126, Fig. 1) were studied in detail. Dr. Jean-Claude Rage (Muséum National d'Histoire Naturelle, Paris), who has access to the original specimen, kindly provided photographs and confirmed our observations. In addition, fossil and extant tetrapod specimens were examined at MCZ, FMNH, and RM. *Czatkobatrachus* has recently been described in great detail (Evans & Borsuk-Białynicka, 2009), and the information on this taxon is based on the published descriptions and photographs.

Most notable among the other fossil taxa we examined were the primitive caecilian *Eocaecilia micropodia* (MCZ 9163), and the possible proto-lissamphibians *Amphibamus grandiceps* (casts) from the Lower Carboniferous of Mazon Creek, Illinois, and *Doleserpeton annectens* (Bolt, 1969; Sigurdsen & Bolt, 2010) from the Lower Permian of Oklahoma. *Prosalirus bitis* (MNA V 8725) from the Lower Jurassic Kayenta Formation was also studied. Among modern forms, we examined ethanol-preserved specimens representing Ranidae (*Lithobates pipiens*, RM 2812 [= *Rana pipiens*], and *L. catesbeianus* [= *Rana catesbeiana*], RM 2785); Bufonidae (*Anaxyrus americanus* [= *Bufo americanus*], RM 4999); Ascaphidae (*Ascaphus truei*, RM 4430); Leiopelmatidae (*Leiopelma hochstetteri*, RM 2215; *Leiopelma archeyi*, RM 2193–2195); Pipidae (*Xenopus laevis*, RM 2230); and Pelobatidae (*Scaphiopus holbrookii*, RM 2425). We also examined and dissected *Conraua goliath* (Petropedetidae *sensu* Frost et al., 2006). These specimens were dissected to compare the musculature and osteology of the thorax and forelimbs. We attempted to examine species exemplifying each of the anuran locomotor modes identified by Emerson (1978) and Wells (2007) but, unfortunately, no specimens of "running frogs," such as *Kassina* sp., were available for study. For comparison, we also examined the forelimb anatomy of the salamander families Hynobiidae (*Hynobius nigrescens*, MCZ 22513); Cryptobranchidae (*Andrias davidianus*, FMNH 166872); and Ambystomatidae (*Ambystoma tigrinum*, RM 2161).

Results

Skeletal Anatomy of Amphibian Pectoral Girdles and Forelimbs

FROGS (ANURA)—The pectoral girdle of ranid frogs consists of several ossified elements. These include the scapula, coracoid, clavicle, omosternum, sternum, and the partially ossified suprascapula and cleithrum (Fig. 2). However, the sternum and omosternum remain unossified in many anurans, such as *Ascaphus*, *Leiopelma*, and *Discoglossus* (Stephenson, 1951; Ritland, 1955a; Pugener & Maglia, 1997). The median epicoracoid cartilages may be either overlapping, as in salamanders (arcifery), or fused along the midline (firmisterny). The scapula is usually roughly hourglass shaped, with the dorsal part expanding to meet the suprascapula, and the ventral expansion accommodating the posteromedially facing glenoid and the anterior contact with the clavicle. There is often a short anteriorly pointed process between the dorsal and ventral expansions (Fig. 2), which serves as a point of origin for part of the deltoid muscle. Although this edge is most pronounced in ranid anurans, it was also found in *Leiopelma* (T.S., pers. obs.). On the medial surface of the scapula of *Lithobates*, there is a strong vertical ridge posterior to the scapular cleft (= supraglenoid foramen; Borsuk-Białynicka & Evans, 2002). This ridge meets the coracoid medially, and according to Gaupp (1904) serves as additional attachment (origin) for the deltoid muscle on the internal face of the pectoral girdle in *Rana*. However, the ridge was found to be lacking or indistinct in primitive taxa. The forelimb may be somewhat more adducted than that of salamanders in the resting position. The humerus is robust, and the zeugopodium consists of a fused radio-ulna. The distal end of the anuran humerus resembles that of salamanders (Fig. 3), but is frequently more highly ossified. It is dominated by the capitulum, which is often even larger than that of salamanders. The capitulum articulates with both the radial and ulnar parts of the fused radio-ulna (Sigurdsen & Bolt, 2009). The radio-ulna also has a smaller articulating facet that fits between the capitulum and the entepicondyle. The proximal head of the humerus is rounded, except for the anterior concavity formed by the deltopectoral crest (described below). In anurans, the humeral shaft often has a more pronounced curvature than in most other sprawling tetrapods, including salamanders. In most of the specimens examined, the bone bends slightly ventrally toward the distal end, whereas there is a strong dorsal curvature toward the proximal head, giving the shaft as a whole a shallow sigmoid curvature (Fig. 3B). It is tempting to interpret the frequently strong curvature of anuran humeri in light of the work of Bertram and Biewener (1988), which emphasizes the relationship of bone curvature and increased load predictability; the shape of the anuran humerus may indicate that forces on the anuran forelimb are highly variable. However, because the degree of curvature varies considerably, even intraspecifically, this trait is difficult to interpret.

The deltopectoral crest (crista ventralis) serves as insertion for the deltoideus and pectoralis muscles, as well as for several smaller muscles (described below). In most anurans, this crest extends further distally than in salamanders and most other tetrapods. The deltopectoral crest of the basal genus *Leiopelma* is relatively short, tapering distally to disappear near the midpoint of the shaft (Fig. 4B). This morphology is also found among extinct subfossil species of the same genus (Worthy, 1987). In strong jumpers such as *Lithobates catesbeianus*, the deltopectoral crest is a prominent, elongate ridge that extends for almost half the length of the bone, reaching an abrupt distal terminus (Fig. 3B). Proximally, the

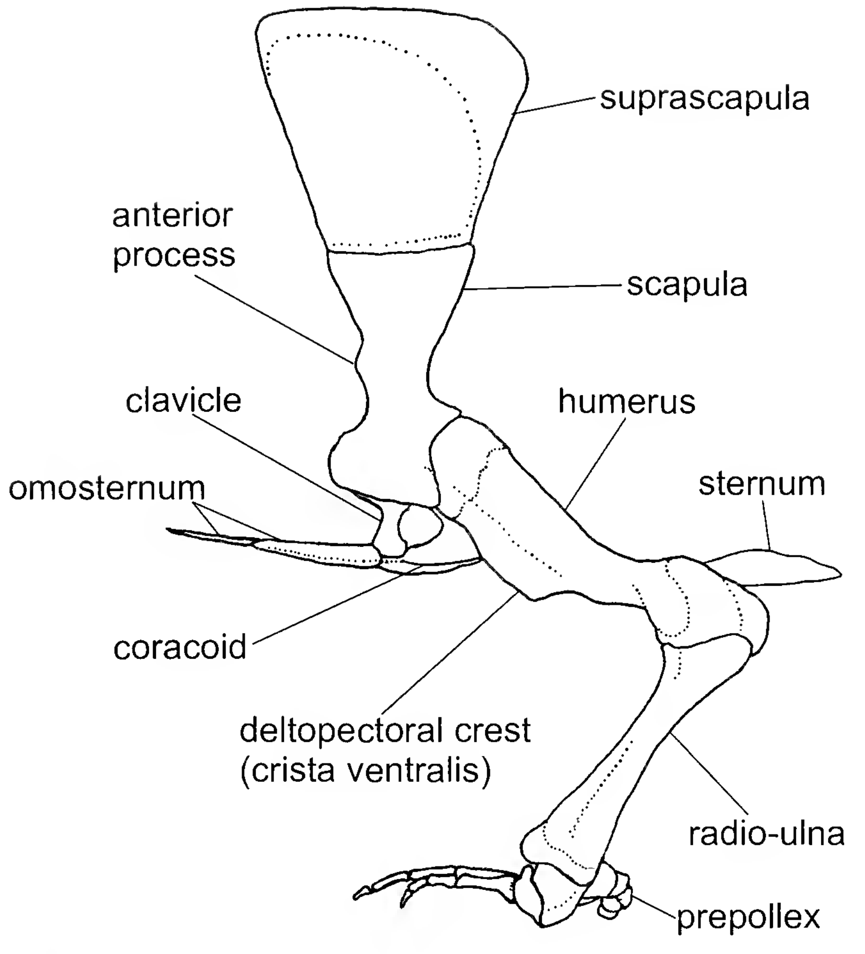

FIG. 2. The pectoral girdle and forelimb of a ranid anuran. Left lateral view. Note the laterally leaning deltopectoral crest, the strong torsion of the manus, and the anterior process of the scapula. The radio-ulna is a wide bone, but is here seen from the ulnar side. Based on female *Lithobates catesbeianus*.

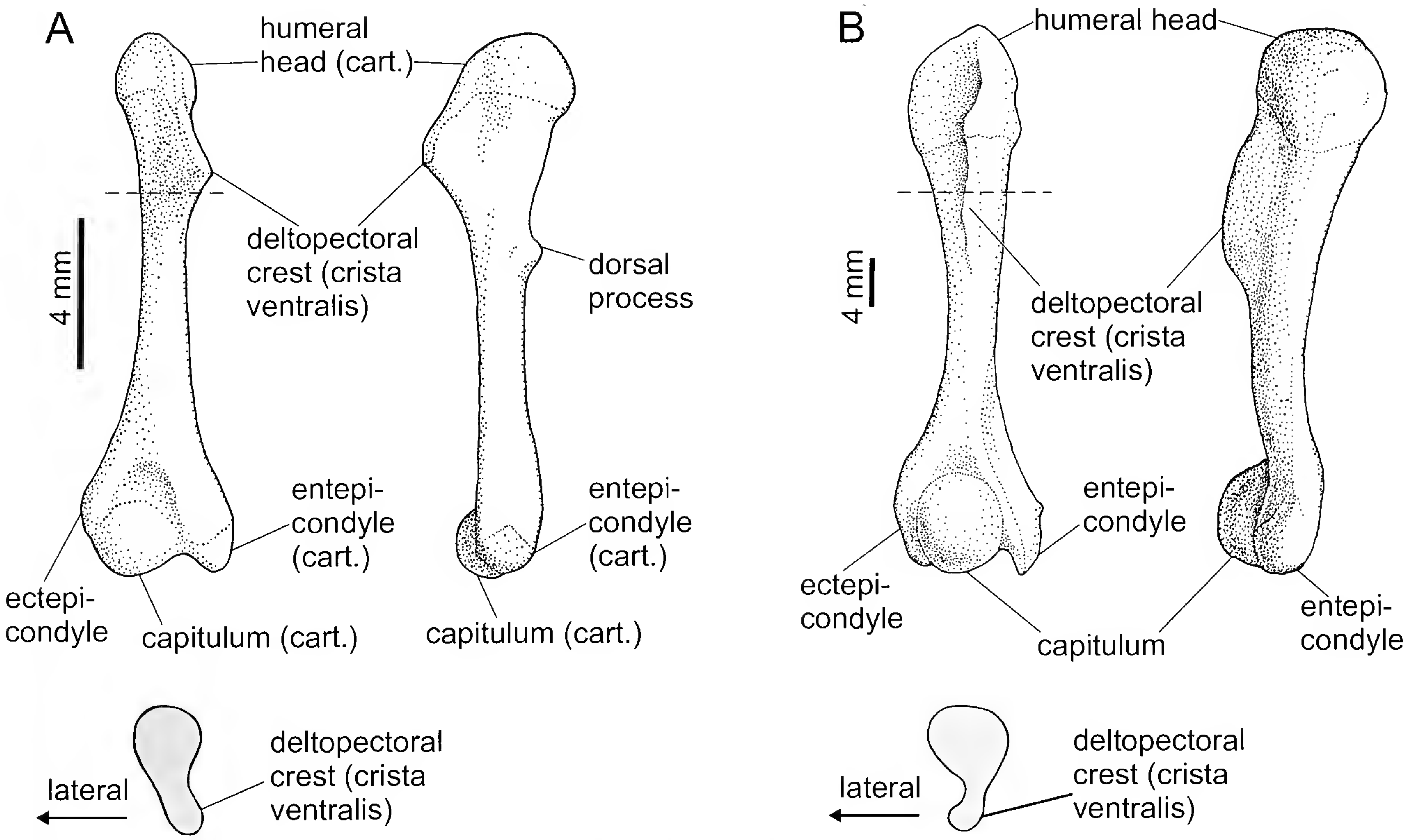

FIG. 3. The right humeri of modern amphibians. (**A**) *Ambystoma tigrinum* in ventral (flexor) and medial (posterior) views. (**B**) *Lithobates catesbeianus* in ventral and medial views. Dashed lines indicate the level of the schematic section shown below. Note the differing orientation of the ventral edge of the deltopectoral crest. The deltopectoral crest seen in *Ambystoma* is similar to that of sprawling amniotes and the primitive caecilian *Eocaecilia* (Jenkins et al., 2007; Sigurdsen & Bolt, 2009), but unlike anurans.

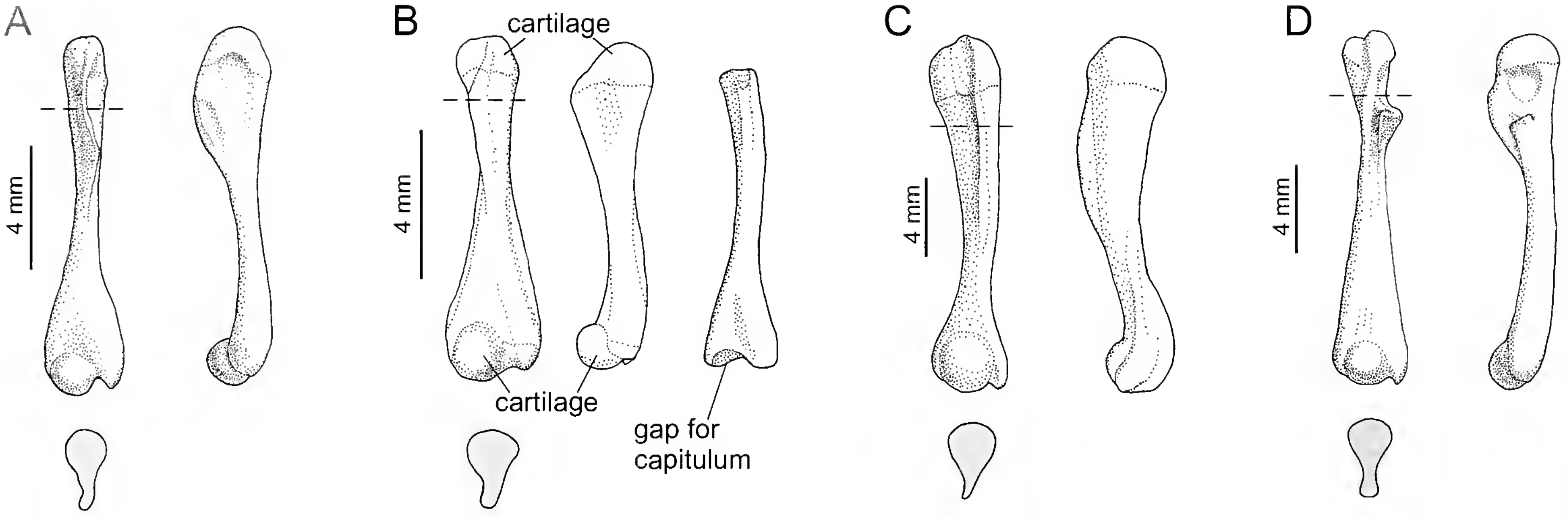

FIG. 4. The humeri of modern anurans. (**A**) *Ascaphus truei*, ventral and posterior views. (**B**) *Leiopelma hochstetteri*, male in ventral and posterior views and partly ossified female humerus in ventral view (cartilage removed). (**C**) *Scaphiopus holbrookii* in ventral and posterior views. (**D**) *Xenopus laevis*, in ventral and posterior views. Schematic sections shown below as in Fig. 2.

crest continues on to the head of the humerus, sometimes being interrupted by a slight break between the main part of the ridge and the head of the humerus (Fig. 3B). In most anurans, the deltopectoral crest curves laterally (anteriorly), forming a concavity on its lateral face (Figs. 2, 3B, 4A–C). This lateral concavity distinguishes anurans from salamanders and the early caecilian *Eocaecilia*, as well as lizards and most Paleozoic tetrapods, in which the deltopectoral crest usually is medioventrally concave. In anurans, the lateral concavity is most prominent in strong jumpers such as *Lithobates catesbeianus* (Fig. 3B), but it is also distinct in *Leiopelma hochstetteri* (Fig. 4B) and *Scaphiopus holbrookii* (Fig. 4C). On the other hand, it is weakly developed in the semiaquatic *Ascaphus truei* (Fig. 4A) and the terrestrial hopper/walker *Anaxyrus americanus*. The weak lateral concavity of the crest in *Ascaphus* is reversed more distally, so that the crest appears to be inclined toward the pectoralis muscle in this area (Fig. 4A). However, we were unable to find a single extant anuran in which the deltopectoral crest resembles that of salamanders (but see *Czatkobatrachus* below).

The most atypical anuran humeri are those of the specialized aquatic pipids. In *Xenopus laevis*, the deltopectoral crest is relatively short. It is almost straight in cross section (i.e., directed ventrally) and the proximal area is best described as biconcave (Fig. 4D). In this species a prominent boss for the insertion of the pectoralis musculature is located close to the posterior edge of the deltopectoral crest. Immediately lateral to this boss, there is a partially covered groove running from the deltopectoral crest down part of the ventral surface of the shaft; this groove accommodates the long tendon extending from the coraco-radialis muscle to the radio-ulna. Ritland (1955a) reported a similar groove in *Alytes*.

As pointed out by Jenkins and Shubin (1998) and others, the anuran manus usually is strongly twisted, so that the digits point medially. There are exceptions to this, the most obvious being the aquatic pipids, but the medial twist of the manus is also absent, or nearly so, in *Ascaphus* and *Leiopelma* (Figs. 5, 6B; see also Ritland, 1955b). The description of Jenkins and Shubin (1998, p. 503), which posits that the radio-ulna is twisted in the opposite direction to the foot, is slightly misleading. In primitive temnospondyls and modern salamanders, the radius is somewhat anterior (lateral in the adducted position) to the humeral axis (e.g., Jenkins & Shubin, 1998; Fig. 6A). In anurans, the radius and ulna, which are easily distinguishable within the radio-ulna, are virtually in the same position (relative to the humerus) as in salamanders, or slightly twisted in the same direction as the manus, bringing the radius and ulna into the same plane as the humeral axis (Fig. 2; Sigurdsen & Bolt, 2009). The details of the carpus vary, but there is usually a considerable amount of carpal fusion. However, the pattern seen in *Ascaphus*, *Leiopelma*, *Spea*, and *Discoglossus* correspond so closely that these may indeed represent the plesiomorphic condition of crown Anura (Stephenson, 1951; Ritland, 1955a; Pugener & Maglia, 1997). The proximal elements usually consist of a radiale (often fused to one of the centralia) and a fused ulnare-intermedium as in salamanders (Fabrezi & Alberch, 1996), though these bones are sometimes fused to other elements as well (Gaupp, 1904; Stephenson, 1952; Ritland, 1955a; Trueb et al., 2000). The medial rotation of the manus is most strongly apparent at the level of the proximal carpals. The distal carpals increase in size from the small distal carpal II (assuming digit 1 is lost) to the very large distal carpal V. The manus also contains a large element Y, and an often finger-like prepollex. The usual phalangeal formula is 2-2-3-3.

SALAMANDERS (CAUDATA)—The largely cartilaginous pectoral girdle of salamanders is a relatively simple structure (Reese, 1906; Francis, 1934), particularly when compared to that of frogs (Fig. 2; see also Gaupp, 1904; Noble, 1931; Trueb, 1973). It consists of an osseous scapulocoracoid (or scapula), surrounded by large suprascapular and coracoid cartilages. The coracoid part of the scapulocoracoid is pierced by a supracoracoid foramen or a homologous incision in the bone (incisura coracoidea; see Borsuk-Białynicka & Evans, 2002). The coracoid cartilages are equivalent to the epicoracoid cartilages of anurans and usually have a broad medial overlap, as in arciferous anurans. There is also a short, cartilaginous sternum of variable shape (Reese, 1906; Noble, 1931; Francis, 1934). The salamander humerus consists of a well-developed shaft (in contrast with the earliest tetrapods; e.g., Carroll & Holmes, 2007) that usually bears cartilaginous ends (Fig. 3A). In general, salamanders share with anurans and the primitive fossil caecilian *Eocaecilia* a large capitulum (radial condyle or capitellum), a distally directed entepicondyle, and the absence of foramina (Sigurdsen & Bolt, 2009). The humeral shaft of caudates usually is straight or only slightly curved. As in

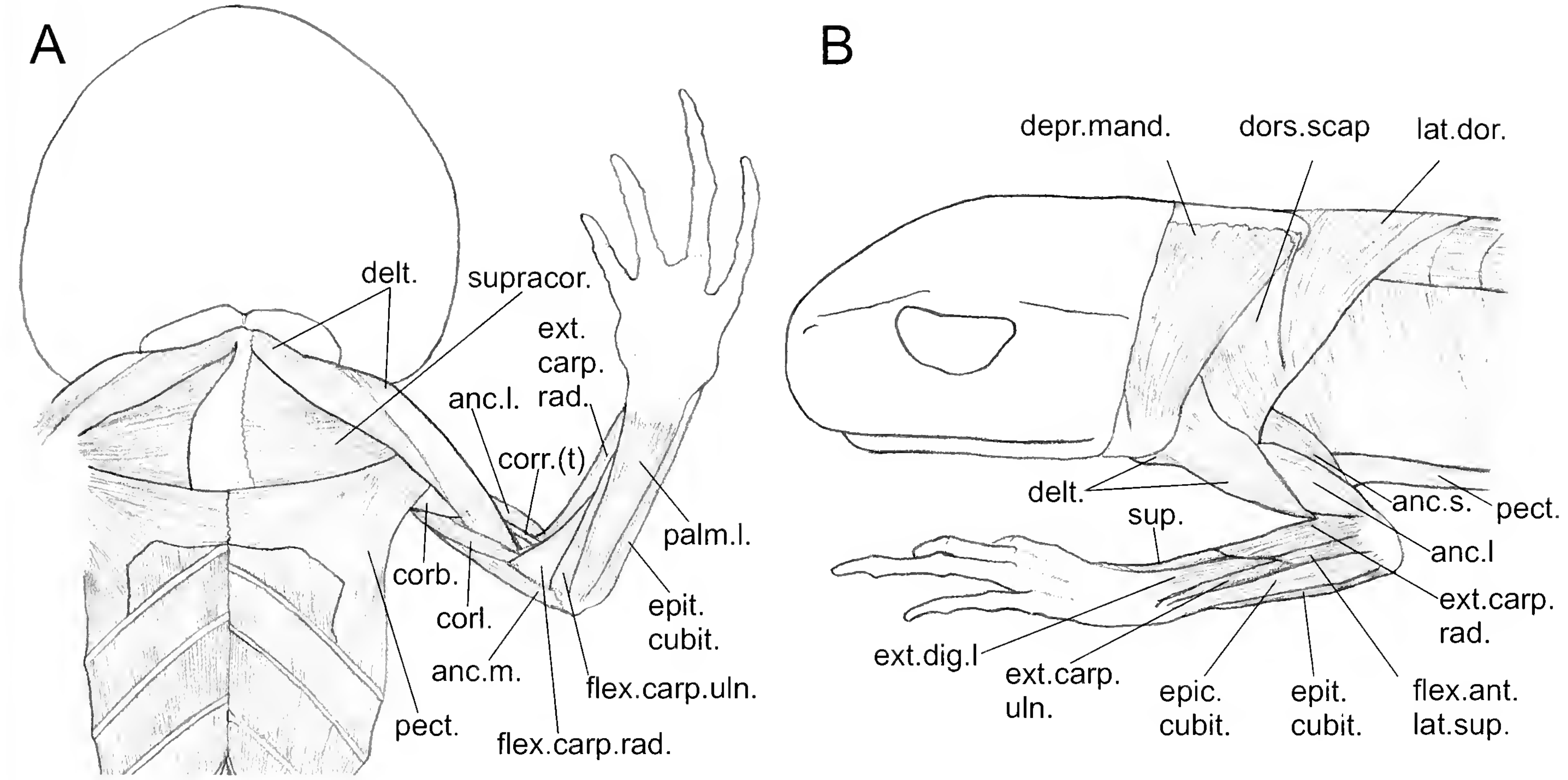

FIG. 5. The superficial chest and forelimb musculature of *Leiopelma archeyi*. (**A**) Ventral view. (**B**) Lateral view. Abbreviations: anc.l., anconeus caput lateralis; anc.m., anconeus caput medialis; anc.s., anconeus caput scapularis; corb., coracobrachialis brevis; corl., coracobrachialis longus; delt., deltoideus; depr. mand., depressor mandibulae; dors. scap., dorsalis scapulae; epic. cubit., epicondylo-cubitalis; epit. cubit., epitrochleo-cubitalis; ext. carp. rad., extensor carpi radialis; ext. carp. uln., extensor carpi ulnaris; ext. dig. l., extensor digitorum communis longus; flex. ant. lat. sup., flexor antibrachii lateralis superficialis; flex. carp. rad., flexor carpi radialis; flex. carp. uln., flexor carpi ulnaris; lat. dor., latissimus dorsi; palm. l., palmaris longus; pect., pectoralis; sup., supinator manus; supracor., supracoracoideus.

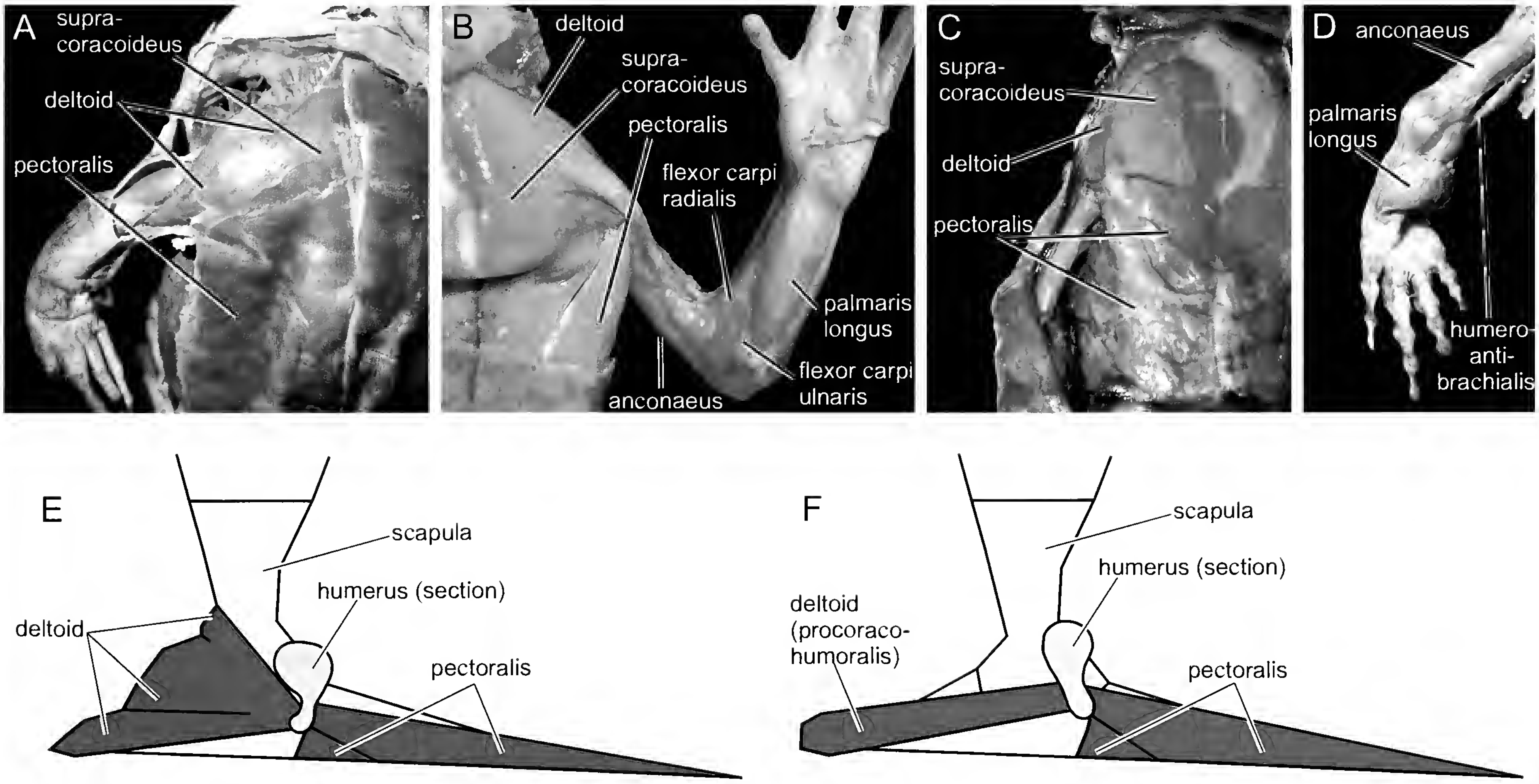

FIG. 6. The chest and forelimb musculature of modern amphibians. (**A**) *Lithobates catesbeianus* (Ranidae). (**B**) *Ascaphus truei* (Leioplematidae), showing the palmaris musculature of the lower arm. (**C**) *Ambystoma tigrinum* (Ambystomatidae). (**D**) The ventral forelimb musculature of *Ambystoma tigrinum*. (**E**) Schematic illustration of the pectoral region in a jumping anuran, showing the pectoral girdle, humerus, the pectoralis musculature, and the partially subdivided deltoid in lateral view. Note the large deltoid and the orientation of the deltopectoral crest (ventral crest). (**F**) Schematic illustration showing the same features in the pectoral region of a salamander.

Eocaecilia, but unlike frogs, there is often a dorsal process (crista dorsalis), which is the insertion point of the subscapularis muscle. However, this process is absent in some caudates, such as *Cryptobranchus* (Reese, 1906) and *Necturus* (T.S., pers. obs.). As in most tetrapods with a sprawling posture, the ventral edge of the deltopectoral crest (crista ventralis) curves medially and ventrally, creating a medial or ventro-medial concavity near the proximal end of the bone (Fig. 3A). This feature is almost universally present in tetrapods with a sprawling posture, the major exception being anurans (see above). The radius and ulna are unfused in salamanders, but both of these elements articulate with the large capitulum, though a rounded edge on the ulnar articulation surface also fits in the trochlear region between the capitulum and entepicondyle (sometimes erroneously called the ulnar condyle). The radius is usually expanded distally. The carpus shows none of the medial rotation of anurans. It often includes a number of elements that are fused in different ways, but distal carpals 1 and 2 are always fused. The phalangeal formula also varies, but 1-2-3-2 or 2-2-3-3 are common (Duellman & Trueb, 1994). Peculiarly, the digits and carpals develop preaxially rather than postaxially, contrary to the situation in most other tetrapods including frogs (Fröbisch et al., 2007).

Musculature of the Chest and Forelimbs of Amphibians

The musculature that is most relevant to the present discussion originates on the trunk and inserts on the forelimb (Fig. 5), but other muscles are also discussed when necessary, with emphasis on features that differ markedly between anurans and caudates. For a full description of the amphibian musculature see Gaupp (1904), Francis (1934), Miner (1925), Ritland (1955b), Duellman and Trueb (1994), and Walthall and Ashley-Ross (2006). The present description is based on original observations of *Leiopelma* and *Lithobates* (T.S.), with comparative information from *Ambystoma*. We follow Gaupp (1904), Francis (1934), and Ritland (1955b), except when otherwise noted. The nomenclature followed is that of the literature on anuran anatomy, so that the term "deltoid" is equivalent to the "procoracohumeralis" in caudates, and "deltoideus clavicularis" of amniotes, whereas the "dorsalis scapulae" of anurans and caudates (e.g., Francis, 1934) is equivalent to the "deltoideus scapularis" of amniotes (see Abdala & Diogo, 2010).

The dorsal musculature between the trunk and forelimb is largely similar in frogs and salamanders. This includes the latissimus dorsi and dorsalis scapulae muscles. However, unlike salamanders, these two muscles converge in anurans, to insert on the lateral face of the deltopectoral crest (crista ventralis) by a common tendon (Fig. 5).

The anconeus muscle (triceps, see Abdala & Diogo, 2010), which extends the elbow joint, is well defined in both anurans and salamanders. It has three heads in anurans—the caput mediale, laterale, and scapulare (Fig. 5)—whereas salamanders have a fourth point of origin at the coracoid (Francis, 1934).

The coraco-brachialis muscles originate from the coracoid and insert on the medial face of the humerus. Unlike Ritland's (1955b) description of *Ascaphus*, *Leiopelma* clearly has both coraco-brachialis muscles (Fig. 5) as described in *Rana* (Gaupp, 1904). However, the difference appears to be one of nomenclature, as the subcoracoscapularis of Ritland (1955b) appears to correspond to the longus slip of the coraco-brachialis. The coraco-brachialis muscles of salamanders resemble those of frogs. The subscapularis muscle of salamanders, inserting on the humeral dorsal process, has no clear homologue in frogs. The deltoid muscle (m. procoracohumeralis of Francis, 1934) of salamanders is relatively simple; it originates from the procoracoid cartilage of the pectoral girdle and inserts laterally on the deltopectoral crest of the humerus (Francis, 1934). In contrast, the deltoid of anurans is a complex and often massive muscle (Figs. 5, 6). Gaupp (1904) divided the deltoid muscle into three parts (pars episternalis, clavicularis, and scapularis) with separate origins and insertions. In *Leiopelma*, the muscle is a more unified mass with two or three origins (heads) and two regions of insertion, as in *Ascaphus* (Ritland, 1955b). Nevertheless, Gaupp's (1904) classical description is still largely accurate, and the major divisions given by that work are used here, although the fibers do not always follow the patterns described by Gaupp (1904). The antero-medial part (pars episternalis of Gaupp, 1904) originates from the anterior part of the epicoracoid and inserts on the distal end of the deltopectoral crest of the humerus. This slip of the anuran deltoid is closely associated with the underlying coraco-radialis muscle. The scapularis slip of the deltoid is the most robust part (Figs. 5A, B, 6). In *Leiopelma* and *Ascaphus*, it originates from the anterior edges of the scapula and clavicle, the dorsalmost part originating at the anterior process of the scapula (Fig. 2). In *Rana* and *Lithobates* parts of the deltoid also originate from the interior surface of the scapula. The muscle inserts on the deltopectoral crest of the humerus. However, fibers from this slip also continue on to insert more distally on the humerus. This situation was found in both *Leiopelma* and *Lithobates*, but in the latter it continues even further along a low ridge running from the deltopectoral crest, to insert near the entepicondyle (ulnar epicondyle) of the humerus. Finally, the pars clavicularis of the deltoid originates from the lateral end of the clavicle. It inserts inside the lateral concavity of the deltopectoral crest of the humerus. In most frogs, the deltoid muscle is considerably thicker than the surrounding musculature (Fig. 5A), and it seems to be the most powerful of the muscles originating on the trunk and inserting on the forelimb. The exception is the aquatic pipids, in which the deltoid is thinner than in most other anurans.

The pectoralis muscle of anurans was divided into three parts by Gaupp (1904): partes epicoracoidea, sternalis, and abdominalis. However, in *Leiopelma* the pars epicoracoidea is clearly separate from the rest of the pectoralis complex, and is strikingly similar to the supracoracoideus muscle described in salamanders (Francis, 1934). We therefore follow Noble (1931) and Abdala and Diogo (2010) in identifying this muscle as the supracoracoideus (Figs. 5, 6). As in salamanders, it originates from the epicoracoid cartilage and from the medial end of the coracoid, to insert on the medial side of the crista ventralis of the humerus. Ritland's (1955b) figures, which show the pectoralis meeting at the midline as far anteriorly as the edge of the deltoid, appear to be misleading, as the situation in the specimens of *Ascaphus* examined in the present study is similar to that of *Leiopelma* (Fig. 5) and not unlike salamanders.

The pars sternalis of the pectoralis originates from the midline connective tissue and the sternum, and inserts on the distal edge of the deltopectoral crest (crista ventralis). The pars abdominalis is the largest part, originating from the septa of the rectus muscle in the abdomen, or the inscriptional ribs of *Leiopelma*, and inserting near the sternalis part on the humerus. This posterior part of the pectoralis covers a large area of the abdomen, but it is thin and slightly transparent even in large ranids (Fig. 6A). This condition contrasts with the thicker pectoralis musculature in salamanders, in which the posterior muscle slips are more powerful than the deltoid (Fig. 6C, F).

In salamanders, the supracoracoideus muscle (= pectoralis pars epicoracoidea) covers the deeper coraco-radialis. According to Francis (1934) the latter is indistinct from the supracoracoideus, and is presumably a relatively small muscle. Although apparently somewhat larger in anurans, the fibers of this muscle were found to be difficult to discern from those of the supracoracoideus in *Leiopelma*, and the problems Francis (1934) had in distinguishing the two in salamanders is therefore equally true for primitive anurans. In ventral aspect, the muscle is covered by the supracoracoideus and deltoid. It originates from the epicoracoid cartilage, and continues as a long tendon (Fig. 5A) that enters a canal through part of the deltoid muscle and inserts on the proximal radial end of the radio-ulna, close to the articulation with the humerus. Whereas salamanders have a humero-antibrachialis muscle (perhaps equivalent to the biceps brachii; Francis, 1934), anurans have no such muscle. Lacking a biceps, the anurans presumably use the coraco-radialis to flex the elbow (Gaupp, 1904), but contraction of the radial flexors and extensors could also serve to flex this joint, given the extended origins of these muscles on the humerus.

The flexor muscles of the hand and digits are well developed in both salamanders and frogs, and are described in full by Francis (1934) and Gaupp (1904). The asymmetry found in the forearm muscles of anurans is a striking difference from the condition seen in salamanders. For instance, in salamanders, the flexor carpi radialis and ulnaris are located symmetrically on either side of the forearm, partially covered by the palmaris (primordialis) longus, which is situated between the two. In anurans, the flexor carpi ulnaris has shifted position so that it now is situated next to the flexor carpi radialis muscle (Figs. 5A, 6B). The latter muscle is also larger and more triangular than in salamanders. On the dorsal side of the forearm, the extensor carpi radialis is also enlarged and triangular. In *Leiopelma* it partially covers the extensor digitorum muscle (Fig. 5B). This is again contrasting to a more symmetrical arrangement in salamanders.

Pectoral Girdles and Forelimbs of Fossil Salientians

The following account is based on descriptions in the literature, but with additional original observations on *Triadobatrachus* and *Prosalirus*. The Lower Triassic Malagasy salientian, *Triadobatrachus massinoti*, was described by Piveteau (1937), Rage and Roček (1989), and Roček and Rage (2000), with additional comments by Estes and Reig (1973). Another Early Triassic form, *Czatkobatrachus polonicus*, was described by Evans and Borsuk-Białynicka (1998, 2009). *Czatkobatrachus* is similar to *Triadobatrachus* in many ways (Evans & Borsuk-Białynicka, 1998, 2009), but the limb bones are more highly ossified. Borsuk-Białynicka and Evans (2002) described the pectoral girdles of both *Czatkobatrachus* and *Triadobatrachus* in the great detail, and the information will only be briefly summarized here. There are many similarities between the scapulocoracoids of *Czatkobatrachus* and *Triadobatrachus*. The fact that the scapulocoracoid forms a single element pierced by two foramina is obviously a primitive feature (although this is less clear in *Triadobatrachus*). However, the glenoid is not the primitive screw shape found in early tetrapods, being rounded and facing more laterally. *Triadobatrachus* is somewhat more typical for salientians in general in that it possesses a wider scapular blade. Interestingly, an anterior ridge marks the origin of the deltoid in *Czatkobatrachus*, and this region appears to have a slightly protruding process in *Triadobatrachus* (Borsuk-Białynicka & Evans, 2002, figure 13), as in modern anurans.

Previous descriptions of *Triadobatrachus* gave little information on the humeri, other than that they resemble modern anurans (Piveteau, 1937). The bone is about 17.5 mm long as preserved. The humeral shaft of *Triadobatrachus* is sigmoidally curved, much like the humeri of most modern frogs (Fig. 7), and the Jurassic genus *Notobatrachus* (Báez & Basso, 1996; Báez & Nicoli, 2004). There is no dorsal process. The deltopectoral crest tapers distally and disappears at not quite the midlength of the shaft (preserved length of crest ~8 mm). There is a slightly raised area on the medial side of the bone, near the ventral apex of the deltopectoral crest. Presumably, this was the insertion point of the pectoralis musculature as in modern pipids (Fig. 7D). However, the ventral edge of the deltopectoral crest is deflected laterally, so that the proximal part of the humerus is concave on the lateral side, as in true jumping anurans. The distal and proximal ends of the bone are poorly preserved, owing to the lack of ossification of these parts. There is a large, rounded gap at the distal end of the bone, located lateral to the entepicondyle (Fig. 7C). The size and shape of this gap indicate that *Triadobatrachus* had a large, unossified capitulum; this feature is better preserved in the Polish taxon *Czatkobatrachus polonicus* (discussed below). The gap continues on to the dorsal side of the bone, again resembling the condition in modern anurans, in which part of the cartilaginous capitulum extends dorsally into a trough-like depression. The preserved parts of the medial condyle also indicate a distally directed entepicondyle as in anurans. In general, Piveteau's (1937) observation that the humeri of *Triadobatrachus* are much like those of modern anurans is confirmed here.

The radius and ulna are unfused in *Triadobatrachus* (Fig. 7A, B), and their shapes do not differ strongly from the situation in salamanders. However, *Triadobatrachus* appears to lack the broad distal expansion of the radius seen in salamanders and *Doleserpeton* (Francis, 1934; Sigurdsen & Bolt, 2010). The carpus of *Triadobatrachus* is poorly known, but appears to include separately ossified radiale, ulnare, and intermedium.

Interestingly, whereas the humerus of *Triadobatrachus* has a deltopectoral crest leaning slightly laterally (the side of the deltoid insertion) and a prominent muscle attachment scar on the medial side for the pectoralis, *Czatkobatrachus* appears to be the exact opposite, with the crest leaning slightly medially (the side of the pectoralis insertion), but with a muscle scar for the deltoid on the lateral side (Evans & Borsuk-Białynicka, 2009, figure 6). The bone is clearly more slender than that of *Triadobatrachus*, but this is to be expected in a smaller animal. The shaft is gently sigmoidally curved. It preserves some parts not seen in *Triadobatrachus*. The large capitulum is ossified in *Czatkobatrachus* (Evans & Borsuk-Białynicka, 1998, 2009). However, the general similarities of these two forms, as well as the large gap in the distal end of the humerus of *Triadoba-*

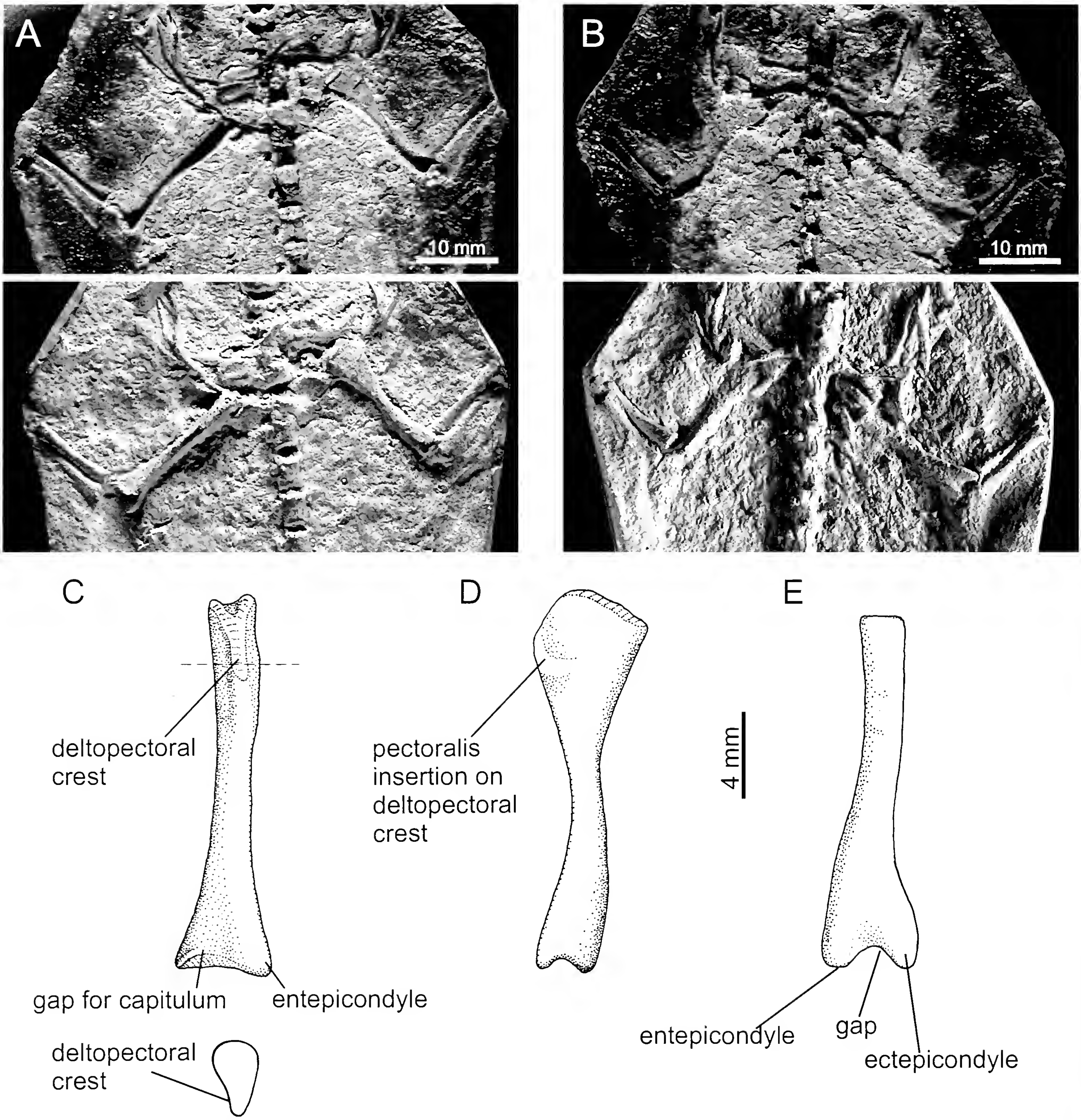

FIG. 7. The humeri of the Lower Triassic salientian *Triadobatrachus massinoti*. (**A**) Original specimen (top) and cast (bottom) in ventral view showing the forelimbs. (**B**) Dorsal view of original specimen (top) and cast (bottom). (**C**) Humerus, ventral (flexor) view, with schematic section below. (**D**) Medial (posterior) view. (**E**) Dorsal (extensor) view. The line drawings are based on both sides of the specimen, but reoriented to correspond to the right side. The casts have been flipped horizontally to correspond to the original specimens.

trachus, make it likely that this typically batrachian feature was present in both Triassic taxa. The ulna of *Czatkobatrachus* is not unlike that of salamanders (Sigurdsen & Bolt, 2009), and it preserves a well-ossified olecranon. Although the higher degree of ossification in *Czatkobatrachus* may be a sign of terrestriality, this pattern does not follow our observations of modern anurans, in which the semi-aquatic and aquatic genera *Ascaphus* and *Xenopus* have fully ossified humeri, whereas the more terrestrial *Leiopelma* usually retains cartilaginous parts. Alternatively, the single specimen of *Triadobatrachus* may be somewhat immature.

Prosalirus bitis, an early jumping anuran from the Lower Jurassic of Arizona, was described by Shubin and Jenkins (1995; see also Jenkins & Shubin, 1998). By this time, the pectoral girdle had reached an essentially modern anuran stage, including a separate scapula and coracoid. The best preserved humerus is somewhat crushed, and only partially ossified distally. The bone is notable for its robustness. The presence of strong medial and lateral ridges may indicate that the specimen is male, judging from similar features on the male humeri of *Ascaphus* (Ritland, 1955a; see also Trueb, 1973) and *Leiopelma* (Fig. 4B). The deltopectoral crest is mediolaterally crushed, making its orientation somewhat difficult to discern. Jenkins and Shubin (1998; Fig. 2) reconstructed the crest as being slanted laterally, as in most modern anurans. The bone resembles that of *Ascaphus* in having a rounded outline of the deltopectoral crest, whereas it is closer to *Leiopelma* in its greater robustness. Our observations confirmed a slight sigmoidal curvature, although apparently less so than in both *Triadobatrachus* and many modern anurans, but similar to *Ascaphus*. There is some evidence for medial rotation of the manus in *Prosalirus*, as in many modern anurans (Jenkins & Shubin, 1998).

The stem anuran *Vieraella* is from the Early Jurassic of Patagonia (Báez & Basso, 1996). It is known from only one specimen. The scapula appears to be more slender than that of *Prosalirus*. The humerus has a well-developed deltopectoral crest, which appears to taper toward the shaft distally, as in *Leiopelma*. Interestingly, the forefoot appears to be strongly rotated medially as in many modern anurans, except that this feature is absent or poorly developed in *Ascaphus* and *Leiopelma* (e.g., Ritland, 1955a,b). The femur is considerably longer than the humerus in *Vieraella*.

The primitive genus *Notobatrachus* from the Jurassic of Patagonia was described in detail by Báez and Basso (1996) and Báez and Nicoli (2004). Although *Vieraella* is the earliest recorded frog from Patagonia, *Notobatrachus* is far better known (Báez & Basso, 1996). The pectoral girdle of this form is very similar to that of *Leiopelma* in that the scapula has a robust hourglass shape and a distinct scapular cleft, and the coracoid being relatively wide (Estes & Reig, 1973). The humerus of *Notobatrachus* has a well-developed deltopectoral crest which appears to taper distally, as in *Leiopelma*. The crest appears to be oriented laterally such that a concavity is formed on the lateral side of the bone (Báez & Nicoli, 2004; Fig. 2). The shaft is relatively robust, and Báez and Basso (1996) noted a slight sigmoidal curvature. The proximal and distal ends are unossified. The manus appears to lack medial rotation. The overall impression given by all of these elements are nearly identical to those of *Leiopelma*. A series of specimens show that many carpals initially ossify as individual bones, only later to fuse with other carpal elements (Estes & Reig, 1973).

Discussion

Frogs use their forelimbs both in the takeoff and landing phases of a jump (Peters et al., 1996; Essner et al., 2010) and occasionally in feeding, head-bobbing signaling behavior, and, in males, mating and even fighting. The added muscular attachment ridges of the humeri are male specializations for amplexus; otherwise, the features discussed here are found in both males and females. The pectoral musculature of anurans is similar to that of salamanders in many ways, but the two groups differ profoundly in some important features. In anurans, this is most pronounced in the enlarged and elaborated deltoid, the lack of a humero-antibrachialis muscle (biceps), and the marked asymmetry seen in the muscles of the forearm, with enlarged flexors and extensors on the radial side. The asymmetry of the forearm musculature may be linked to the strong medial rotation of the manus, which would affect the position of the muscles flexing and extending this part of the limb. Rotation of the manus is nearly absent in *Ascaphus* and *Leiopelma* (Figs. 5, 6B). Even so, the musculature does not resemble that of salamanders in these forms but represents a slightly rearranged anuran condition in which the extensor digitorum is partially covered by other muscles and the radial extensor and flexor are somewhat smaller.

The deltoid (= procoracohumeralis) muscle inserts on the proximal portion of the humerus in salamanders, whereas, in frogs, the different slips of this muscle insert proximally, as well as further distally, with one slip inserting almost at the distal end of the bone. The extended insertion of the deltoid of frogs reinforces the impression of the increased importance of this muscle in anurans relative to other tetrapods. The action of the deltoid is enhanced by this elongated insertion on the humerus because the force of muscle contraction is applied further from the fulcrum (i.e., the glenoid).

A functional interpretation of the enlarged and complex deltoid of frogs remains somewhat elusive. Contraction of the deltoid pulls the humerus forward, and rotates it so that the radio-ulna and manus are directed anteriorly (Gaupp, 1904; Duellman & Trueb, 1994). This function appears to have limited use during takeoff, but ranid anurans almost certainly use this muscle during landing, when the forelimbs are stretched anteriorly to resist the impact (Peters et al., 1996; Nauwelaerts & Aerts, 2006; Essner et al., 2010) and this behavior is also observed in hylids (P.J.B., pers. obs.). The fusion of the radio-ulna strengthens the forelimb further against the force of impact. Even in poorer jumpers (e.g., *Bufo*, *Scaphiopus*), the movement of the forelimb during short hops usually differs from that of crawling animals such as salamanders and, presumably, primitive tetrapods.

However, new observations of primitive extant anurans reveal a quite different mode of jumping behavior from that of ranids (Essner et al., 2010). In *Ascaphus*, the forelimbs are not extended forward during the landing phase, and the animal lands on its belly or head. *Leiopelma* are best characterized as hoppers rather than strong jumpers, although they are capable of longer jumps when agitated (Abourachid & Green, 1999). Like *Ascaphus*, *Leiopelma* rarely lands directly on its forelimbs (Essner et al., 2010); however, unlike in *Ascaphus*, our own observations show that *Leiopelma* rotates the forelimbs so that the radio-ulna and manus are directed anteriorly when jumping. Thus, the landing behavior of *Leiopelma* more closely resembles that of other modern anurans than does *Ascaphus*. Therefore, the primitive condition of modern anurans is equivocal, and the odd behavior of *Ascaphus* either may be plesiomorphic or a secondary adaptation to its torrent-dwelling habits.

Some evidence suggests that the locomotor behavior of *Ascaphus*, and perhaps also *Leiopelma*, is derived rather than primitive, as suggested by Ritland (1955b). For instance, the fused radio-ulna of all modern anurans is usually interpreted as a shock-absorbing adaptation (Liem et al., 2001), which seems to be hard to reconcile with the landing behavior seen in *Ascaphus* (Essner et al., 2010). This is further supported by Jenkins and Shubin (1998), who concluded that the fusion of the radio-ulna and tibiofibula, along with other morphological features, indicate that terrestrial saltation was primitive, at least for Anura (but perhaps not Salientia). Evans and Borsuk-Białynicka (1998) interpreted the pectoral girdles of the Triassic salientian *Czatkobatrachus* as an initial stage in the evolution of the pectoral girdle and forelimb as a shock-absorbing complex, emphasizing the anterior movement of the forelimb during landing. This result is consistent with our observations of the forelimb of *Triadobatrachus*, although it is contradicted by the behavior of *Ascaphus*, and somewhat less by *Leiopelma*. If Evans and Borsuk-Białynicka (1998) are correct, then the behavior of *Ascaphus* must be viewed as uniquely derived rather than primitive.

Fossil evidence suggests that the medial manual rotation of anurans had evolved by the Lower Jurassic (Table 1). However, this rotation of the manus is much less pronounced in both *Ascaphus* and *Leiopelma* (Figs. 5, 6) than in some early anurans such as *Vieraella* and, perhaps, *Prosalirus* (Báez & Basso, 1996; Jenkins & Shubin, 1998). Ritland (1955b) suggested a correlation between the position of the manus, locomotion (usually crawling or even climbing), and habitat in *Ascaphus*. The lateral slant of the deltopectoral crest of *Ascaphus* is less pronounced compared to most other salientians including *Leiopelma* and, as we have shown, *Triadobatrachus*, although it is far from the salamander condition. The forelimb musculature of *Leiopelma* and *Ascaphus* is recognizably anuran, but the deltoid is not as enlarged as seen in ranids (Figs. 5, 6), and the forearm musculature seems to be even more specialized than seen in ranids in that the extensor digitorum is partially covered by other muscles. One plausible explanation for this is that the forearm muscles of *Ascaphus* and *Leiopelma* have been rearranged twice, once during the evolution of medal manual rotation, and once again when this feature was reversed.

All of these features seem to confirm Ritland's (1955b) conclusion that the behavior of both *Ascaphus* and *Leiopelma* is uniquely derived and adapted to their habitat, and may not reflect the primitive condition of anurans. The situation is further complicated by the fact that *Ascaphus* and *Leiopelma* may or may not constitute a monophyletic taxon. Although Green and Cannatella (1993) argued that the two genera are not related closely enough to be considered part of the same family, Frost et al. (2006) concluded that they may indeed belong together in a monophyletic Leiopelmatidae. If this phylogeny is accepted, then the most parsimonious distribution of the three states of landing behavior (i.e., those of *Ascaphus*, *Leiopelma*, and other anurans, respectively, treated as an ordered character with three character states) is that either the behavior of *Leiopelma* (rotating forelimbs anteriorly, but landing on the belly) or that of advanced anurans (rotating forelimbs anteriorly, and landing on forefeet) is the primitive state; one more step is required if we designate the behavior of *Ascaphus* (no rotation of the forelimbs, landing on belly) as primitive.

Although the humeri of frogs, salamanders, and *Eocaecilia* are surprisingly similar in the elbow region (Sigurdsen & Bolt, 2009), salientians (frogs and basal proanurans) seem to differ from all other tetrapods in the muscle attachments of the humeri. In this regard, the humeri of *Eocaecilia*, salamanders, and lizards are functionally equivalent in having a deltopectoral crest that is deflected medially and ventrally, creating a medial concavity proximally. This condition also is present in temnospondyls, such as *Dissorophus* and *Doleserpeton* (Sigurdsen & Bolt, 2009). Overall, the forelimbs of salamanders are remarkably similar to those of the Lower Jurassic caecilian *Eocaecilia* (Jenkins et al., 2007) and the possible "proto-lissamphibian" *Doleserpeton*, an amphibamid from the Lower Permian (Sigurdsen & Bolt, 2010). Although lepospondyl limb elements often are poorly preserved, the medial concavity of the deltopectoral crest is confirmed in the microsaurs *Pantylus*, *Cardiocephalus* (Carroll & Gaskill, 1978), and *Euryodus* (FMNH PR 983). This similarity to possible lissamphibian sister-groups indicates that the forelimb morphology of modern salamanders is close to the primitive lissamphibian condition (Sigurdsen & Bolt, 2009). The deltopectoral crest found in most sprawling tetrapods ensures a strong edge for the attachment of the pectoralis musculature, which is important in moving the animal forward during locomotion.

The most striking differences between an anuran humerus and that of a salamander are associated with the deltopectoral crest (the lack of a dorsal process in anurans is also shared with some salamanders). The fact that the proximal area of the humerus of most salientians is concave laterally, rather than medially, probably reflects a shift in the importance and strength of the muscles attached to the deltopectoral crest. The lateral concavity of the anuran deltopectoral crest serves as an insertion site for the proximal parts of the powerful deltoid musculature in frogs (Fig. 6). The enlarged deltoid is also reflected by the elongation of this crest.

The deltopectoral crests of *Czatkobatrachus* and *Triadobatrachus* taper distally, and are slightly extended relative to those of salamanders, but less so than in the strongest jumpers among modern frogs. Apart from this, these early salientians show marked differences in the deltopectoral crest. The orientation of the crest in *Czatkobatrachus* is essentially as in salamanders, but with a more marked deltoid attachment on the lateral surface of the bone. The slight lateral concavity of the proximal part of the humerus of *Triadobatrachus* (Fig. 7) may indicate a beginning elaboration of the deltoid in this early salientian, and this observation is confirmed by the area of the origin of the deltoid at the anterior edge of the scapula, which shows a practically modern anuran configuration including an anteriorly projecting edge (compare Fig. 2 to Evans & Borsuk-Białynicka, 2009, figure 13). Thus, the anatomy of *Triadobatrachus* suggests that the musculature of the proximal part of the forelimb was more similar to frogs than to salamanders, but this conclusion is less certain for *Czatkobatrachus*. The latter shows evidence of strong deltoid musculature attachments in both the humeri and the scapulocoracoid. However, in both of these cases, the situation appears to be somewhat less similar to most modern anurans than in *Triadobatrachus*. On the other hand, the higher degree of ossification seen in *Czatkobatrachus* is typical of anurans. It is possible that the lack of this feature relates to the ontogenetic stage of the single specimen of *Triadobatrachus*. When compared to fossil and extant anurans, and keeping in mind the missing cartilaginous parts, the humerus of *Triadobatrachus* appears to resemble that of the genera *Leiopelma* and *Notobatrachus* most.

Roček and Rage (2000) argued that few features point unequivocally towards jumping in *Triadobatrachus*, and concluded that saltation probably evolved after this early salientian stage. According to these authors, the anterior and posterior limbs are of nearly the same length, the tibia and fibula being shorter than the femur, and the trunk having a relatively high number of vertebrae. However, we should point out that nearly all of these features are actually intermediate between such forms as *Doleserpeton* and modern anurans, a point also made by Jenkins and Shubin (1998). For instance, the number of presacrals (14) is fewer than in any amphibamid,

TABLE 1. Features purportedly associated with jumping.

	No. presacral vertebrae	Tail/caudal vertebrae	Iliac blade orientation	Epipodial fusion	Femur-to-humerus length ratio	Deltopectoral crest orientation	Medial manual torsion
Doleserpeton[1] (Lower Permian)	22–25	tail present	posterior	absent	1.03	medial	absent
Eocaecilia (Lower Jurassic)	>30	tail present	?	absent	0.98	medial	?
Caudata (recent)	10–60[2]	tail present	posterior	absent	0.85[3]	medial	absent
Triadobatrachus (Lower Triassic)	14	tail reduced	anterior	absent	1.22	lateral	?
Czatkobatrachus[4] (Lower Triassic)	? (~14)	tail reduced	anterior	absent	1.13	medial (?)	?
Prosalirus[5] (Lower Jurassic)	?	fused coccyx	anterior	present	1.42	lateral (?)	present (?)
Vieraella[6] (Lower Jurassic)	10	?	anterior	present	>1.60	lateral	present
Notobatrachus[6,7] (Middle Jurassic)	9	fused coccyx	anterior	present	1.30	lateral	absent (?)
Ascaphus (recent)	9 (10)	fused coccyx	anterior	present	1.50	— (ventral)	absent
Scaphiopus (recent)	8	fused coccyx	anterior	present	1.34	lateral	present
Lithobates (recent)	8	fused coccyx	anterior	present	1.80	lateral	present

[1] Sigurdsen and Bolt (2010).

[2] Duellman and Trueb (1994).

[3] Highly variable feature; figure given is derived from Francis (1934).

[4] Evans and Borsuk-Białynicka (2009).

[5] Jenkins and Shubin (1998).

[6] Báez and Basso (1996).

[7] Báez and Nicoli (2004).

and one less than the short-bodied salamander *Karaurus* (Ivachnenko, 1978). The hind limb is somewhat elongated, the femur being 22% longer than the humerus. This is longer than any of the salamanders studied here, and also longer than in the possible lissamphibian sister-taxon *Doleserpeton* (Sigurdsen & Bolt, 2010), although some other amphibamids seem to have elongated femora. Finally, the structure of the deltopectoral crest, the anteriorly directed ilium, and the reduced tail could also be associated with jumping. The anatomy of the humeri is certainly closer to modern anurans than to salamanders, suggesting a change in locomotion. Such major anatomical changes as are found in modern frogs are unlikely to take place rapidly, and *Triadobatrachus* appears to be anatomically intermediate between the presumed ancestral state of lissamphibians and that of modern jumping anurans (Table 1).

There is evidence of reversals and unique specializations early in the salientian fossil record. For instance, both the deltopectoral crest and ilio-sacral configuration (Evans & Borsuk-Białynicka, 2009) differ in the Triassic forms *Czatkobatrachus* and *Triadobatrachus*, and in the Jurassic *Notobatrachus* shows less manual rotation than does *Vieraella*. The latter appears to have been a strong jumper (Table 1), a condition that is reversed in numerous modern anurans. In this, we disagree with Reilly and Jorgensen (2011), who placed the origin of jumping much later based on the morphology of the pelvic region alone. The situation is further complicated by the fact that all extant anurans, with their variable modes of locomotion, are likely derived from jumping forms. Therefore, their anatomy may reflect a mixture of inherited features and apomorphic adaptations, making them difficult to compare to the most primitive members of Salientia. Gomes et al. (2009) showed that both phylogeny and ecology can affect anuran postcranial morphology, and that these influences sometimes can be hard to tease apart.

Although the anatomy of *Triadobatrachus* precludes its possibility of being as strong a jumper as some modern taxa, the presence of several frog-like features in its postcranial anatomy, including the evidence for a strong deltoid musculature, may suggest that hopping or jumping was an important form of locomotion for this early salientian, perhaps combined with salamander-like crawling. *Czatkobatrachus* shows some of the same features, but lacks a few of the typical anuran features seen in the humerus and pectoral girdle of *Triadobatrachus*, indicating some morphological, and presumably behavioral, diversity among early salientians.

It is difficult to say whether or not *Triadobatrachus* habitually landed on its forefeet after jumps in view of the variable landing behaviors of *Ascaphus*, *Leiopelma*, and other anurans. The advanced frog-like attachment sites of the deltoid muscle on the forelimb and pectoral girdle suggests that a powerful forward extension the forelimbs may have been important in the locomotion of *Triadobatrachus*, perhaps to absorb the forces of impact during the landing phase of a jump. Alternatively, it may have rotated the forelimbs forward as *Leiopelma* does, a behavior which somewhat resembles a reflex during free-fall situations (Wassersug, 2001).

The fused radio-ulna and medial rotation of the manus in Early Jurassic forms and most modern anurans, combined with the elaboration of the deltoid muscle, could indicate that landing on the forefeet is indeed the plesiomorphic condition of anurans. If this is the case, we would have to conclude that *Leiopelma*, and especially *Ascaphus*, are poor models for the primitive condition among extant frogs, as is indeed suggested by their unusual forelimb musculature. However, further studies are clearly needed to assess what constitutes the primitive mode of jumping behavior in anurans and the importance of forelimb anatomy and musculature in salientian locomotion.

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Chapter 7: A New Coelurosaurian Theropod from the La Buitrera Fossil Locality of Río Negro, Argentina

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Abstract

A new coelurosaurian theropod, *Alnashetri cerropoliciensis*, is reported here based on articulated hind limbs of a single individual discovered at the locality of La Buitrera (Candeleros Formation, Cenomanian–Turonian), Río Negro Province, Argentina. The new taxon differs from other coelurosaurs in the possession of a low ridge that separates the rostral tibial surface from the outer face of the lateral malleolus, and which extends proximally beyond the tip of the ascending process of the astragalus, and in the possession of ventral notches on the hemicondyles of the distal articulations on pedal phalanges III-1 and III-2. *Alnashetri* is easily distinguished from the dromaeosaurid *Buitreraptor*, the only other known small theropod from La Buitrera. Phylogenetic analysis supports alvarezsauroid affinities. The evidence supporting this relationship comes from the detailed anatomy of the ankle, however, and this concentration of character support within a single anatomical region may bias our results. If our proposed phylogenetic placement is accurate, *Alnashetri* antedates all other Argentinian alvarezsaurids and indicates that alvarezsaurids were present in the Neuquén Basin throughout the entire Late Cretaceous.

Introduction

Non-avian coelurosaurian theropods were largely unknown and considered to be absent from the Mesozoic record of South America until the 1990s. The recognition of both alvarezsaurid and paravian theropods from Late Cretaceous strata of Argentina in the mid-1990s (Novas, 1996, 1997; Novas & Puerta, 1997) challenged the paradigm that Laurasian and Gondwanan dinosaur faunas of the Cretaceous were comprised of distinct and vicariously distributed lineages (Bonaparte, 1986). Since the initial discoveries of *Alvarezsaurus* (Bonaparte, 1991) and *Unenlagia* (Novas & Puerta, 1997), several more alvarezsaurid (Novas, 1997; Salgado et al., 2009; Agnolin et al., 2012) and dromaeosaurid (Makovicky et al., 2005; Novas & Pol, 2005; Novas et al., 2009) taxa and specimens have been discovered principally from the Late Cretaceous Neuqúen Group of northern Patagonia.

The oldest unit within the Neuqúen Group is the Cenomanian–Turonian Candeleros Formation, which has produced a rich fauna of both large and small dinosaurs and other vertebrates (Leanza et al., 2004). The bulk of the known small- to medium-sized vertebrates derive from a large tract of exposures of the upper Candeleros Formation on the Río Negro shore of the Ezequiel Ramos Mexía reservoir known as La Buitrera (Fig. 1), which were discovered by the second author in 1999.

In 2005, the senior author discovered a partial skeleton of a very small theropod dinosaur at La Buitrera, comprising parts of both hind limbs, but with the left more complete than the right. Preparation of the specimen has revealed that it can be distinguished from other Cretaceous theropods of South America and elsewhere. In this paper we describe and name this new taxon.

Institutional Abbreviations

FMNH, Field Museum of Natural History, Chicago; IGM, Institute of Geology, Mongolia, Ulaanbataar (currently held at American Museum of Natural History, New York); MPCA, Museo Provincial Carlos Ameghino, Cipoletti; MUCPV, Museo de Ciencias Naturales, Universidad del Comahue, Neuqúen (currently reposited at Centro Paleontologico los Barreales); MCF-PVPH, Museo Carmen Funes, Plaza Huincul; UA, Université de Antananarivo, Antananarivo.

Systematic Paleontology

Theropoda Marsh, 1891
  Coelurosauria Von Huene, 1926
    Maniraptora Gauthier, 1986
      Alvarezsauridae Bonaparte, 1991
        Alnashetri cerropoliciensis gen. et sp. nov.

Holotype

MPCA-477—Partial left femur, distal portions of left and right tibiae, right fibula, proximal tarsals of both ankles, a nearly complete right metatarsus, proximal and distal parts of the left metapodials, left pedal digit III.

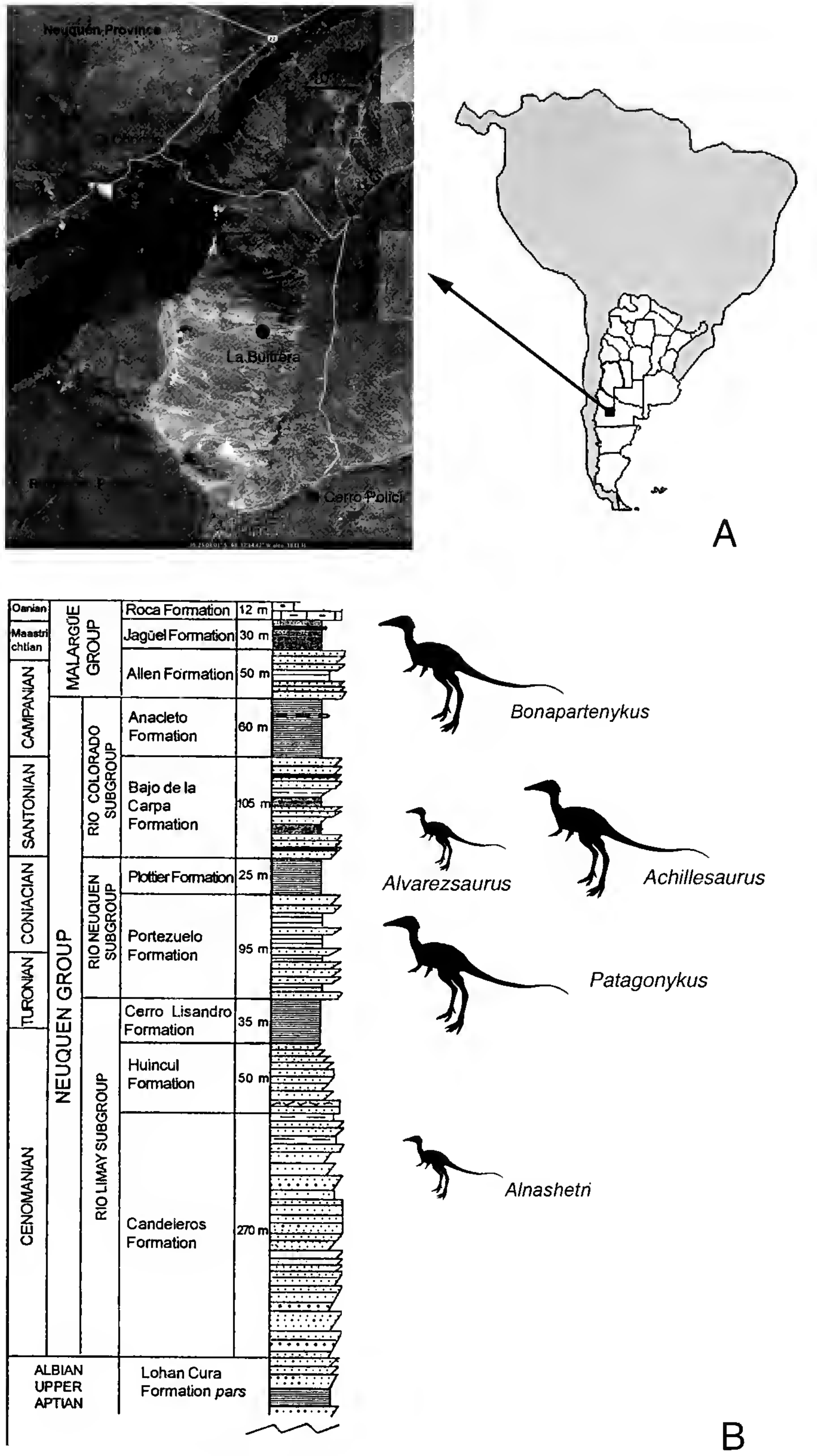

FIG. 1. (**A**) Satellite map of the La Buitrera locality, with inset providing geographic context within South America. (**B**) Stratigraphy of the Upper Cretaceous Neuquén Group calibrated against the geologic timescale, and showing which formations yield alvarezsaurid remains. The silhouettes approximate relative size of taxa. Specific specimen and coordinate data for La Buitrera specimens are on file with the second author. Map sourced from Google Earth.

Etymology

Alnashetri, meaning "slender thighs" in the Günün-a-kunna dialect of the Tehuelchan language, in reference to long and slender hind limbs of the holotype. The specific name is coined in honor of the nearby hamlet of Cerro Policía, whose residents have generously assisted fieldwork efforts at La Buitrera since the locality was discovered by the second author in 1999.

Diagnosis

A small non-avian coelurosaur exhibiting the following two autapomorphies: presence of a low ridge on the distal end of the tibia, which separates the rostral surface for articulation with the astragalus from the outer face of the lateral malleolus, and which extends up the shaft of the tibia dorsal to the tip of the ascending process of the astragalus. Small notches extending ventrally from the collateral ligament pits at the base of the distal articular hemicondyles on phalanges III-2 and III-3 appear to be unique to *Alnashetri* among described non-avian theropods.

Locality and Horizon

The specimen was found at the "Hoyada de los esfenodontes" sublocality, part of the main fossiliferous locality of La Buitrera, about 30 km south of the village of El Chocón (Fig. 1). It was recovered from massive red sandstones that form the upper part of the Candeleros Formation, close to the contact with the Huincul Formation. However, the specimen comes from the lower levels of the outcrops in this region, where the lowermost section of the Candeleros Formation is not exposed. This unit produces a rich fauna of small vertebrates, including dozens of specimens of the large eilenodontine rhynchocephalian *Priosphenodon avelasi* (Apesteguía & Novas, 2003), the basal snake *Najash rionegrina* (Apesteguía & Zaher, 2006), the notosuchian crocodile *Araripesuchus buitreraensis* (Pol & Apesteguía, 2005), several specimens of the unenlagiine dromaeosaurid *Buitreraptor gonzalezorum* (Makovicky et al., 2005), and also mammals (Rougier et al., 2011) and pterosaurs. Many of the small vertebrate fossils recovered from this unit are articulated, suggesting that they were entombed by rapid overbank flooding events (Apesteguía, 2008). The Candeleros Formation is regarded as Cenomanian–Turonian in age (Leanza et al., 2004).

Description

The proximal half of the left femur is preserved (Fig. 2). An isolated fragment of bone has a shape suggestive of being the femoral head. It is roughly conical in form and has a broken triangular base, with the most prominent point likely representing the ventral edge of the femoral neck. If this inference is correct, the neck of the femur would have been relatively short and thick. Its surface is generally rounded, except for a flat zone surrounding the break, and the entire fragment ends in a rounded but eroded apex. The femur is missing the proximal part of both the anterior and greater trochanters. There is no evidence of a groove separating the anterior and greater trochanters, and it is likely that the trochanters were separated by only a small notch as in the alvarezsauroid *Patagonykus* (Novas, 1997), or not at all. Only the base of the anterior trochanter is preserved. It arises just below the level of the neck for the femoral head. The preserved section of the anterior trochanter is straight (Fig. 2A), but protrudes only very slightly beyond the femoral shaft, and there is no evidence of an accessory trochanter as observed in several coleurosaurian lineages including ornithomimosaurs (Makovicky et al., 2010), tyrannosauroids (FMNH PR 2081), and *Microvenator* (Makovicky & Sues, 1998). A small neurovascular foramen occupies the medial face of the shaft slightly anterior and distal to the anterior trochanter (Fig. 2A). A fourth trochanter is absent (Fig. 2A) as in many Maniraptora, including Paraves and parvicursorine alvarezsaurids. The trochanteric shelf (Hutchinson, 2001) is also

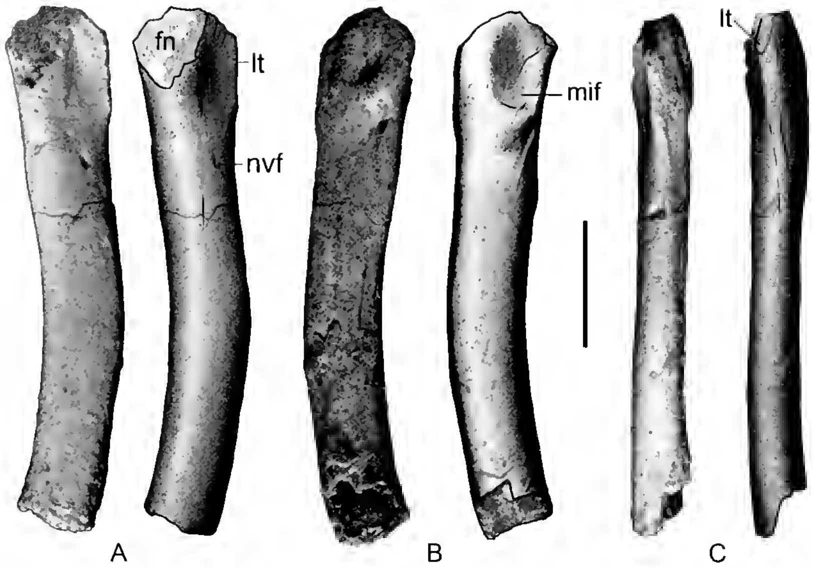

FIG. 2. Partial left femur of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciencis* in (**A**) medial, (**B**) lateral, and (**C**) rostral views. Abbreviations: fn, femoral neck; lt, lesser trochanter; mif, insertion for m. iliofemoralis; nvf, neurovascular foramen. Scale bar = 1 cm.

reduced and represented by a low mound on the lateral face of the femur (Fig. 2C) located just below the level of the neck for the femoral head. Similar development of the trochanteric shelf is observed in a number of basal tetanurans, but not in paravian taxa, which bear a prominent and dorsally directed tubercle. The preserved section of the femoral shaft is mediolaterally compressed and much wider in lateral view than in rostral view (Fig. 2). The lateral and posterior surfaces of the shaft are nearly continuous, only separated by a rounded posterolateral edge, unlike most alvarezsaurids, in which the caudal face of the shaft is flat between the posterolateral ridge and the fourth trochanter (MUCPV 53; Novas, 1997). The medial surface is largely flat, and separated from the anterior and posterior sides by more conspicuous and marked edges. Consequently, the transverse section of the shaft is elliptical in cross section immediately below the anterior trochanter and more elliptical to D-shaped at the level of the midshaft. The shaft is strongly bowed distally as is typical of Maniraptora.

The right tibia (Fig. 3) is more complete than the left, though both are missing the proximal end including the cnemial and fibular crests. The shaft is cylindrical and slightly bowed medially. The distal end bears a shallow groove for articulation with the astragalus, and is only slightly expanded across the malleolli. The triangular depression for articulation with the ascending process of the astragalus is offset laterally with its apex toward the lateral border of the tibia (Fig. 4B). In contrast, most coelurosaurs lack a well-defined medial ridge on the tibia that buttresses the astragalar ascending process, and the rostral aspect of the distal tibia is flat. However, the tibia of *Mononykus* (IGM 7/106) exhibits a well-defined groove for reception of the ascending process of the astragalus.

A low ridge extends along the shaft of the tibia toward the distal end and defines the border between the lateral and rostral faces of the distal tibia (Fig. 4B). It is about twice as long as the ascending process of the astragalus, which it braces distally. To the best of our knowledge, all other coelurosaurs lack an extended ridge that reaches above the ascending process of the astragalus along this part of the tibial shaft, although the fibula may obscure such a ridge in articulated specimens. We interpret the extent of this ridge to be an autapomorphy of *Alnashetri*. The distal end of the tibia is only slightly wider than the tibial shaft and does not flare broadly as in, e.g., ornithomimosaurs, oviraptorosaurs, and tyrannosauroids. The tibia is trapezoidal and block-like in distal view, as in some enantiornithine birds and the parvicursorine taxa *Shuvuuia* and *Mononykus*, but unlike the more rostrocaudally flattened distal tibiae of most other maniraptorans (e.g., Norell & Makovicky, 1999, figure 11). The caudal surface of the distal end is marked by low medial and lateral ridges extending towards the malleolli and defining a shallow sulcus between them. The outer malleolus of the tibia is broad and about as wide as the maximum width of the calcaneum. In this regard, *Alnashetri* resembles the condition observed in parvicursorine taxa such as *Mononykus*, whereas most other non-avian coelurosaurs have an outer malleolus that is narrower than the calcaneum (Novas, 1997).

A short distal section bordering the right ankle is the only part of the fibula preserved with MPCA 477 (Fig. 3). The fibula clearly reached the ankle as in most non-avian theropods, but unlike parvicursorine taxa. The articulation between the distal fibula and the proximal tarsals is not preserved in MPCA 477.

The astragalus is restricted to the extensor face of the tibia in distal view unlike the majority of coelurosaurs (Fig. 4E), in which the astragalus wraps over much of the distal end of the tibia. The astragalus is also largely restricted to the rostral face of the tibia in *Achillesaurus* (Martinelli & Vera, 2007), *Shuvuuia* (Suzuki et al., 2002), and the Tugrikin Shireh alvarezsaurid (IGM 100/1305) though it wraps further onto the distal surface of the tibia in *Mononykus* (IGM 107/6) and *Patagonykus* (MCF-PVPH 53). The astragalar articular surface is smaller than the exposed end of the tibia in distal view, an unusual proportion among theropods, although this is in part due to poor preservation and possible breakage of the bottom of the astragalus. The ascending process is more complete on the left ankle, and is tall and triangular as in other coelurosaurs. Its lateral edge is relatively straight for most of its length and parallels the lateral edge of the tibia (Fig. 4B). The medial edge is inclined dorsolaterally as revealed by the underlying groove on the rostral face of the tibia. The astragalus of *Alnashetri* lacks the robust buttress for articulation with the distal fibula observed in *Patagonykus* (Novas, 1997) and *Achillesaurus* (Martinelli & Vera, 2007), nor is there evidence for a cup-like depression on the calcaneum for reception of the end of the fibula as seen in ornithomimosaurs, *Patagonykus*, and tyrannosauroids.

The calcaneum is fused to the astragalus in *Alnashetri* (Figs. 3, 4) and the lateral face of the calcaneum on the better preserved left ankle appears to be flat and smooth. The lateral condyle of the astragalocalcaneum is distinctly taller than the medial one, a condition also observed in the basal alvarezsaurids *Patagonykus* and *Alvarezsaurus* (Martinelli & Vera, 2007, figure 9). By contrast, the proximal tarsal condyles are generally subequal in height in most coelurosaurian theropods, including dromaeosaurids (IGM 100/985), oviraptorosaurs (IGM 100/3003), tyrannosauroids (FMNH PR 2081), and parviscursorine alvarezsaurids (IGM 106/7), with the notable exception of a juvenile troodontid (Currie & Peng, 1993). The medial condyle of the astragalocalcaneum of *Alnashetri* is narrow and terminates in a sharp arc as in the parvicursorines *Albinykus* (Nesbitt et al., 2011) and *Mononykus* (Perle et al., 1994), and it projects farther anteriorly than the broader lateral condyle. The condyles are separated rostrally by a wide and deep sulcus forming a deep saddle in end view (Fig. 4E) as in the alvarezsaurids *Shuvuuia* and *Mononykus*, but in contrast

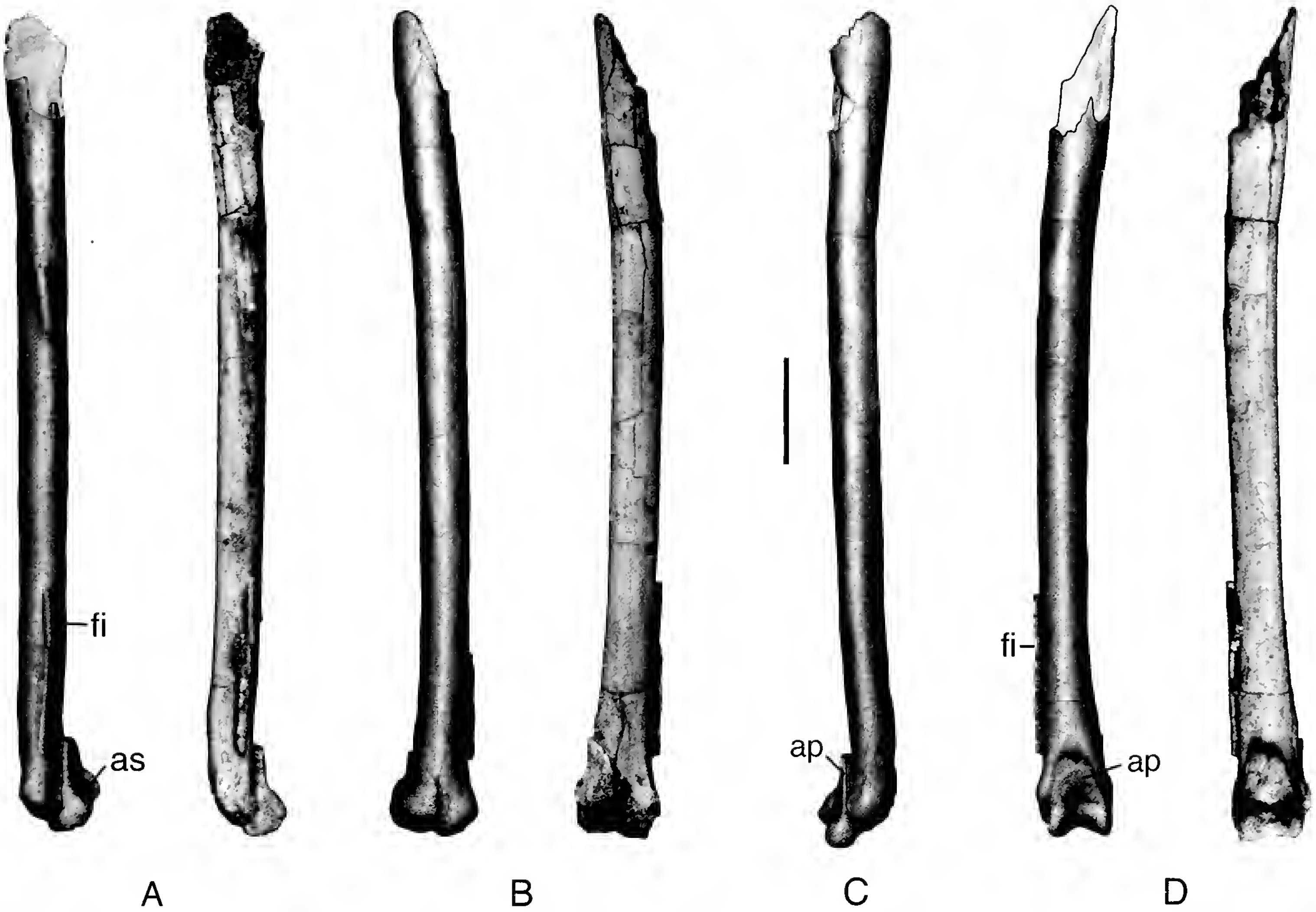

FIG. 3. Right tibia, fibula, and proximal tarsals of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciencis* in (**A**) lateral, (**B**) caudal, (**C**) medial, and (**D**) rostral views. Note that medial view is represented by drawing only, whereas all other views are represented by drawing and photograph. Abbreviations: as, astragalus; ap, ascending process of the astragalus; fi, fibula. Scale bar = 1 cm.

to the majority of other non-avian coelurosaurs. However, unlike these parvicursorine taxa, there is no tendinal fossa on the extensor surface of the sulcus that separates the condyles in *Alnashetri* (Figs. 4B, 5B). The supracondylar fossa is very broad and deep laterally and is truncated laterally by the tall lateral condyle, which it excavates medially. Naish and Dyke (2004) noted that a large, elliptical, and laterally situated supracondylar fossa is a synapomorphy of alvarezsaurids. A

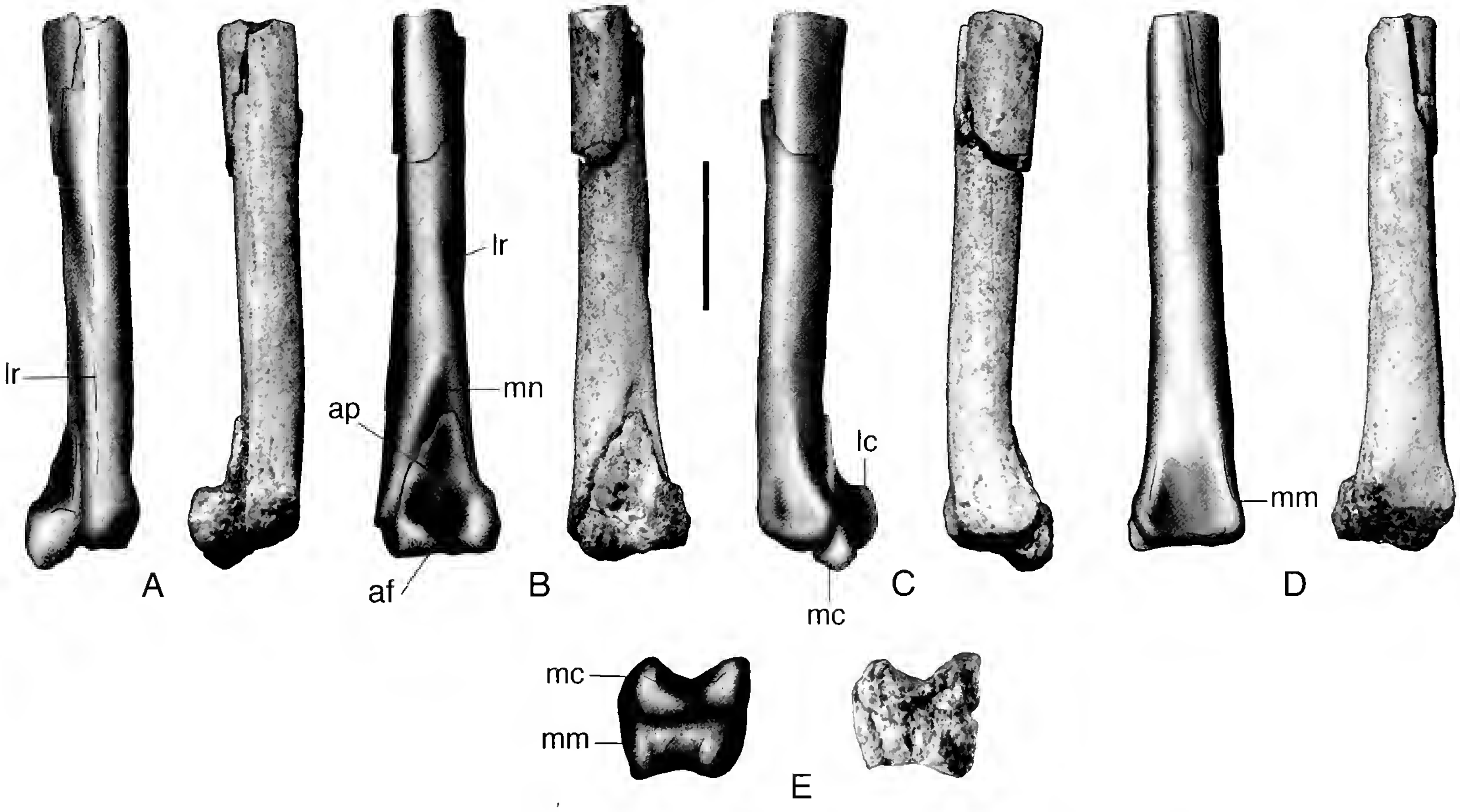

FIG. 4. Left tibia and astragalocalcaneum of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciencis* in (**A**) lateral, (**B**) rostral, (**C**) medial, (**D**) caudal, and (**E**) distal views. Abbreviations: af, fossa at base of ascending process; ap, ascending process of astragalus; lc, lateral condyle; lr, lateral ridge; mc, medial condyle; mm, medial malleolus; mn, medial notch on tibia for reception of ascending process of astragalus. Scale bar = 1 cm.

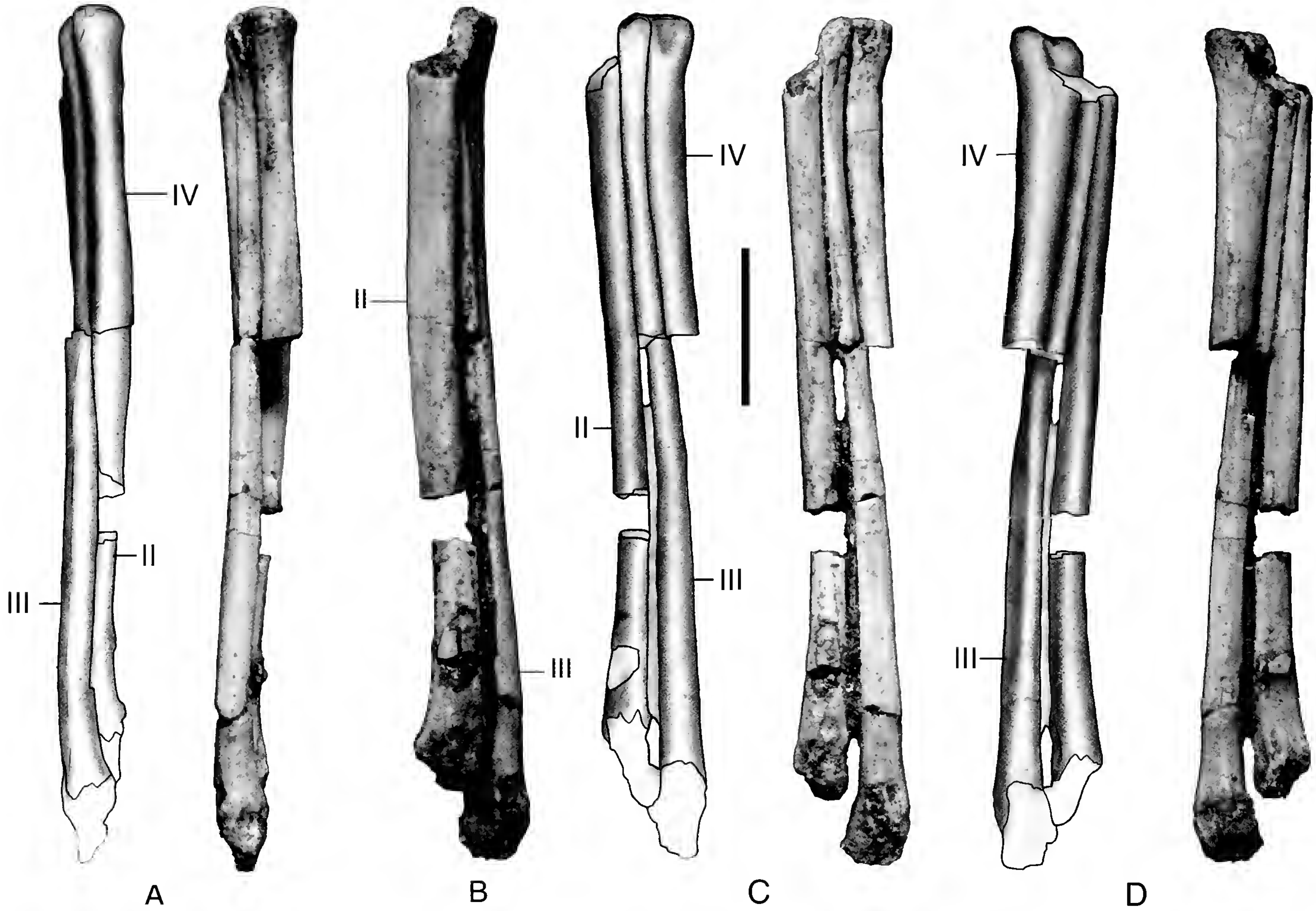

FIG. 5. Right metatarsus of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciensis* in (**A**) lateral, (**B**) medial, (**C**) rostral, and (**D**) caudal views. Note that medial view is represented by photograph only, whereas all other views are accompanied by halftone drawings. Abbreviations: II–IV, metatarsals II–IV. Scale bar = 1 cm.

similar deep excavation of the medial face of the lateral condyle is observed in the alvarezsaurids *Achillesaurus* (Martinelli & Vera, 2007), *Patagonykus* (Novas, 1997; MCF-PVPH 47), and to a lesser extent in *Alvarezsaurus* (MUCPV 54). The fossa bears a small pit at its deepest point in *Alnashetri*. Several accessory fossae are observed on the better-preserved left ankle of *Patagonykus* (Novas, 1997), and the depression is also marked by pitting in the parvicursorine *Mononykus* (IGM 106/7). Such pits are not limited to alvarezsaurid taxa, however, and pits are also observed within a fossa at the base of the ascending process of the astragalus in *Tyrannosaurus rex* (FMNH PR 2081), and a single pit can be observed within the supracondylar groove of the unenlagiine *Rahonavis* (UA 8656). No distal tarsals are preserved with the holotype specimen of *Alnashetri*.

The right metatarsus (Fig. 5) is fairly complete, whereas only fragments of the left one were recovered. Metatarsal (MT) II is incomplete proximally on the right foot, but the proximal end is preserved on the left side. The proximal articulation is slightly expanded relative to the shaft and is roughly square in end view. The shaft is mediolaterally compressed and deeper in the extensor–plantar plane. The lateral and medial surfaces of the shaft converge posteriorly to form a low plantar crest. This crest reaches its maximum depth along the middle of the shaft, and is posteriorly convex in lateral view. Below the midshaft, the crest attenuates and is replaced by a rounded border. The shaft is slightly curved and laterally concave.

Alnashetri does not possess an arctometatarsalian foot, and MT III is exposed along the full length of the foot. Metatarsal III has a proximal articulation that is deeper than wide in end view, with straight medial and lateral edges (Fig. 5). The shaft is slender and is constricted at midlength, but still fully exposed in both plantar and extensor views as in *Alvarezsaurus*. The shaft is slightly medially curved in extensor view. The distal half of the shaft bears narrow facets on its medial and lateral faces for articulation with the shafts of MT II and MT IV, respectively (Fig. 6A). The facet for MT II extends farther distally than that for MT IV, suggesting that the shaft of MT IV diverges laterally from the axis of the metatarsus distally as is observed in *Alvarezsaurus* (MUCPV 54). This condition differs from parvicursorines as well as from outgroups, in which the flattened zone of contact for MT IV reaches roughly the same level as that for MT II. The shaft adjacent to the distal articulation exhibits a gentle anteriorly convex curvature (Fig. 6A, C), which serves to bring the distal articulation into the same plane as the articulation of MT II and MT IV in distal view. A similar curvature of the distal part of MT III is observed in *Albertonykus* (Longrich & Currie, 2009) and *Xixianykus* (Xu et al., 2010). The distal articulation is preserved on the left element, and is narrow in extensor view (Fig. 6C). A break extends obliquely through the articulation, rendering it uncertain as to whether it is ginglymoid or not. A shallow, but conspicuous extensor fossa lies proximal to the intercondylar groove.

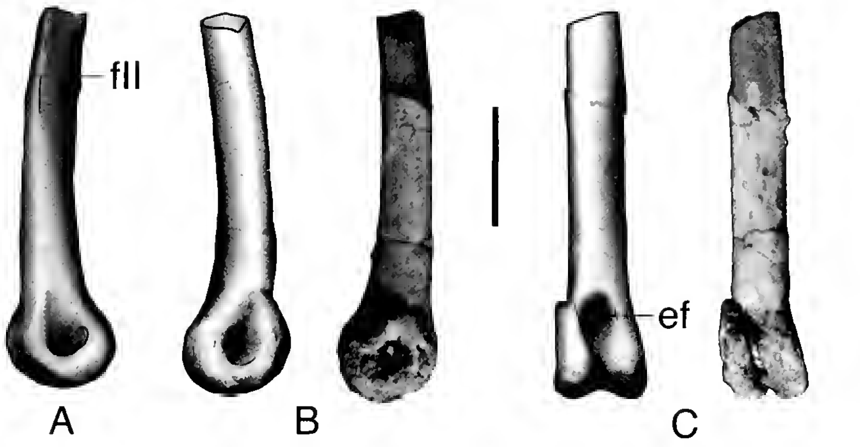

FIG. 6. Distal end of right metatarsal III of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciencis* in (**A**) medial, (**B**) lateral, and (**C**) rostral views. Note that medial view is represented by halftone drawing only, whereas the other views are represented by photographs accompanied by halftones. Abbreviations: ef, extensor fossa; fII, facet for metatarsal II. Scale bar = 5 mm.

Only the proximal half of the left MT IV is preserved. Both its proximal articulation and shaft are more robust than the corresponding parts of the other two major metatarsals. The proximal part of the shaft is mediolaterally expanded in plantar view. In end view, the proximal articular surface is slightly triangular and mainly expanded mediolaterally.

Three articulated phalanges from the left foot (Fig. 7) likely represent the end of digit III, given their slender proportions and the symmetrical appearance of their shafts and articular surfaces. Phalanx III-2 is elongate with a shaft that is slightly constricted at midlength. The distal collateral ligament fossae are relatively large. A conspicuous extensor pit is observed on the dorsal surface just proximal to the condyles. Small notches are present immediately proximal to the distal articulation on the medioventral and lateroventral borders of the shaft (Fig. 7), and represent a unique trait of *Alnashetri*. Phalanx III-3 is almost as long as III-2 (Fig. 8). As in phalanx III-2, notches are observed proximoventral to the collateral ligament fossae. The ungual is incomplete, but is clearly the shortest element in the toe. The flexor tubercle is deep and positioned close to the proximal articulation (Fig. 7). The dorsal edge of the ungual is relatively straight in lateral view, whereas the lower edge is deeply concave. In ventral view, the lower face of the ungual is formed as a low ridge adjacent to the tubercle, but becomes more rounded distally.

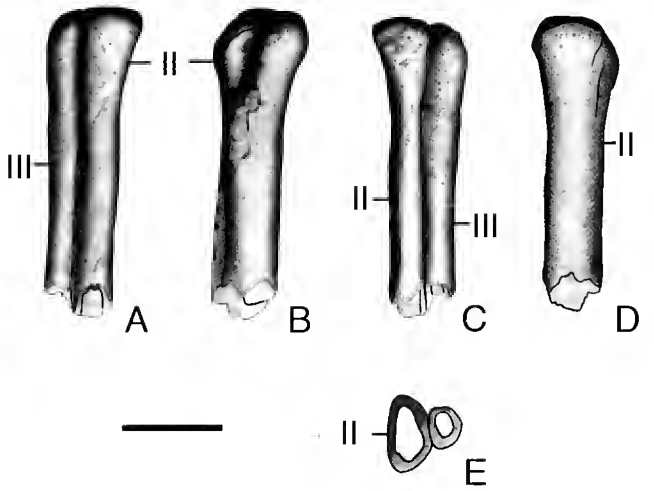

FIG. 7. Proximal ends of left metatarsals II and III of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciencis* in (**A**) caudal, (**B**) lateral, (**C**) rostral, and (**D**) medial views. (**E**) Distal cross sections of the preserved sections. Abbreviations: II–III, metatarsals II–III. Scale bar = 5 mm.

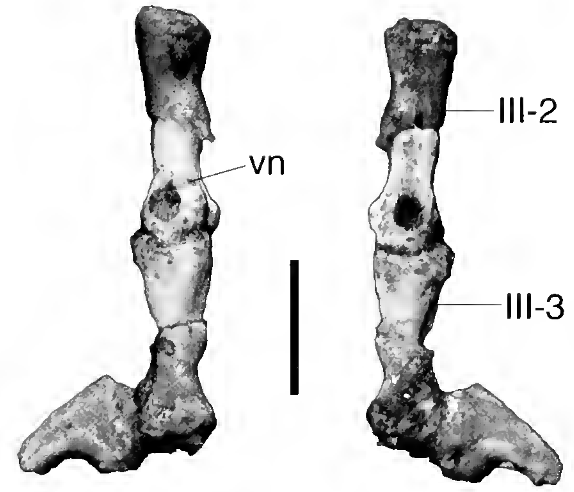

FIG. 8. Right pedal digit III of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciencis:* Left, medial view; Right, lateral view. Abbreviations: III-2, phalanx III-2; III-3, phalanx III-3; vn, ventral notch on distal articulation below ligament pit. Scale bar = 5 mm.

Phylogenetic Methods and Results

Due to its fragmentary nature, the holotype skeleton of *Alnashetri* lacks clear-cut synapomorphies that would allow unambiguous referral to a particular coelurosaurian clade, necessitating a more comprehensive analysis to determine its affinities. As a first pass, we added *Alnashetri* to a recent and relatively comprehensive cladistic matrix used to explore coelurosaurian interrelationships (Zanno & Makovicky, 2011). This preliminary analysis found *Alnashetri* to nest within Alvarezsauroidea. To further explore this potential relationship, we added four recently described alvarezsauroid taxa (*Linhenykus* Xu et al., 2011; *Xixianykus* Xu et al., 2010; *Albinykus* Nesbitt et al., 2011; and *Bonapartenykus* Agnolin et al., 2012) and eight characters with relevance for *Alnashetri* or for alvarezsaurid relationships to the matrix. Several other alvarezsauroid taxa were omitted either due to their highly incomplete preservation, including *Albertonykus* (Longrich & Currie, 2009), *Ceratonykus* (Alifanov & Barsbold, 2009), and *Kol* (Turner et al., 2009), or because of a lack of sufficiently detailed description (*Haplocheirus*). The first category of omissions is less likely to have an impact on the position of *Alnashetri* as these taxa all exhibit an arctometatarsal pes and are therefore more derived alavarezsaurids than is *Alnashetri*. The omission of *Haplocheirus* is of greater concern as it is considered the basalmost alvarezsauroid (Choiniere et al., 2010) and is therefore critical for understanding trait distributions at the base of the clade. The basal Argentinean taxon *Achillesaurus* (Martinelli & Vera, 2007) was not included as a separate terminal taxon, as it may be a junior synonym of *Alvarezsaurus*, which is known from the same formation and from which it differs trivially. Because we could not code the majority of traits for *Haplocheirus* from the brief preliminary description (Choiniere et al., 2010), and because information on *Alnashetri* is restricted to the hind limb, the results of our present analysis should be viewed as provisional. The character list and data matrix (in Nexus or TNT formats) are available upon request from the senior author, or online at http://fieldmuseum.org/users/peter-makovicky.

The data matrix was analyzed with parsimony using TNT (Goloboff et al., 2008), with all characters treated as unordered. Analysis was performed using the following parameters: searches employing the Tree Bisection and Reconnection algorithm were run on 200 randomly generated

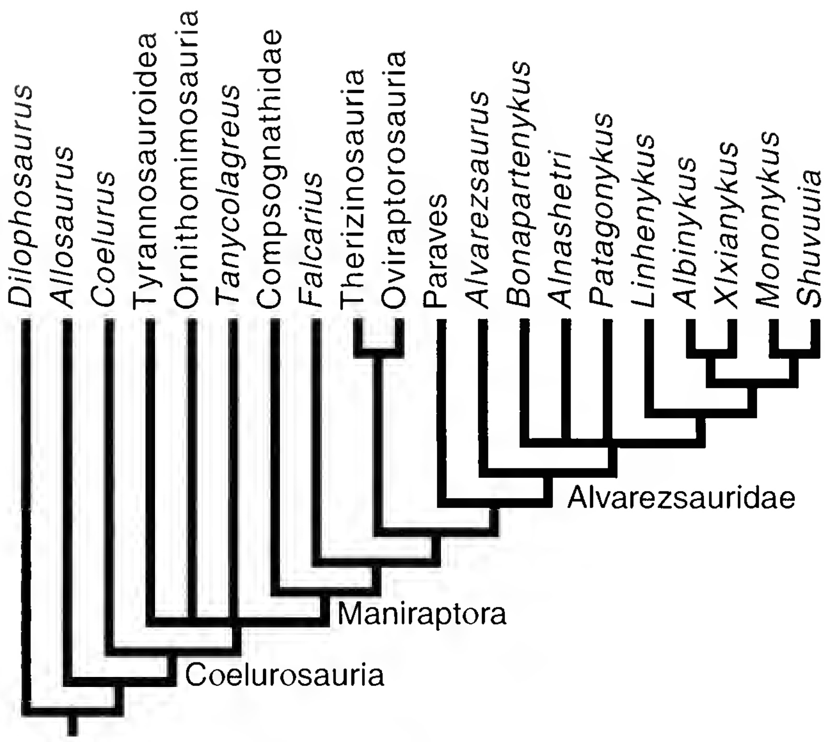

Fig. 9. Strict consensus of 28,980 most-parsimonious trees derived from the phylogenetic analysis of 304 characters in 80 coelurosaurian and outgroup taxa. Clades outside of Alvarezsauridae have been collapsed to suprageneric lineages for simplicity. Clade names follow usage and definitions by Sereno et al. (2005) and Choiniere et al. (2010). All shown relationships have a Bremer support of 1, although some nodes within collapsed clades enjoy higher support.

Wagner trees, with 10 trees for held at each iteration. The analysis produced 390 most-parsimonious trees (MPTs) with a length of 1052 steps, the consensus of which is shown in Figure 9. Further branch swapping using the Subtree Pruning and Regrafting strategy was performed on the recovered 390 MPTs, resulting in a total population

of 28,980 MPTs, but the additional resolutions caused no changes to consensus topology, indicating that all MPTs derive from a single tree island. *Alnashetri* is recovered as a basal alvarezsaurid, falling within a basal polytomy of other Argentinean taxa from the Neuqúen Basin. The character support for this placement, and a qualitative evaluation of it, will be presented in the Discussion.

Discussion

Alnashetri represents only the second coelurosaurian taxon known from the rich La Buitrera fauna. This locality has produced a remarkable diversity of small vertebrates (e.g., Apesteguía & Novas, 2003; Apesteguía & Zaher, 2006; Rougier et al., 2011), but Coelurosauria was only known from several specimens of the unenlagiine dromaeosaurid *Buitreraptor* (Makovicky et al., 2005; Gianechini & Apesteguía, 2011) prior to the preparation of *Alnashetri. Alnashetri* can clearly be distinguished from *Buitreraptor* in its lack of a pronounced lateral ridge or tuber (= posterior trochanter of Gauthier [1986]) on the proximal femur. With few exceptions such as *Vorona*, almost all paravian taxa exhibit a prominent lateral tuber regardless of size or developmental stage. A large lateral tuber is observed in specimens of *Buitreraptor* with femoral lengths ranging from approximately 80 mm to approximately 150 mm, and can thus be confidently interpreted as ontogenetically invariant. Currie and Peng (1993) also noted the presence of a large lateral tuber on the hind limb of a juvenile troodontid, and all specimens of *Archeopteryx* exhibit a prominent tuber regardless of size (Wellnhofer, 1974; Mayr et al., 2007).

Alnashetri also differs from *Buitreraptor* in traits of the tibia, proximal tarsals, and metatarsus. The lateral malleolus of the tibia is relatively broad and flat with little or no lateral projection in *Alnashetri*, whereas it is narrow and projects as a pointed process beyond the fibula and lateral margin of the atragalocalcaneum in *Buitreraptor* (MPCA 238). The astragalocalcaneum of *Alnashetri* differs significantly from that of *Buitreraptor* in having asymmetrical condyles with the lateral one taller than the medial one, and in the possession of an expanded fossa at the base of the ascending process, bearing a small pit presumably for insertion of tendons of the foot extensor musculature (Nesbitt et al., 2011). The third metatarsal of *Alnashetri* is more uniformly exposed in caudal view than in *Buitreraptor*, where the diaphysis of MT III is pinched distally between MT II and MT IV. The diaphysis of MT III has a gently rounded rostral face rather than flat to concave rostral shaft surface as observed in the unenlagiines *Buitreraptor* (MPCA 238) and *Rahonavis* (UA 8656), and the proximal half of the shaft of the third metatarsal is not rostroplantarly compressed as in *Buitreraptor* (MPCA 238).

Although the preserved parts of the anatomy are limited, the holotype of *Alnashetri* does exhibit two autapomorphies. The first of these is an expanded longitudinal ridge that separates the rostral and lateral faces of the distal tibial shaft and extends well above the top of the ascending process of the astragalus. Many other coelurosaurs such as ornithomimosaurs (*Beishanlong*, Makovicky et al., 2010), dromaeosaurids (*Velociraptor* IGM 100/985; *Rahonavis* UA 8656), alvarezsaurids (*Achillesaurus*, Martinelli & Vera, 2007; *Shuuvuia*, IGM 100/1305), and oviraptorosaurs (*Conchoraptor* IGM 100/3003) have a sharp edge separating the rostral and lateral faces of the lateral malleolus of the tibia, but the ridge is restricted to the articular surface for the astragalocalcaneum and does not extend above the proximal tarsals. *Alnashetri* also appears to be unique in having small notches or indentations on the edges of the lateral and medial hemicondyles of the distal articulations on phalanges III-2 and III-3, proximoventral to the collateral ligament pits. Such notches have not been reported in other coelurosaurian taxa to our knowledge, although detailed information on phalangeal anatomy is admittedly scant for many taxa.

Besides unenlagiine dromaeosaurids, other coelurosaurian clades known from South America include avialans, alvarezsaurids, and compsognathids. Although *Alnashetri* resembles Cretaceous stem avialans in lacking a fourth trochanter and in having a block-like distal ankle with rostrally projected astragalocalcanear condyles, it differs in having a fibula that reaches the ankle and in having narrower astragalar condyles separated by a wide sulcus. Furthermore, unlike South American enantiornithines (Chiappe & Walker, 2002) and many other stem birds such as *Patagopteryx* (Chiappe, 2002), it lacks a lateral tubercle on the proximal ends of the femur. Although the Malagasy stem avialan *Vorona* also lacks a lateral tubercle, its fibula does not reach the ankle and it has a fully fused tarsometatarsus with a proximolateral foramen between MT III and MT IV (Forster et al., 2002) unlike *Alnashetri. Alnashetri* differs from compsognathids and several other non-paravian coelurosaurian lineages such as tyrannosauroids, ornithomimosaurs, and therizinosauroids in the absence of a fourth trochanter, and the probable partial or complete development of a trochanteric crest. It furthermore is distinguishable from these clades in the more block-like outline of the ankle in distal view, with rostrally projected astragalar condyles separated by a deep saddle-like sulcus.

Our phylogenetic analysis posits *Alnashetri* as a basal alvarezsaurid in a polytomy with two other Argentinean basal alvarezsaurids, *Bonapartenykus* and *Patagonykus*. Eleven unambiguous synapomorphies (characters [chars.] 112, 114, 117, 157, 164, 181, 265, 297, 298, 299, 301; see character list) unite alvarezsaurid taxa in our phylogenetic result, but only three of these (chars. 297, 298, 299) can be scored in *Alnashetri*. These three synapomorphies include: asymmetrical astragalocalcanear articulation with a taller lateral condyle (char. 297, shared with *Alvarezsaurus*, *Patagonykus*, and *Albinykus*, reversed in *Mononykus* and *Shuuvuia*); presence of a laterally displaced expanded fossa at the base of the ascending process of the astragalus (char. 298, shared with *Patagonykus*, *Alvarezsaurus*, and *Mononykus*, absent in *Shuuvuia* and *Albinykus*, not observable in other taxa due to preservation); and presence of small pits, presumably for tendinal insertion, within the supracondylar groove or fossa (char. 299, shared with *Mononykus*, *Patagonykus*, and probably *Alvarezsaurus*, although preservation is poor in the latter, absent in *Shuvuuia*, unknown in other alvarezsaurids).

Although we find unambiguous character support for placing *Alnashetri* within the Alvarezsauridae, all of these traits derive from the ankle and may therefore be functionally interrelated and therefore not fully independent of each other. Nevertheless, *Alnashetri* does exhibit other traits, such as reduction or absence of a fourth trochanter, only a small cleft between anterior (lesser) and greater trochanters or no separation at all, and absence of a lateral ridge and posterior trochanter that are all compatible with alvarezsaurid anatomy, though these characters also enjoy a wider distribution among coelurosaurian theropods. We also note that there are a few other anatomical traits in *Alnashetri* that are only known in some alvarezsaurid taxa among maniraptorans. For example, the rostral face of the distal tibia bears a clearly delimited depression for reception of the astragalar ascending process in the holotype of *Mononykus*, as in *Alnashetri*, and Agnolin et al. (2012) noted that the distal tibia of *Bonapartenykus* bears an oblique ridge for reception of the medial edge of the ascending process. Such structures cannot be evaluated in *Patagonykus*, *Albinykus*, *Linhenykus*, and *Xixianykus* and *Alvarezsaurus* due to fusion or articulation between the tibia and proximal tarsals, or due to preservation, and they are absent *Shuuvuia* and virtually all maniraptoran outgroups.

Alnashetri predates all other South American alvarezsaurids by 5 to 10 million years. All other described alvarezsaurids from Argentina derive from younger strata within the Neuquén Group of Neuquén and Río Negro provinces. Should future discoveries confirm our preliminary phylogenetic findings, the discovery of *Alnashetri* within the lowest unit of the Neuquén Group provides evidence that this clade was present in the Neuquén Basin throughout the entire span of the Late Cretaceous (Salgado et al., 2009; Agnolin et al., 2012) and that alvarezsaurids were a stable, if rare, component of South American Late Cretaceous faunas.

The holotype skeleton of *Alnashetri* is remarkably small and comparable to *Shuuvuia* in size. Besides *Ligabueino*, it is the smallest non-avian theropod yet collected from Argentina, although it is impossible to determine if the holotype represents a juvenile individual or not without histological sampling of the long bones. By contrast, *Achillesaurus*, *Patagonykus*, and *Bonapartenykus* represent relatively large taxa, whereas the holotype of *Alvarezsaurus* derives from a young juvenile (and is possibly a senior synonym of *Achillesaurus*). Continued fieldwork and future discoveries hopefully will provide more information on the anatomy of *Alnashetri* and allow a more definitive evaluation of its affinities and its significance for understanding biogeography and evolutionary trends such as body size evolution within alvarezsaurids.

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Chapter 8: "Regressed" Macrostomatan Snakes

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Abstract

On some morphology-based phylogenies of extant snakes the capacity to ingest prey of a diameter larger than the snake's head optimizes as a derived condition of macrostomatan snakes such as boas and pythons. The evolution of macrostomatan jaw mechanics can be traced in the more basal scolecophidian and anilioid snakes, such as blind snakes, thread snakes, pipe snakes, and shield tails. Several recent morphology-based phylogenetic analyses of snake interrelationships including fossil snakes have placed fossil taxa of large body size and/or with a macrostomatan skull structure basal to either all extant snakes, or basal to the Alethinophidia (Anilioidea plus Macrostomata, excluding Scolecophidia). This has led to the characterization of scolecophidians and/or anilioids as "regressed macrostomatans". These snakes would have lost their macrostomatan feeding capacities in adaptation to a fossorial or secretive mode of life, correlated in some forms such as scolecophidians and uropeltines with miniaturization. However, the characterization of scolecophidians and/or anilioids as regressed macrostomatans is not only a matter of character optimization on a phylogeny, but is also incompatible with morphological and physiological aspects of feeding mechanics in snakes.

Introduction

Oppel (1811: 14) introduced the order Squamata, which he divided into the "Saurii" possessing distinct limbs and non-dilatable maxillaries, and the "Ophidii" that lack (external) limbs and are characterized by dilatable maxillaries. Oppel's (1811: 19) grouping of "lizards" and snakes as two subsections within the same order reflects his concern that there seems to be hardly any single character that would unambiguously separate lizards from snakes. With respect to the genus *Ophisaurus*, named an intermediate between snakes (*Ophi-*) and lizards (*-saurus*) by Daudin (1803: 346), Oppel (1811: 17) confessed to having difficulties in deciding whether it should be placed "at the end of the lizard [series], or at the beginning of the snake [series]." Oppel's (1811) work introduced themes that still resonate in contemporary discussions of squamate interrelationships, in particular the position of scolecophidians as the basal-most extant snakes in spite of their extreme trophic specializations (Haas, 1930; Kley & Brainerd, 1999; Kley, 2006), and the possible relationships of snakes with other limb-reduced squamates.

A basal position of the fossorial scolecophidians would indicate a terrestrial origin of snakes from some clade of limb-reduced lizards (Bellairs & Underwood, 1951; Rieppel, 1988; Conrad, 2008). This scenario has traditionally clashed with the interpretation of the marine, monitor-like, Cretaceous mosasauroid lizards as possible snake ancestors. Cope (1869: 253) referred to mosasaurs as Pythonomorpha on account of the fact that they share with snakes an intramandibular joint in the lower jaw, as well as a loose mandibular symphysis. He later (Cope, 1872, 1878; see Caldwell, 1999, and Rieppel et al., 2003, for further discussion) used similarities of inferred jaw mechanics in defense of the phylogenetic derivation of snakes from mosasaurs. With his description of *Pachyophis*, a mid-Cretaceous marine squamate, Nopcsa (1923) thought he had identified the perfect intermediate between mosasauroids and snakes.

The discovery of mid-Cretaceous snakes with well-developed hind limbs in marine sediments of the Middle East (Haas, 1979, 1980a, b; Caldwell & Lee, 1997; Lee & Caldwell, 1998; Rage & Escuillié, 2000; Tchernov et al., 2000; Rieppel & Head, 2004) triggered a controversy as to whether these symoliophiid snakes (Rieppel & Head, 2004; pachyophiids in Lee et al., 1999) provided, indeed, a link with mosasauroids (Carroll, 1988), or whether they were derived, i.e., marcostomatan snakes related to boas and pythons (the debate is summarized and referenced in Rieppel et al., 2003). The first morphology-based analysis of squamate interrelationships that included both mosasauroids and *Pachyrhachis* corroborated mosasauroid relationships of snakes (Lee, 1998), relegating the signal that links snakes with limb-reduced, burrowing squamates to convergence (the "burrowing ecomorph" of Lee, 1998; but see Rieppel & Zaher, 2000; Conrad, 2008). Whereas some authors continue to defend a marine origin of snakes from mosasaurs, on the basis both of morphological and molecular data (e.g., Lee, 2000, 2005; Lee & Scanlon, 2002; Caldwell, 2006; Palci & Caldwell, 2010), a terrestrial origin of snakes has recently been defended on morphological grounds (Conrad, 2008). The latter study corroborated the basic structure of the squamate tree first found by Estes et al. (1988), yet recovered a monophyletic clade Scincophidia (Conrad, 2008: 137) that is nested within the Scincoidea and comprises (Feyliniidae (Acontidae (Dibamidae (Amphisbaenia, Serpentes)))). This result based on morphology stands in stark contrast to recent molecular analyses of squamate interrelationships (Fig. 1).

Molecular data support a position of snakes deeply nested within Squamata, in an unresolved trichotomy with Anguimorpha and Iguania (Townsend et al., 2004; Vidal & Hedges, 2005, 2009; Fig. 1B). Most recently, the morphological data offered by Conrad (2008) were combined with molecular data for an analysis that broke the scincophidian clade of limb-reduced squamates (Wiens et al., 2010). In this combined analysis, the snakes were found to be the sister group of the Anguimorpha; the mosasauroids in turn were found to nest within anguimorphs. In summary, the alternatives proposed during the last decade of research into squamate relationships remain the same "traditional" ones that had been identified before (Rieppel, 1988): snakes are related to other limb-reduced squamates; snakes are related to anguimorphs; or snakes are related to mosasauroids nested within anguimoprhs.

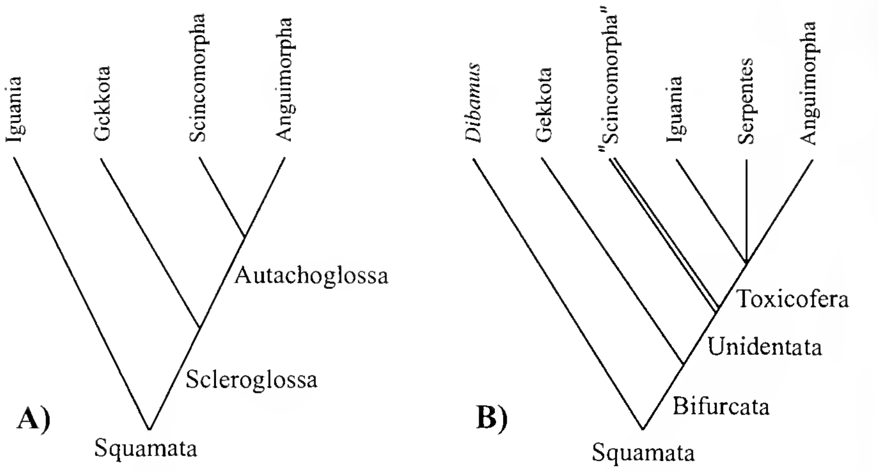

FIG. 1. Phylogenetic relationships of major groups of squamates. (**A**) The morphological tree. Snakes are alternatively considered to be nested within Anguimorpha (Estes et al. 1988) or Scincomorpha (Conrad, 2008). (**B**) The molecular tree.

Jaw Mechanics and Snake Origins

A terrestrial origin of snakes from other limb-reduced squamates is robustly supported by an unweighed morphological data set (Conrad, 2008), but has been rejected as a misleading signal due to convergent evolution that results from an adaptation to a burrowing life style (Lee, 1998; Wiens et al., 2010). Conversely, a marine origin of snakes from the mosasauroids is supported with reference to a position of the mid-Cretaceous marine symoliophiids with well-developed hind limbs and a macrostomatan skull structure at the root of the snake tree (e.g., Caldwell & Lee, 1997; Lee, 1998; Lee & Caldwell, 2000; Lee & Scanlon, 2002; Caldwell, 2006; Scanlon, 2006; Palci & Caldwell, 2010). This latter hypothesis clashes with the recognition of a non-macrostomatan terrestrial basal snake with well-developed hind limbs and a pelvis from the Late Cretaceous of Patagonia (Apesteguía & Zaher, 2006; Zaher et al., 2009; see also Wilson et al., 2010), and also renders the macrostomatan skull structure primitive for snakes in general (Lee et al., 1999; Rage & Escuillié, 2000). Such a conclusion is in conflict with earlier interpretations of the evolution of ophidian jaw mechanics (Greene, 1983; Cundall & Greene, 2000; Greene & Cundall, 2000), as it renders scolecophidians and other non-macrostomatan snakes (*Anilius*, *Cylindrophis*, *Anomochilus*, and uropeltines) so-called "regressed macrostomatans" (Underwood, pers. comm.) that have lost macrostomatan features in adaptation to a fossorial or secretive mode of life. Macrostomatan snakes are characterized by the capacity to engulf prey with a diameter exceeding that of the snake's head (Greene, 1983; Cundall & Greene, 2000), which requires musculoskeletal correlates as discussed below (see also Rieppel, 1988; Rieppel et al., 2003).

The skull of macrostomatan snakes is characterized by features permitting a wide gape that involve the dentigerous elements of the upper and lower jaws, and of the dermal palate. In macrostomatans, the supratemporal bone extends backward into a free-ending posterior process of variable length that carries the quadrate suspension beyond the craniovertebral joint. The quadrate, furthermore, is rotated backward to a variable degree, thus carrying the mandibular joint further backward, which, with a correlated elongation of the mandible, contributes to an increasing gape size. The mandibular tooth row is extended through the development of a posterior dentigerous process on the dentary. The basicranium (basioccipital and basisphenoid) develops a ventrally projecting longitudinal crest to provide additional area of origin for the constrictor internus dorsalis musculature, which moves the elements of the dermal palate, and coupled with them, the maxillaries, in alternate steps across the prey ("pterygoid walk": Boltt & Ewer, 1964; see also Cundall & Greene, 2000). All of these skeletal correlates of macrophagy are present in the marine mid-Cretaceous symoliophiids with well-developed hind limbs (Rieppel et al., 2003). Macrophagy has, indeed, been the key evolutionary innovation that has been claimed to link the symoliophiids to mosasaurs (Lee et al., 1999). However, as the snake jaws work themselves across the relatively large prey item, the jaw adductor muscles undergo significant passive stretching, which in turn requires changes in the jaw adductor muscle architecture.

The action range of a muscle fiber is dependent on its absolute length, for the degree of passive stretching is distributed across a greater number of sarcomeres that bridge the distance from the point of origin to the point of insertion. The longer a muscle fiber is, the less will an individual sarcomere be stretched and the closer it will remain to the length-tension optimum for any given distance of passive stretching. But long- and parallel-fibered jaw adductor muscles that characterize macrostomatan snakes (Zaher, 1994) do not represent the plesiomorphic sauropsidan condition. It has long been recognized that the complex multipinnate jaw adductor muscle architecture is remarkably conservative across Sauropsida (Lakjer, 1926; see also Haas, 1973). A pinnate structure increases the physiological cross-section of a muscle, but at the cost that the individual fiber is not exerting force at optimal mechanical advantage. The latter can be the case in parallel-fibered muscle bundles, which bulge upon contraction, however, unlike pinnate muscles. The complex multipinnate muscle architecture of sauropsidan jaw adductors may have had its origin in the evolutionary optimization of the physiological cross-section of the jaw adductor muscle mass within a closed space, i.e., the temporal fossa of an ancestral anapsid reptile skull, which would not have allowed for bulging of enclosed parallel-fibered muscle bundles unless space within the temporal fossa would have been left unoccupied by musculature.

Non-macrostomatan snakes (scolecophidians, *Anilius*, *Cylindrophis*, *Anomochilus*, and uropeltines) all retain a complex multipinnate jaw adductor musculature, a muscle architecture that is furthermore closely comparable with that of lizards (Haas, 1930; Rieppel, 1980), and hence represents the ancestral condition for snakes (given that snakes are deeply nested within squamates in all phylogenetic analyses reviewed above). Two genera of basal snakes, variably included or excluded from macrostomatans (Cundall & Greene, 2000), i.e., *Loxocemus* and *Xenopeltis*, show intermediate steps of reduction of the internal tendinous skeleton of their jaw adductors (Zaher, 1994), which are vestigial in all other macrostomatans examined. To make macrophagy possible, macrostomatans had to reorganize their jaw adductor muscles into long- and parallel-fibered muscle bundles (Haas, 1973; Zaher, 1994). Assuming macrophagy for the marine mid-Cretaceous symoliophiids with well-developed hind limbs, as the skeletal correlates in the skull would indeed suggest, makes it necessary to assume that they, too, reduced the internal tendinous skeleton of their jaw adductors to at least some significant degree.

Whereas it may seem plausible to entertain the concept of regressed macrostomatans with respect to the skull structure of non-macrostomatan snakes, especially in view of the pedomorphosis evident in the skull anatomy of scolecophidians (Kley, 2006, Rieppel et al., 2009) and other miniaturized non-macrostomatan snakes (Rieppel & Maisano, 2007), the same is less plausible with respect to jaw adductor muscle architecture. Depending on the choice of a phylogenetic analysis from those available, it may remain equivocal whether the internal tendinous skeleton was reduced twice in snakes (in the fossil stem macrostomatans and in the extant crown macrostomatans), or whether the non-macrostomatan snakes re-evolved the complex squamate jaw adductor muscle architecture. The concept of *regressed* macrostomatans, however, would seem imply the re-evolution of a complex jaw adductor muscle architecture closely comparable with that of lizards in non-macrostomatan snakes, which would be hard to explain. In all snakes, the jaw adductor musculature lies superficial to the skull and thus is free to expand, whereas the soft diet of non-macrostomatan snakes does not require the strong bite force that characterizes insectivorous lizards and the ancestral stem reptiles (Carroll, 1969).

Conclusions

Between paleontologists on the one side (Cope, 1869, 1872, 1878; Nopcsa, 1923) and zoologists on the other (Walls, 1940, 1942; Bellairs & Underwood, 1951), there emerged the two classic hypotheses concerning snake origins. Paleontological research related snakes to Cretaceous mosasauroid lizards, which would imply a marine origin of snakes. Zoological research related snakes to other limb-reduced squamates, which would imply a terrestrial origin of snakes. With the discovery of marine mid-Cretaceous macrostomatan symoliophiids with well-developed hind limbs, the debate became intertwined with the issue as to whether macrophagy is plesiomorphic, or derived within snakes (see discussion in Lee, 1998; Rage & Escuillié, 2000; Rieppel et al., 2003; Rieppel & Head, 2004). So far, cladistic analyses of squamate interrelationships have not conclusively resolved that debate. Indeed, recent molecular studies have tended to blur the distinction between macrostomatan and non-macrostomatan snakes (Slowinsky & Lawson, 2002). There exists a recurrent molecular signal for a basal position of the macrostomate genera *Tropidophis* and *Tachyboa* outside the conventional macrostomatan clade (Wilcox et al., 2002), possibly close to *Anilius* (Vidal & David, 2004; Vidal & Hedges, 2002, 2004; Wiens et al., 2008; Scanlon & Lee, 2011). Conversely, the non-macrostomate genus *Cylindrophis* and the related uropeltines nest inside basal macrostomatans (Wilcox et al., 2002; Vidal & David, 2004; Vidal & Hedges, 2004; Wiens et al., 2008; but see Scanlon & Lee, 2011, for a combined analysis). The redevelopment of a complex multipinnate jaw adductor musculature comparable with that of lizards would unequivocally have to be assumed for *Cylindrophis* and the uropeltines, if their position within booid macrostomatans is accepted on the basis of this molecular signal.

This is yet another example of the profound incongruences obtained from analyses of squamate interrelationships based on morphology or molecules (see also the discussion in Rieppel et al., 2008). Patterns of squamate interrelationships differ in morphology-based analyses, molecular-based analyses, and combined analyses (for the latter compare Wiens et al., 2010 with Scanlon & Lee, 2011). An additional difficulty in the analysis of squamate interrelationships relates to different interpretations of morphological traits by different authors (e.g., Lee, 1998; Rieppel & Zaher, 2000; Scanlon, 2005). So far there has been little discussion as to the reasons that may cause these discrepancies in morphological, molecular, or combined signals. The solution to this problem cannot be, however, to simply declare the molecular tree as the correct one, and to claim discovery of morphological synapomorphies by mapping morphological traits onto a molecular scaffold (Siegel et al., 2011). Any trait—morphological or molecular—earns the status of synapomorphy through phylogenetic analysis, not through optimization on a pre-existing phylogeny (Assis & Rieppel, 2010).

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Chapter 9: Healed Fractures in the Neural Spines of an Associated Skeleton of *Dimetrodon*: Implications for Dorsal Sail Morphology and Function

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Abstract

Hyperelongate neural spines forming a prominent dorsal "sail" are known in eight genera distributed between two families of pelycosaurian-grade synapsids. Although the function(s) of the sail remain disputed, most researchers assume that resilient soft tissue stretched between the elongate neural spines, extending to the distal tips. Hypotheses to explain the purpose of the sail have included thermoregulation (Romer & Price, 1940; Bramwell & Fellgett, 1973; Haack, 1986; Tracy et al., 1986; Bennett, 1996; Florides et al., 1999) and sexual selection (Tomkins et al., 2010). In this paper, we analyze the natural pathologies found in the neural spines of a very large pelycosaur, *Dimetrodon giganhomogenes*, as a natural experiment: What would ensue in the event of sail breakage and what does that tell us about sail structure, development, maintenance, and the orientation of the sail?

A series of seven associated neural spines from FMNH UC 1134 demonstrate subtle though distinctly abnormal rugosities, a sign most often indicative of a well-healed hard callus of bone fracture. Microstructural examination revealed surprising facts: not only did the abnormal bone areas prove NOT to be fracture hard callus, but the abnormal tissue reflected underlying material failure resulting from slippage between adjacent lamellae of bone. Moreover, the characteristic cranial and caudal orientation of the deep longitudinal grooves contributing to the classic dimetrodont figure-8 spine cross section was rapidly reestablished *in vivo* by a combination of osteoclastic resorption and additional lamellar deposition of bone to regain the "correct" pre-injury orientation, underscoring the architectural importance of the dumbbell shape in resisting lateral bending. This bone disruption and repair occurred at least five seasons before death, which explains the well-healed external appearance of the lesions. The absence of vascular communicating canals casts doubt on the widely held hypothesis that these grooves contained blood vessels that supplied a thermoregulatory sail. Furthermore, the distal morphology of spines in more complete specimens, including the type FMNH UC 112 and OMNH 01727, suggests that the dorsal margin of the sail was located well proximal to the tips of the elongate neural spines. The cross-sectional architecture of the spines suggests a further hypothesis: that the proximal portion of the sail may have also functioned as an energy storage device, facilitating fast locomotion in this top predator.

Introduction

The dramatic sails of many Permian pelycosaurian-grade synapsids are the earliest "bizarre" structures in the terrestrial fossil record. These elongate neural spines, often more than three times the standing height of the animal, have suggested various hypotheses of function, including thermoregulation and display. Dorsally elongate components of the axial skeleton have arisen independently in Paleozoic amphibians, pelycosaurian-grade synapsids, and dinosaurs. Although the Early Permian dissorophid amphibian *Platyhistrix* possessed dermally sculptured, elongate neural spines, it is not clear that they were supported by a soft-tissue web (Vaughn, 1963). Spinosaurid theropod dinosaurs also possessed elongate spines, as did the iguanodontian *Ouranosaurus*, albeit shorter and wider anterio-posteriorly than those of pelycosaurs (Taquet, 1976; Buffetaut, 1992; Sereno et al., 1996). A sail-like soft tissue structure stretching between spines is most often assumed for these dinosaurian forms, although the alternative of a fatty hump resembling the 'buffalo hump" has been proposed (Bailey, 1997).

Hyperelongate neural spines of the presacral vertebrae evolved in at least two lineages of Late Paleozoic synapsids, including the omnivorous and herbivorous Edaphosauridae and the carnivorous Sphenacodontidae. A partial series from the sphenacodontid *Dimetrodon* is shown in Figure 1. Among

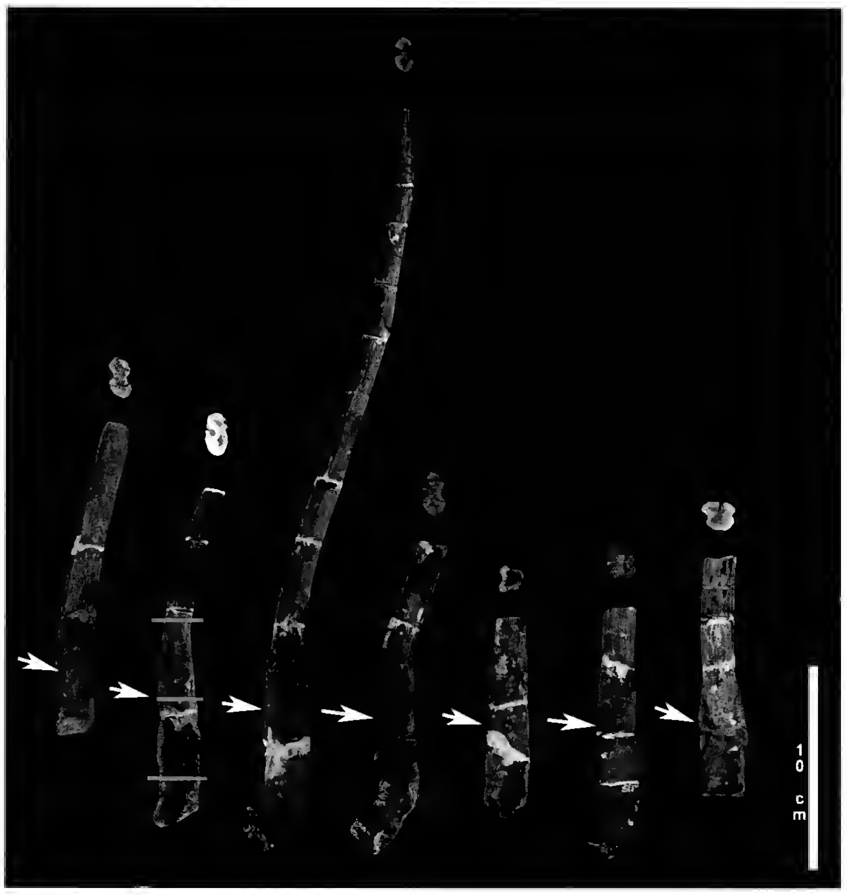

FIG. 1. FMNH UC 1134, *Dimetrodon giganhomogenes*. Right lateral view of a series of seven associated vertebral neural spines demonstrating a line of healed fractures. Elements are in cranial to caudal order as explained in text. Dorsal cross-sectional view of each element is shown above lateral view of spines. Arrows indicate position of abnormal rugosities. Lines indicate portion from which serial thin sections were obtained.

these forms, the sphenacodontids persisted as the dominant terrestrial amniote predators in North America and Europe from the latest Pennsylvanian through the Early Permian periods (~300 Mya to 270 Mya) until they were ultimately replaced by their therapsid relatives during the Middle Permian (Vaughn, 1969; Reisz, 1986; Hook & Hotton, 1991; Reisz & Berman, 1992; Rubidge & Sidor, 2001). The earliest known fossils that can be attributed to this group are represented by the type species *Sphenacodon ferox* from Upper Pennsylvanian and Lower Permian deposits of north-central New Mexico, USA (Romer & Price, 1940; Eberth, 1985; Reisz, 1986). The species *Sphenacodon ferocior* appears to have succeeded *S. ferox* in the Lower Permian Cutler Group deposits of New Mexico and is distinguished by its slightly (20%) larger size and relatively elongate neural spines, which are up to 45% longer than are those of *S. ferox* (Berman, 1978), indicating positive allometry of the neural spines with respect to body size in the genus (Romer & Price, 1940; Berman, 1978).

Dimetrodon is undoubtedly the best known of elongate-spined tetrapods. The evolutionary radiation of *Dimetrodon* species in the North American Southwest and midcontinent has been characterized by temporal trends in phyletic size increase associated with a relative increase in the surface area of the putative dorsal sail, which displays positive allometry with respect to body size (Romer & Price, 1940; Tracy et al., 1986). In general, the neural spines of *Dimetrodon* are more than 18 times taller than the vertebral centrum (and as much as 30 times taller in the massive *Dimetrodon grandis*). They are subdivided into a medio-laterally compressed to subquadrate proximal region, and a distal region having a more figure-8 (or rarely subcircular) cross-sectional shape (Figs. 1, 2). This change in cross-sectional geometry between the proximal and distal portions of the spine, which occurred to a lesser degree in the genus *Ctenospondylus*, has been termed "dimetrodont" differentiation (Romer & Price, 1940).

FIG. 2. FMNH UC 1134, *D. giganhomogenes*. Close-up of fourth in series of seven associated vertebral neural spines illustrated in Figure 1. From left to right: left lateral, caudal, and right lateral views demonstrating lesion resembling healed fractures. Arrow indicates slight deflection of caudal longitudinal groove.

The common occurrence of such elongate-spined taxa in Permo-Carboniferous deposits and their frequent popular reconstruction with well-developed webbing between the spines has fostered a general acceptance of this morphology. With rare exceptions (e.g., Jaekel, 1910), it has been generally accepted that an epidermal webbing joined the neural spines into a single structure. However, surface morphology and histological structure of the spines did little to confirm its specific presence. The report of a single spine with a healed fracture in *Dimetrodon milleri* by Romer and Price (1940) supported this hypothesis by suggesting a mechanism for splinting the damaged bone by a soft tissue interspinous structure. A partial neural spine (UCLA-VP 526, *Dimetrodon* sp., Lower Permian, Arroyo Formation, Texas, USA) also displays the macroscopic appearance of fracture healing and may be evidence for splinting.

In this study, the natural experiment provided by a series of traumatic injuries greatly enlarges evidence for the sail presence, as well as casting light on neural spine dynamics. In this chapter, we concentrate on a remarkable illustration of the dynamics of injury and healing in a single specimen. FMNH UC 1134 is an associated but partial and highly fragmentary adult skeleton that can be assigned with confidence to *Dimetrodon giganhomogenes*. In this study, examination of the series of pathological neural spines derived from this very robust and mature Late Paleozoic sphenacodontid pelycosaur determined that traumatic damage to the series functioned as a "natural experiment" – whereby histological examination was able to characterize post-perturbation healing and subsequent growth and well as ontogenetic shape change.

Materials and Methods

A prior survey of pelycosaur specimens from collections of the Field Museum of Natural History (FMNH), the Carnegie

Table 1. Differential diagnosis for neural spine lesions in fmnh UC 1134.

Category of etiology	Disease entity	Quality of "fit" to observed data?
Traumatic	neural spine fracture periostosis due to blunt trauma	good
Infectious	infectious osteomyelitis by innoculation	poor—pattern and localized shaft involvement do not match expectations
Degenerative	enthesopathy	poor—location on shaft inappropriate for potential interspinous musculature

Museum of Natural History , Oklahoma Musuem of Natural History (omnh) University of California Los Angeles Vertebrate Paleontology (ucla-vp), Museum der Natur, Gotha, Germany and the American Museum of Natural History revealed that healed traumatic injury of axial elements is the most common form of pathology in Late Paleozoic pelycosaurian-grade synapsids (Rega et al., 2004). As the majority of these diagnoses were based upon macroscopic evaluation and because the microstructure of *Dimetrodon* neural spine bone is complex (Enlow & Brown, 1957; Huttenlocker et al., 2010), accurate characterization at the histological level was necessary to confirm the diagnosis and characterize the healing process.

Of the series of neural spines from fmnh UC 1134 showing consecutive lesions, we sectioned the second spine in the series, to minimize destruction of the more prominent lesions. Additional comparative histological sections of *Dimetrodon* neural spines as well as a tibia from fmnh UC 1134 (Huttenlocker et al., 2010) were sectioned to establish a baseline of normal long bone and neural spine histomorphology. Thin-sectioning was performed using standard protocols for fossil bone found in Chinsamy and Raath (1992) and Wilson (1994). A basal (proximal) section, a mid-lesion section distal to the changing point, and a midpoint (distal) section were selected along the length of the spine to ensure that the data obtained were not only useful, but also comparable across genera. The sectioning levels are indicated in Figure 1. A more detailed account of sectioning procedures, materials, and histomorphometric measurements is presented in Huttenlocker et al. (2010).

Results

Macroscopic Morphological Overview

fmnh UC 1134 is a single associated adult specimen of *Dimetrodon giganhomogenes* from the Kungurian-aged (Lower Permian) Clear Fork Group of north-central Texas (Arroyo Formation of Romer & Price, 1940). Part of the specimen includes seven incomplete neural spines (Fig. 1) that show abnormal rugosities of their proximal portions. Based on spine cross-sectional morphology, we can confidently assign these spines to the cranial third of the sail, most likely just caudal to the pectoral girdle. The rugosities form a clear linear series, suggesting that these were the effects of healing from a single traumatic event.

The approximate order of the spines was determined by comparison to the classic descriptions in Romer and Price (1940). The cross sections of typical neural spines undergo a marked change beyond the so-called "changing point" (Pivorunas, 1970; Bennett, 1996), defined as a change in histological organization and/or cross-sectional shape from the base of the spine to the more distal portion, especially in spines demonstrating pronounced dimetrodont differentiation (Romer & Price, 1940). Most the spine inferior to this changing point was likely embedded in the epaxial muscle. Distal to this point, the spine cross section becomes craniocaudally compressed and medio-laterally expanded. The most cranial and caudal spines of the *Dimetrodon* vertebral column tend toward a circular cross section, whereas the mid-dorsal spines are elongated transversely and marked by cranial and caudal longitudinal grooves that give the characteristic "figure-8" or dumbbell shape of the spine in cross section.

We determined the cranial-most spines of fmnh UC 1134 based upon their cross-sectional morphology. The first two spines have the most subcircular cross sections of the entire series, whereas the third spine has a more subquadrate shape and zygapophyses, indicating a transition to the mid-dorsal region. The remaining four spines were determined to be more caudal in the series, most likely mid-dorsal spines, due to their typically dumbbell-shaped distal cross sections (Reisz, 1986). The rugosities are most prominent on the fourth and fifth spines of the series, with lesions diminishing in prominence on adjacent spines. A subtle deflection of the deep longitudinal groove is seen on the anterior and posterior aspects of spines 4 and 5 in the series (spine 4 in Fig. 2). We postulate that a single traumatic event occurred, whose effects were most marked on the fourth and fifth spines, and that its effect extended both cranially and caudally to include the remaining spines.

The gross morphological appearance of the permineralized bone, including lesion outline, form and degree of porosity/rugosity, and association of lesions in a linear series, appears consistent with the "diagnosis" of healed neural spine trauma, most likely bony fracture of the adjacent neural spines induced by bending (Table 1). The minimal deformation of the spines—which lack externally observable features of malalignment in the form of subluxation, torsion, or lateral bending—supports the presence of intact interspinous soft tissue splinting the neural spines while osseous healing occurred.

Less likely hypotheses to account for the observations include traumatically induced lifting of the periosteum with ensuing bone deposition without frank bone breakage, greenstick fracture (incomplete fracture of soft bone), infection, or a combination of all of these causes. Traction damage by muscle and ligament (enthesopathy) is far less likely, because the rugosities are located beyond the putative dorsal extent of the epaxial muscles, including the interspinalis, spinalis dorsi, and semispinalis dorsi as well as their tendons and the underlying ligaments. Although other less likely scenarios could not be be ruled out entirely macroscopically, the most consistent and conservative diagnosis of the observed pathology appeared to be healed fractures of the neural spines.

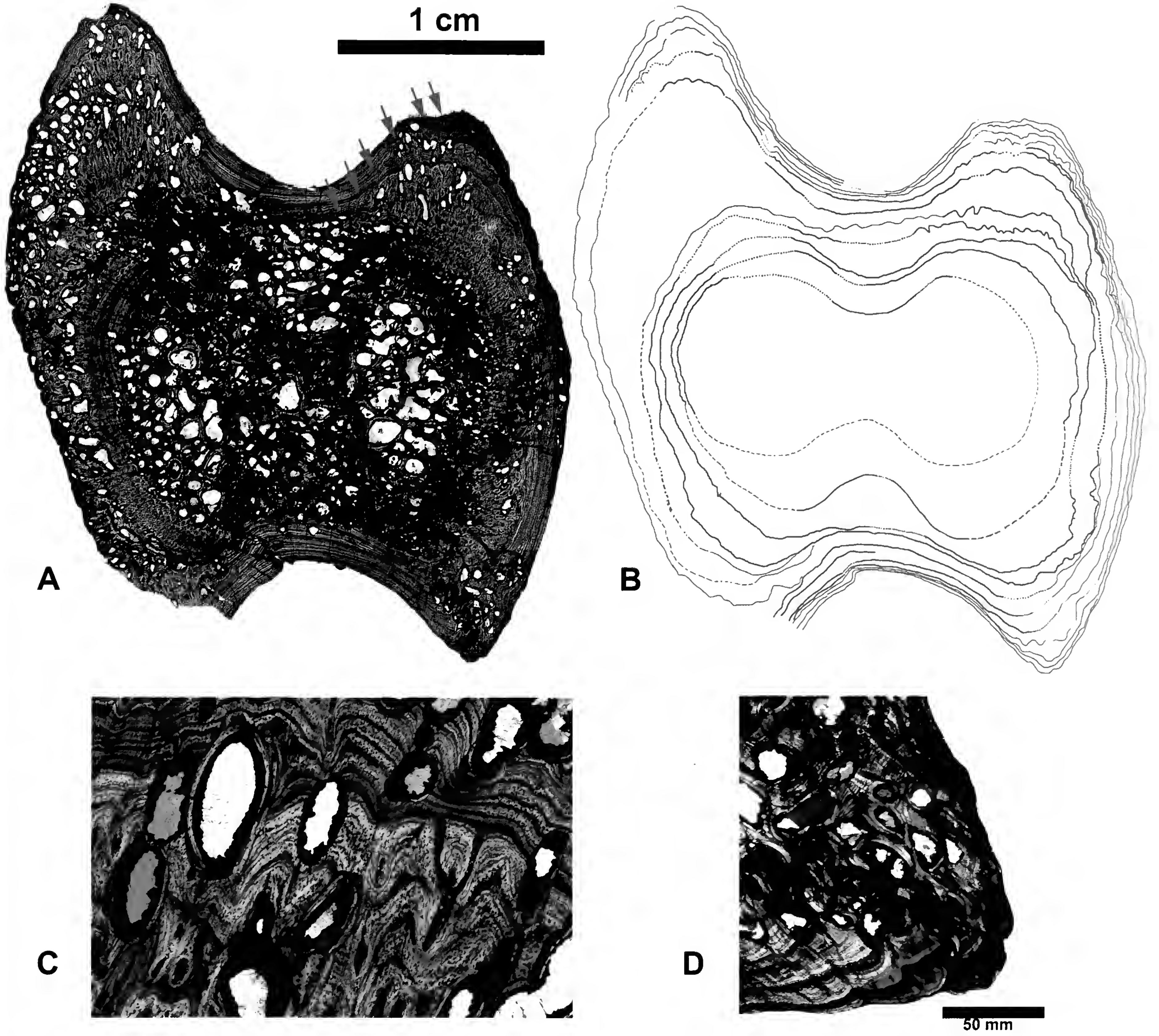

FIG. 3. Life-history data and growth as displayed in histological features of FMNH UC 1134. *D. giganhomogenes* distal spine 2. Scale for A–B at top. Scale for C–D at bottom. (**A**) Proximal cross section micrograph of spine 2 with arrows indicating visible lags subsequent to "growth spurt" of horns. Early lamellae are extensively remodeled to form porous medullary bone. (**B**) Line drawing tracing lamellae indicating cross-sectional shape change during ontogeny. The cortical LAG intervals narrow, indicating approaching maturity. (**C**) False-color polarization of cortex at higher magnification showing fibro-lamellar bone with line of arrested growth (at arrow). Resorption spaces characteristically lined by one to two lamellae are deposited circumferentially. Osteocyte lacunae are visible as black specks. (**D**) False-color polarization at higher magnification of right caudal horn tip. Note four LAGS and extensive remodeling.

Neural Spine Bone Was Highly Dynamic

The neural spine tissue of FMNH UC 1134 was far more dynamic in life than that of the tibia used for comparison, displaying densely vascularized fibrolamellar bone in the cortex and highly remodeled fibrolamellar bone remodeled into cancellous bone in the medullary area (Fig. 3A, C), likely reflecting the rapid distal and circumferential outgrowth of the neural spines relative to the other skeletal elements (Enlow, 1969; de Ricqlès, 1974; Bennett & Ruben, 1986; Rega et al., 2004, 2005; Huttenlocker et al., 2010). In contrast to the neural spines, the tibia of FMNH UC 1134 is characterized by a cortex composed largely of lamellar-zonal bone tissue, interbedded with regions of more rapidly growing fibrolamellar bone. This is consistent with descriptions of other specimens of *Dimetrodon* (Enlow & Brown, 1957; Enlow, 1969; de Ricqlès, 1974) and indicates slower growth than that of the hyperelongated neural spines.

Observable lines of arrested growth (LAGs) indicate 9 to 11 seasons of growth (Fig. 3B), with six seasons' growth accumulating after localized osseous growth spurt (Fig. 3A, arrows). Based on the intervals between the observable internal cortical LAGs, the number of LAGs obliterated by remodeling in the cortex numbers between 6 and 10. Age at death is likely therefore to have been between 15 and 21 years. Pericortical lamellar spacing diminishes substantially toward

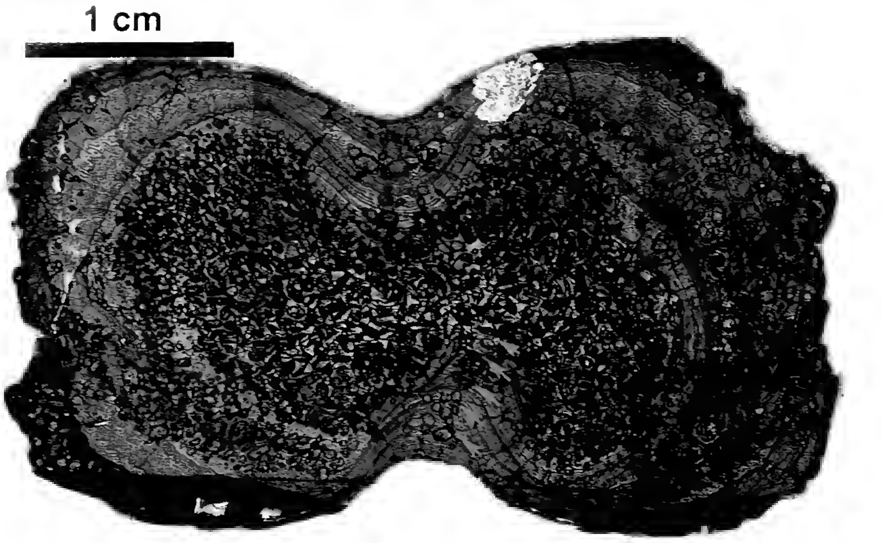

Fig. 4. FMNH UC 1134, the center of the observed pathology, mid-swelling transverse section of distal spine 2. Discontinuity (at arrows) is a linear array of lined secondary resorption centers. Note the lamellar-zonal bone lining grooves and the progressive migration of the lower groove apex from interior to exterior. The entire lateral cortex contains fibro-lamellar cortical bone throughout, containing entrapped blood vessels internally but with increasingly exuberant secondary remodeling of irregular fibrolamellar bone as the cortical surface is approached. The irregular bone deposition and secondary remodeling are responsible for the external appearance of rugosity.

the outer cortex, indicative of the slowing of osseous growth near the attainment of somatic maturity.

Shape Change during Ontogeny

The base of the spines of FMNH UC 1134 display a quadrangular cross-sectional shape with enlarged, paired horns anteriorly and posteriorly. Their elongate shape and the Sharpey's fiber density and orientation provide supporting evidence that these were the attachment sites for a bilaminar interspinous webbing forming the soft tissue sail (Fig. 3D). The inner cortex reveals that these prominent horns were not developed in early ontogeny at this level of the spine (Fig. 3A). If they were present in the young animal, horns or small ridges may have been situated more proximally in the spine but have since been obliterated by tissue remodeling.

The LAG interval marking the change from the figure-8 cross section to the subquadrangular cross section was the largest of the section and indicates that only one season's rapid growth was needed to attain the cross-sectional shape change (Fig. 3A, B). The horns contain considerable localized primary vascularity. Turnover of bone in discrete 3 to 15mm lacunae by osteoclastic resorption and deposition of lamellar new bone forms an "incipient" secondary osteon, whose circumferential infilling is typically limited to one or two lamellae (Fig. 3C). The localized growth spurt may be explained by entheseal migration of the epaxial musculature during normal growth, as evidenced by the deep, obliquely oriented Sharpey's fibers in this region, by interspinous webbing robusticity, and (or) by an overall growth spurt associated with the attainment of sexual maturity or dominance.

The proximal medullary region bears well-vascularized, fibrolamellar cortical bone undergoing prolific cancellous conversion by osteoclastic resorption and deposition of a new circumferential shell of bone similar to that seen in the horns. These spaces are so closely packed as to form well-differentiated, highly cancellous bone, completely filling the medullary cavity. The spaces presumably housed blood vessels and other soft tissue. The remaining but fragmented lamellae cross-cut by these resorption spaces preserve a figure-8 cross-sectional morphology typical of the distal region (Figs. 1, 3A, 4, 5A). This phenomenon was reported by Sumida et al. (2005), who suggested that cross-sectional shape of the spine may not be taxonomically informative unless ontogenetic trajectory is considered.

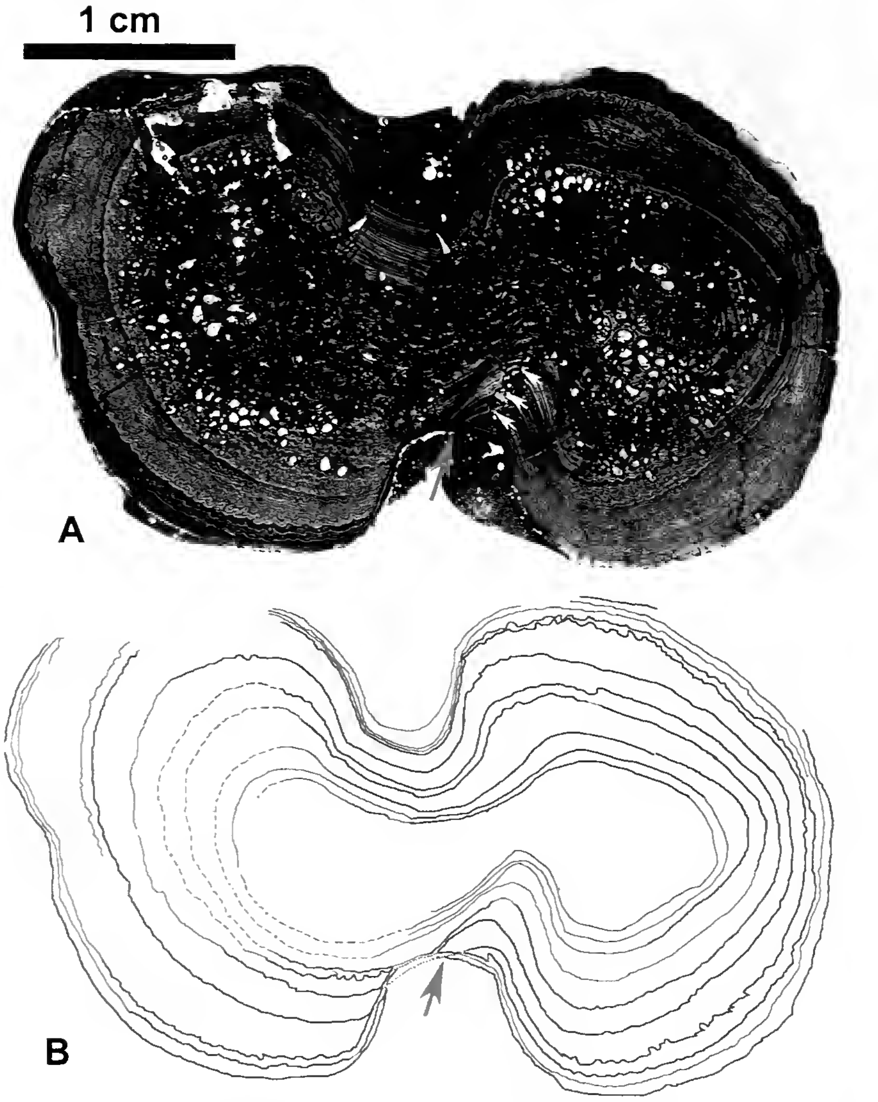

Fig. 5. Transverse section distal spine 2. Gray arrows indicate location of "unconformity" show at higher magnification in Figure 6. (**A**) Micrograph. White arrows indicate linear array of secondary remodeling. (**B**) Lamellar line drawing. At area of "unconformity" in base of groove (gray arrow), blue dotted lines show lamellae that were resorbed.

Dynamics of Microfracture

Sections through both the pathological rugose lesion and a superficially normal-seeming area distal to it illustrate the scope of the injury. The mid-lesion section through the rugose lesion of externally visible pathology (Fig. 4) does not depict the expected shell of periosteally deposited new bone characteristic of the hard callus of fracture. Rather, the actual injury is far more subtle, indicating localized torsional failure by means of interlamellar slippage and potential material failure of traversing the lamellae comprising the groove apex. The lateral portions of the enveloping lamellae in this section are both highly vascularized and highly remodeled.

The orientation of the groove farther distally is markedly distorted, showing that the pathology extended up the spine to the area which, on the surface, appeared normal. The groove is offset by approximately 20 degrees (Fig. 5A). A linear arrangement of 4 to 12 mm lined resorption spaces transects the apical lamellae forming the groove base. This could be an area

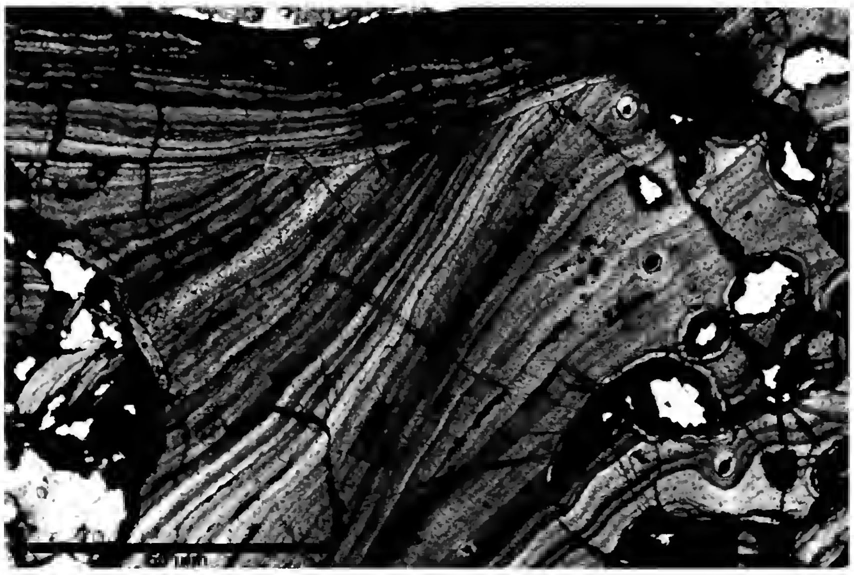

FIG. 6. Transverse section at higher magnification through "unconformity." Resorptive truncation of lamellae and subsequent lamellar deposition reestablishes the groove orientation within one season of growth. Note scalloping at arrows indicative of osteoclastic resorption.

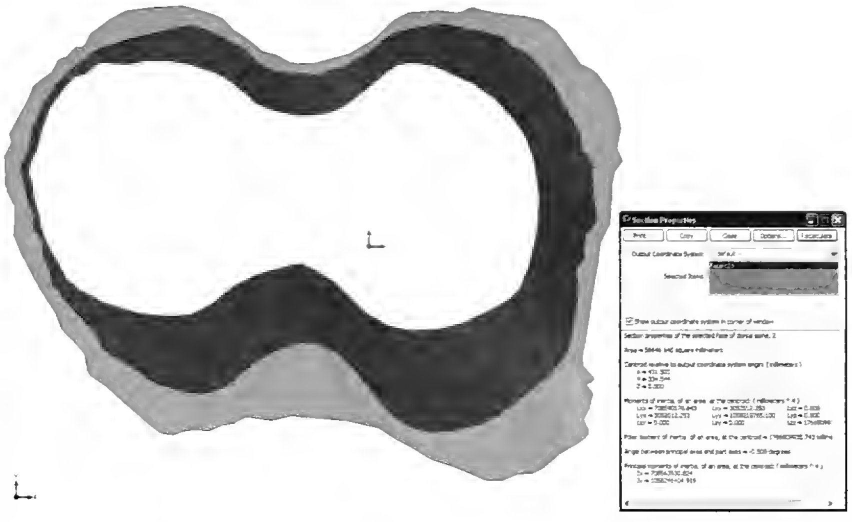

FIG. 7. Finite elements analysis output indicating principal moments of inertia in mid-lesion cross section. The principal moments of inertia at the centroid (intersection of vector arrows) are: I_x= 708,563,530.824 and I_y = 1,058,246,404.909. Note that resistance to lateral bending is higher than cranio-caudally. The horizontal width of the spine is about 3.5 cm.

of frank material failure manifesting as microfracture, although evidence is obliterated by resorption.

Resorption of subperiosteal lamellae and deposition of newer subperiosteal lamellae established the original cranio-caudal orientation of the groove within one season's growth (Fig. 5B). The truncation of lamellae by osteoclastic action and the subsequent lamellar deposition are illustrated at greater magnification in Figure 6, where the scalloping indicative of osteoclastic action can be seen.

Discussion

Much to the surprise of all involved, the sectioning did not reveal the expected hard callus of healed fracture, but rather a far more interesting interplay of bone dynamics, including microfracture, rapid resorption and proliferation, and canalized healing in a highly vascularized bone capable of very rapid growth and dynamic remodeling. Injured neural spine bone tissue left a history that can be read. Loading in excess of the yield point caused slippage between lamellae and consequent plastic deformation in spine 2. Frank material failure manifesting as microfracture may have occurred transecting the apex of the caudal groove, but this was obliterated by subsequent remodeling. This is a very different result than what was initially expected from the external appearance, and it reinforces the observation that it is critical to section pathologies rather than rely on external morphology and imaging alone when making interpretations. The spine chosen for sectioning was not the most severely affected of the series; presumably, the epicenter of the response to injury would show even more marked changes. It remains intact and available for further study.

Experimentally, Haversian bone yields at 1% and fails at 2% stress over strain. The failure point was likely lower in the interlamellar planes than in the surrounding bone, causing slippage and torsion material failure transecting the groove apex in the distal section likely instituted remodeling along the entire microfracture plane. The toughness of the bone resisted frank fracture of the entire bone. In this way, the elongate spines were structurally well suited to the high magnitude of bending imposed upon them regularly by forces such as falling or by a stiff crosswind. The heterogeneous and site-specific healing response in the injured area ranges from slow-growing zonal-lamellar bone in the grooves to fast-growing, highly vascularized fibro-lamellar bone deposited simultaneously in the lateral cortex, indicating a site-specific response to insult. This rapid dynamic response contrasts to the slower regular growth shown in the long bones, as typified by the tibial section. Sub-periosteal osteoclastic resorption and subsequent lamellar deposition within one season rapidly reestablished the orientation of the disrupted longitudinal groove. Preliminary finite element analysis (Fig. 7) suggests a strong biomechanical rationale for shape geometry and groove orientation in resisting lateral deformation. The region affected by the lesions would have been exposed to large bending moments and, thus, greater probability of failure at the fixed point.

The absence of associated vascular canals in the grooves casts doubt on the widely held hypothesis that the grooves of pelycosaur spines contained blood vessels that allowed the sail to assume a strong thermoregulatory function. Moreover, conservative sphenacodontids with relatively low to moderate spine heights had already evolved a dorsal crest of variable height (Huttenlocker et al., 2010). This confounds the hypothesis that the dorsal sail evolved as a thermoregulatory organ, because it was not derived in "advanced" sphenacodontids, nor was it a neomorph in *Dimetrodon* (*contra* Pivorunas, 1970), but rather evolved from the rudimentary crest of more basal sphenacodontids.

In particular, *Dimetrodon* spine microstructure suggests that the dumbbell shape (two intersecting cylinders) is of vital importance. This cross section is highly resistant to deformation, and is used in engineering for structural support requiring lateral stability. Certain morphological features of the neural spines in sail-finned pelycosaurs, especially the dumbbell cross section, also appear in the vertical septum (VS) of some teleost fishes, specifically the dorsal sail of *Thunnus obesus*, the yellowfin tuna. The VS is composed of bone (neural and hemal spines) embedded in a robust web of collagen, whose primary function may be mechanical in minimizing dorsoventral bending that increases efficiency at lateral undulation. By analogy, we propose that a similar function in increasing locomotor efficiency in sail-backed pelycosaurs must be added to the list of hypotheses regarding sail function.

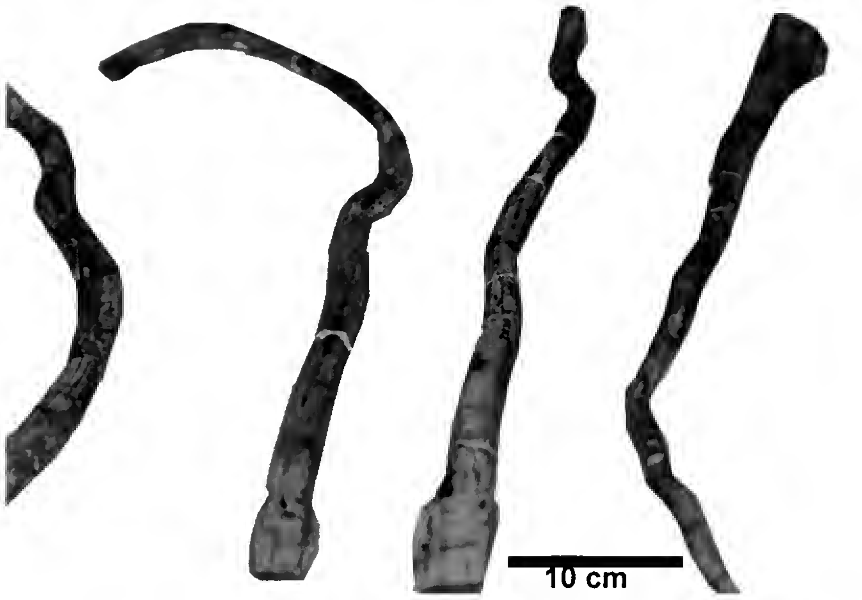

FIG. 8. Distal tips of neural spines from the type of *D. giganhomogenes* FMNH UC 112, indicating eccentric dorsal profile of "sail." The curled tips would have precluded a complete soft tissue sail at the spine margins. The type specimen also manifests a bony spur (enthesopathy), indicative of tension injury to the neural spine, potentially due to interspinous ligament or other sail soft tissue damage.

At high levels of magnification, short bundles of Sharpey's fibers were also found within the lateral cortex of the distal spine under polarized light in FMNH UC 1134. The bundles differed from those found in the proximal region of the spine in their size and distribution, often localized within individual lamellae and varying in orientation. The bundles resemble those figured in the spines of *Edaphosaurus* (Enlow, 1969; de Ricqlès, 1974), although they are not as prominent, and may indicate the migration of the periosteum or that of an associated collagenous sail membrane. Moreover, the presence of profuse resorption chambers lined with new lamellar bone serves a biomechanical purpose in "toughening" the bone at sail attachments. Any crack propagation resulting from tensile stresses would be blunted and halted by these circular features, much the same way that portholes blunt cracks on ship hulls.

As a further consideration of sail morphology, careful examination of the distal morphology of adjacent spines in more complete specimens, including the type FMNH UC 112 and OMNH 01727, suggests that the dorsal margin of the sail *in vivo* was located well proximal to the tips of the elongate neural spines (Fig. 8). These spines curve irregularly at their distal ends like the fingernails of the senescent Howard Hughes, rendering it unlikely that a connected dorsal sail could span these segments.

Conclusions

1. Deformation of elongate neural spines in *Dimetrodon giganhomogenes* FMNH UC 1134 resulted from interlamellar slippage and microfracture. Substantial bending was likely centered on the area of spines 4–5 8 cm above the epaxial musculature. The cross-sectional shape and microstructure created a bone more highly resistant to fracture than are the limb bones.
2. Cranial and caudal groove position was reestablished within one season by resorption and additional lamellar deposition. Preliminary finite element analysis suggests a strong biomechanical rationale for shape geometry and groove orientation in resisting lateral deformation. Localized remodeling chambers in fibrolamellar tissue served to resist crack propagation and thereby "toughen" the bone.
3. Sharpey's fiber orientation suggests a sail attachment at the "horns"; the curled configuration distally in complete specimens does not allow continuous sail attachment.
4. The hypothesized function of thermoregulation is not supported by this histological evidence. Any blood vessels in the soft tissue of the sail were not communicated through bone vasculature, nor are emissary foramena for blood drainage in evidence. Thermoregulation as prime mover for sail evolution is also confounded by the fact that it evolved from the rudimentary crest of variable height in more basal sphenacodontids.
5. Cross-sectional shape, previously used to distinguish among *Dimetrodon* species, is an ontogenetic feature and cannot be used to determine species designations independent of ontogenetic considerations. The neural spines of *Dimetrodon giganhomogenes* show a localized growth spurt in the "horns" lasting one to two seasons. This same growth spurt is not observed in the tibia.

Acknowledgments

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Chapter 10: Ontogeny in the Malagasy Traversodontid *Dadadon isaloi* and a Reconsideration of its Phylogenetic Relationships

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Abstract

New craniodental material of the traversodontid *Dadadon isaloi* from Middle/Upper Triassic basal "Isalo II" beds of southwestern Madagascar is described. These specimens reveal several new autapomorphies of *Dadadon*, including paired foramina on the frontal near the anterior border of the postorbital and lower incisors with denticulated distal margins. The new material covers a broad size range, providing the first information on ontogeny in *Dadadon*. Larger (presumably older) specimens of *Dadadon isaloi* have more postcanine teeth, relatively longer, narrower snouts, and a higher degree of cranial ornamentation than smaller specimens. Postcanine replacement in *Dadadon* was similar to that of other traversodontids: new teeth erupted at the posterior end of the postcanine tooth row and moved forward. Using information from the new specimens, the position of *Dadadon* was tested in a new phylogenetic analysis of traversodontids. In the new analysis, *Dadadon* is strongly supported as a member of a clade also including the South American taxa *Massetognathus* and *Santacruzodon*, here named Massetognathinae subfam. nov. This clade is diagnosed by the presence of denticulated lower incisors, relatively small canines, three cusps in the labial margin of the upper postcanines, and low, flat skulls. Massetognathinae is the sister-group of Gomphodontosuchinae, which includes *Gomphodontosuchus*, *Menadon*, *Protuberum*, *Exaeretodon*, and *Scalenodontoides*. The Laurasian traversodontids (*Arctotraversodon*, *Boreogomphodon*, and *Nanogomphodon*) form a clade that is the sister-taxon of Massetognathinae + Gomphodontosuchinae. Denticulated incisors evolved multiple times in traversodontid evolution (in massetognathines and *Arctotraversodon*), and thus this group represents another possibility (besides various archosauromorphs) to be considered when attempting to identify isolated Triassic teeth with denticulated carinae lacking cingula.

Introduction

Traversodontids, a group of herbivorous Triassic cynodonts, represent perhaps the last unmitigated success story for the therapsids prior to the evolution of mammals. During the Triassic, the once dominant therapsids increasingly played a diminished role in terrestrial vertebrate ecosystems, with sauropsids (particularly archosauromorphs) occupying many of the niches previously filled by therapsids in the Permian. Of the three therapsid clades to survive the Permo–Triassic extinction, therocephalians became extinct early in the Middle Triassic (Rubidge & Sidor, 2001). Several lineages of dicynodonts (emydopoids, lystrosaurids, and kannemeyeriiforms) crossed the end-Permian extinction boundary, but only the kannemeyeriiforms survived into the Late Triassic (Angielczyk & Walsh, 2008; Dzik et al., 2008; Fröbisch et al., 2010). Kannemeyeriiforms were widespread and reasonably abundant within localities, but were a fairly homomorphic group (King, 1988). Within eucynodonts, basal cynognathians (cynognathids, gomphognathids, and trirachodontids) were widespread and abundant, but with low species diversity (Martinelli et al., 2009); basal probainognathians had higher species diversity but were relatively rare (Hopson & Kitching, 2001; Abdala & Ribeiro, 2010). Only traversodontids combined high species diversity, broad geographic distribution, and high abundance within faunas (where they occurred, traversodontids were usually the dominant herbivorous tetrapods [Whiteside et al., 2011]). The earliest traversodontids are known from the Anisian of Argentina and Africa, and the group survived into the Late Triassic, with members of the group (*Scalenodontoides* in southern Africa and *Boreogomphodon* in eastern North America) last known in the Norian (Abdala & Ribeiro, 2010). The richest deposits of traversodontid fossils have been found in South America and Africa, and traversodontids were traditionally considered a Gondwanan endemic group. However, recent discoveries have shown that they also occurred in the northern hemisphere (Sues & Olsen, 1990; Sues et al., 1992; Hopson & Sues, 2006). Indeed, the eastern North American taxon *Boreogomphodon* appears to have been as abundant and long-ranging (Carnian to Norian) as any of the better-known South American traversodontids (Sues & Olsen, 1990; Liu & Sues, 2010; Sues & Hopson, 2010). No traversodontids have been found in western North America, North Africa, non-Indian Asia, Australia, or Antarctica. In some of these areas, the absence of traversodontids may be an artifact of undersampling Middle-to-Upper Triassic faunas (e.g., Australia and Antarctica), whereas in well-sampled areas, the absence of traversodontids is probably a real paleobiogeographic phenomenon, perhaps attributable to climatic or competitive exclusion (e.g., western North America).

One of the more recently discovered traversodontid-bearing areas is Madagascar. Beginning in 1996, numerous traversodontid specimens were recovered from the basal "Isalo II" beds of the southwestern part of the country (Flynn et al., 1999). This material was later described as two new species of traversodontids, *Dadadon isaloi* and *Menadon besairiei* (Flynn et al., 2000). *Menadon* is known from the type skull, an isolated mandible, and a partial skull and postcranium (Flynn et al., 2000; Kammerer et al., 2008). *Dadadon* is known from more extensive material, most of it previously undescribed.

Supplementing the descriptions of the holotype (Flynn et al., 2000) and referred skull and lower jaws (Ranivoharimanana et al., 2011), here we describe additional specimens referable to *Dadadon isaloi*, noting their preservational state, newly recognized anatomical features, and character data of import to understanding *Dadadon*'s phylogenetic position or ontogenetic trajectory. These specimens were collected in the basal "Isalo II" beds of the Morondava Basin in southwestern Madagascar. Precise locality information is on file at the American Museum of Natural History and the Field Museum.

Institutional Abbreviations

FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; UA, Université d'Antananarivo, Antananarivo, Madagascar.

Systematic Paleontology

SYNAPSIDA Osborn, 1903
THERAPSIDA Broom, 1905
CYNODONTIA Owen, 1861
GOMPHODONTIA Seeley, 1894
TRAVERSODONTIDAE von Huene, 1936
MASSETOGNATHINAE **subfam. nov.**

Type Genus

Massetognathus Romer, 1967.

Included Taxa

Dadadon isaloi Flynn, Parrish, Rakotosamimanana, Ranivoharimanana, Simpson, and Wyss, 2000; *Massetognathus pascuali* Romer, 1967; *Massetognathus ochagaviae* Barberena, 1981; *Santacruzodon hopsoni* Abdala and Ribeiro, 2003.

Diagnosis

Traversodontid cynodonts characterized by low, flattened skulls, reduced canine size (relative to basal traversodontids), triangular incisor crowns with roughly denticulated sectorial edges (only on the lowers in *Dadadon*, both uppers and lowers in *Santacruzodon* and *Massetognathus*), and three cusps in the labial margin of the upper postcanines (a large main labial cusp and two anterior accessory labial cusps).

Phylogenetic Definition

The clade containing all traversodontids more closely related to *Massetognathus pascuali* Romer, 1967, than *Gomphodontosuchus brasiliensis* von Huene, 1928 (counterpart to Gomphodontosuchinae *sensu* Kammerer et al., 2008).

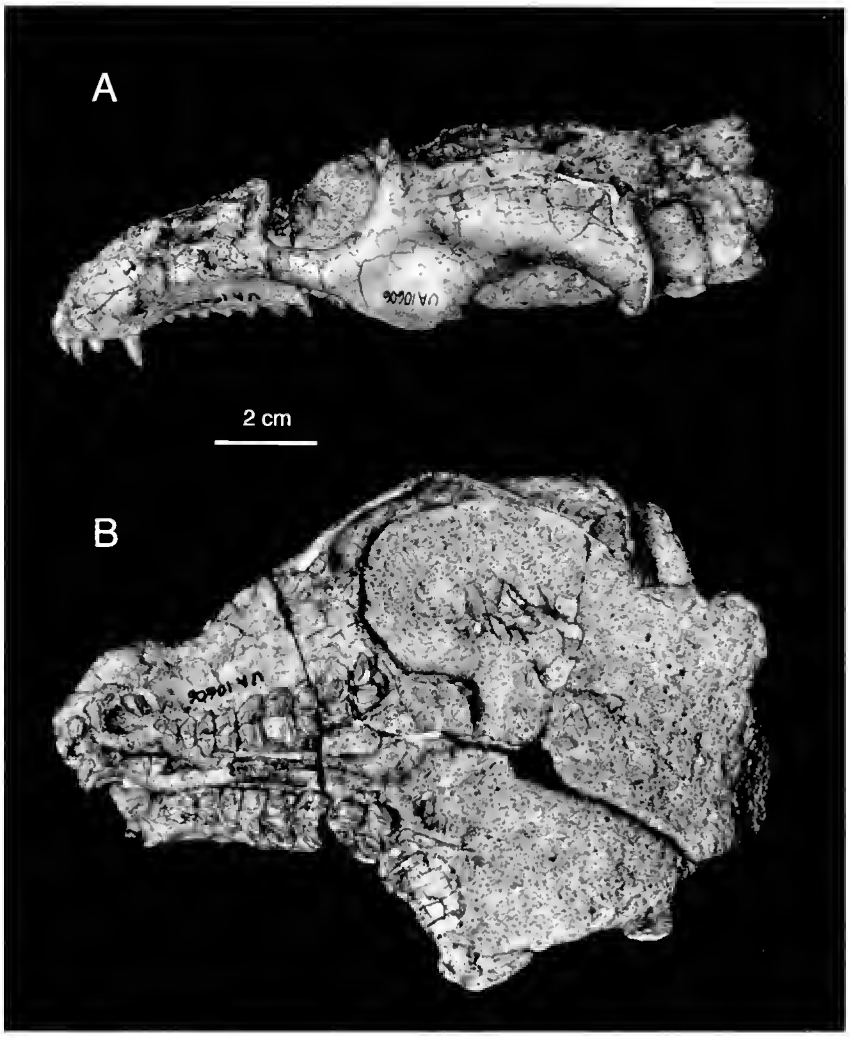

FIG. 1. UA 10606, the holotype of *Dadadon isaloi*, in (**A**) left lateral; and (**B**) palatal views (© American Museum of Natural History, 2012).

DADADON ISALOI Flynn, Parrish, Rakotosamimanana, Ranivoharimanana, Simpson, and Wyss, 2000

Holotype

UA 10606, a fragmentary skull with well-preserved upper postcanine tooth row (Fig. 1).

Referred Specimens

FMNH PR 2232, FMNH PR 3034–3038, UA 10605, UA 10608–10617.

Diagnosis

A massetognathine traversodontid characterized by a fourth upper incisor with posterior accessory cusp, upper incisors with smooth sectorial edges and lower incisors with the lower half of the distal margin denticulated, canine with midline labial groove producing a figure-8-shaped cross section, and a heavily ornamented interorbital region (prominent midfrontal ridge, prefrontal depressions, deep interorbital depressions on the frontal with deep, paired foramina).

Description

UA **10605** was referred to *Dadadon isaloi* by Flynn et al. (2000) and is described in further detail here. This specimen is

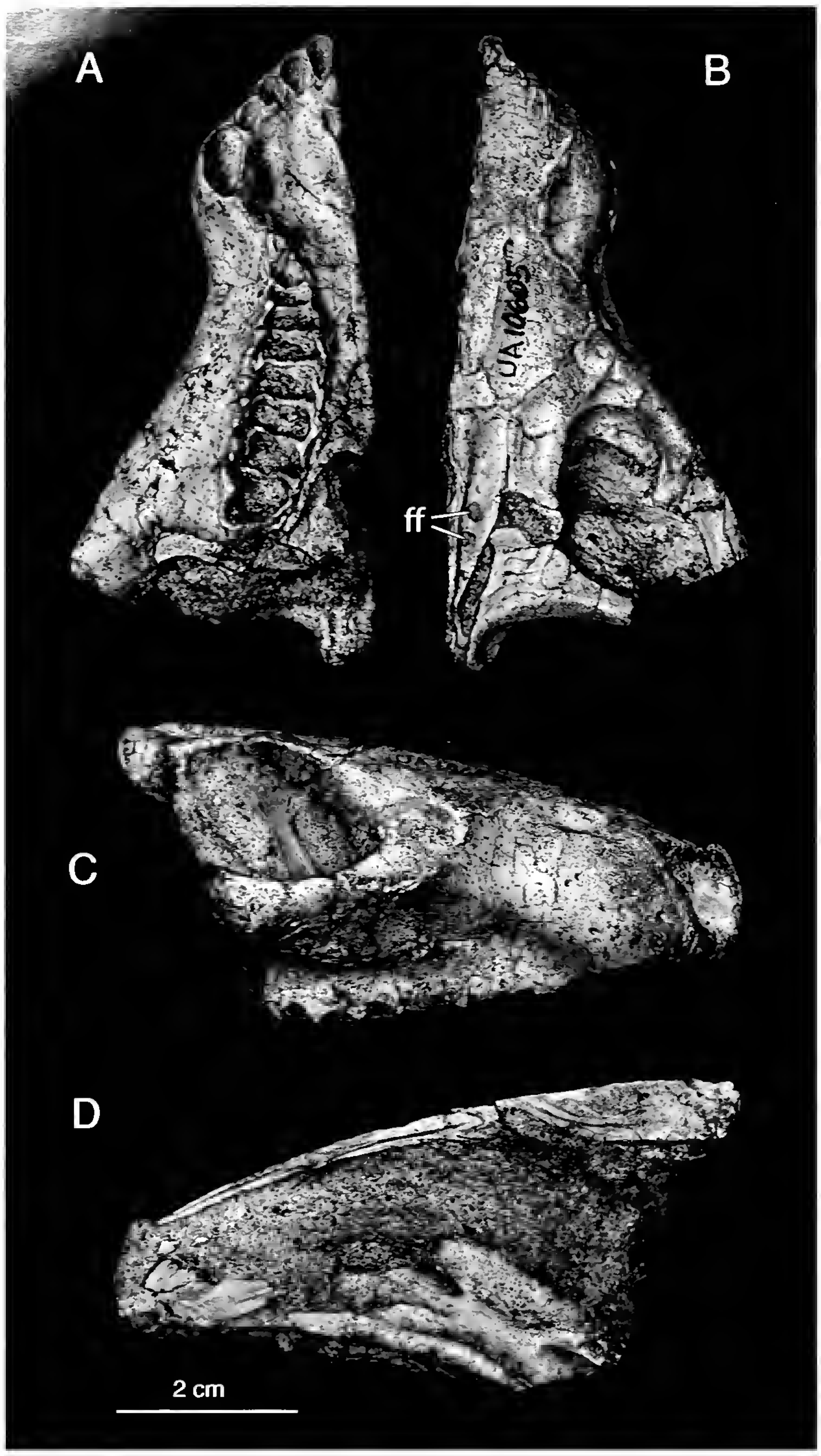

FIG. 2. UA 10605, a partial skull of *Dadadon isaloi*, in (**A**) palatal; (**B**) dorsal; (**C**) right lateral; and (**D**) left medial views. Anterior is up in **A** and **B**. Position of interorbital frontal foramina (**ff**), an autapomorphic feature of *Dadadon*, is indicated in **B**. In this specimen the interorbital depressions are still only weakly developed compared to the condition in larger individuals (e.g., FMNH PR 2232; see Ranivoharimanana et al., 2011) (© American Museum of Natural History, 2012).

an edentulous partial skull (dorsal length from anterior margin of orbits to premaxillary tip 44 mm, dorsal length from postorbital bar to premaxillary tip 68 mm) associated with two partial vertebrae, a thoracic rib, skull fragments, and two incisors. The skull element (Fig. 2) includes the right half of the snout and orbital region (the postorbital bar is broken off posteriorly, but part of the intertemporal bar is preserved). Nine postcanine alveoli are preserved, of which the first is out-of-line (angled anterolaterally) and elevated (positioned more ventrally) with respect to the others. The snout in this specimen is of similar proportions to that of FMNH PR 2232 (Ranivoharimanana et al., 2011), and the same pattern of maxillary foramina is present: two large supracanine foramina dorsal to the alveolar margin, anterior and posterior to the canine, smaller accessory supracanine foramina dorsal to these (unusually, the posterior accessory supracanine position bears two small foramina), and a large lateral maxillary foramen anteroventral to the orbit. Although not as prominent as in FMNH PR 2232, a midfrontal ridge and prefrontal depression are present in the interorbital region of this specimen. Two large foramina, one immediately posterior to the other, are present in the depression between the midfrontal ridge and the frontal-postorbital suture, medial to the anterior margin of the postorbital (Fig. 2B). Reexamination of FMNH PR 2232 reveals that these foramina are present in that specimen as well—they were previously unrecognized because of the great depth of the interorbital depressions, still partially filled with matrix, in that skull. These unusual foramina are not present in any other known traversodontids, and represent a newly recognized autapomorphy of *Dadadon*. Of the two incisors associated with this skull, one is broken at the tip, but the spade-like morphology and presence of a smooth ridge on the distal margin indicate that it is upper incisor 1, 2, or 3 (the fourth upper incisor of *Dadadon* has a prominent accessory cusp that would be visible even if the tip were broken). The other incisor is a well-preserved, intact right lower. This is an asymmetrical, spatulate tooth that is broader at the distal edge of the crown. The posterior face of this tooth is concave with a ridge running from the apex of the crown down the midline towards the root. The lower half of the distal edge of this tooth is denticulated, with three distinct accessory cusps present along the margin—permitting this tooth to be identified as a lower (see FMNH PR 3035 below). This partial denticulation is in contrast to the condition in *Massetognathus* and *Santacruzodon*, wherein both edges of the lower incisors bear cusps.

UA **10613** is a right dentary fragment (Fig. 3) preserving a single intact postcanine tooth in addition to part of a postcanine root and an empty alveolus (fragment is 16 mm long, postcanine 6 mm long on the labial side, 5 mm wide at the anterior edge). The intact postcanine is well preserved and largely unworn, with wear facets on only the top half of the tooth's labial edge and on the transverse crest between the labial and lingual cusps. All three posterior labial accessory cusps are present, although the anteriormost of the three has a broken tip. The posterior cingular crest bears seven tiny cuspules.

UA **10614** is a right maxillary fragment preserving seven postcanine teeth (not figured). Only a fragment of root remains in the small, circular alveolus of PC1. The crowns of PC2 and PC3 are badly damaged but these teeth are clearly wider than long in rectangular alveoli. A clear morphological break is present between PC3 and PC4, the latter of which is twice as large as the former and exhibits the typical adult upper postcanine morphology for *Dadadon*. PC4 is shouldered posteriorly by PC5, but does not shoulder PC3. The cusps of PC4–PC7 are worn and have broken tips, but the general morphology of these teeth is clear, and they increase in size posteriorly. The root of PC7, exposed posteriorly, is relatively short (equal in height to the crown) with a concave posterior edge.

FMNH **PR 3035** is a small, partial mandible (length of the left preserved mandibular ramus is 52 mm, the right is 43 mm, right postcanine tooth row 27 mm long) preserving the precoronoid portion of the dentaries (more of the coronoid process is preserved on the left mandibular ramus, the right side is broken off at the end of the postcanine tooth row). The dentary (Fig. 4) has a straight ventral margin and the anterior margin of the symphysis is obtusely angled relative to the long axis of the jaw. The preserved portion of the left coronoid process is steep. The masseteric fossa extends anteriorly to the level of pc5. A prominent mental foramen is present below the dentary midheight between the positions of the first two

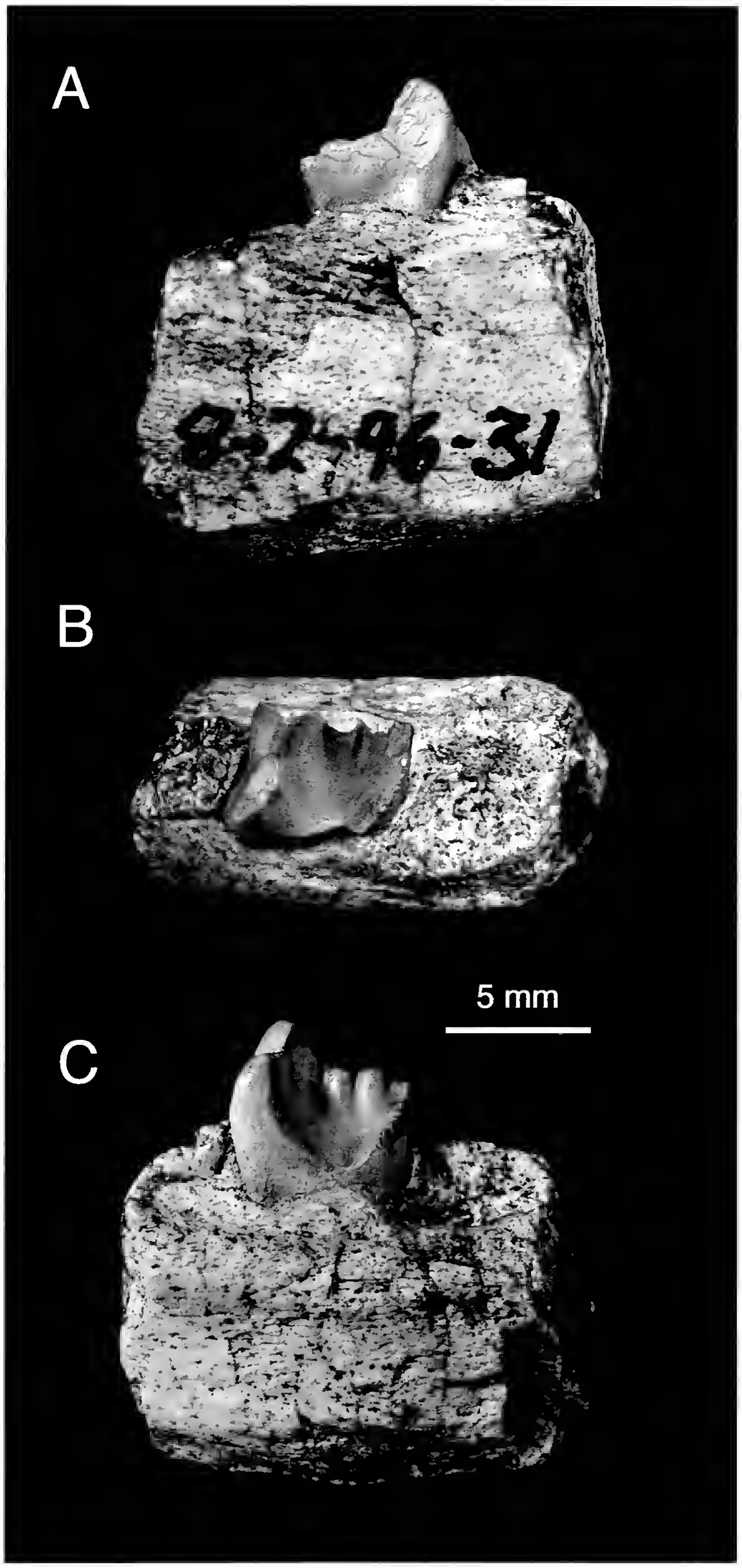

FIG. 3. UA 10613, a right dentary fragment of *Dadadon isaloi*, in (**A**) right lateral; (**B**) occlusal (anterior is left); and (**C**) left medial views. Note the presence of three posterior labial accessory cusps and a densely cuspulated posterior cingular crest on the preserved postcanine tooth (© American Museum of Natural History, 2012).

postcanines. The dentition in this specimen is well preserved and consists of three incisors and a canine on each side, eight right postcanines, and five left postcanines. The incisors are spatulate with spade-shaped crowns with the lower portion of the distal margin denticulated (Fig. 4E, F). The distal margin of the incisors near the tip of the crown is only weakly worn, suggesting that this part of the tooth was naturally devoid of denticulation. The mesial margins of the incisors in this specimen lack denticles entirely, unlike in *Santacruzodon* in which both sides of the incisors are denticulated (Abdala & Ribeiro, 2003). The canines are weakly recurved with smooth anterior and posterior keels. A short diastema (3 mm between tooth bases) separates the right canine and first postcanine. The postcanine tooth row exhibits increasing tooth size and relative width and decreasing wear posteriorly. On the right side, pc1 is 2 mm long labially and 1 mm wide, whereas pc7 is 4 mm long and wide. In pc1, the entire labial surface of the tooth is covered by a wear facet and the labial cusp row is completely obliterated. Distinct (albeit heavily worn) labial and posterior accessory labial cusps first appear in pc3, but all three posterior accessory labial cusps are not observed until pc5, where the labial wear facet is limited to the top half of the crown. Rather than forming a single unit, the labial wear facet in pc6 occurs on the sides of the labial and posterior accessory labial cusps, and in pc7 only weakly on the side of the labial cusp. Only pc3–6 are preserved on the left side, but their sizes and wear levels are similar to their counterparts on the right.

UA **10615** is a small, fragmentary skull (dorsal length from anterior margin of orbits to premaxillary tip 26 mm, dorsal length from postorbital bar to premaxillary tip 43 mm). The largest fragment (Fig. 5) is made up of the majority of the snout, interorbital region, and left zygomatic arch. Other important fragments include the posterior part of the left squamosal and quadrate, two maxillary fragments, and part of the occiput. The midfrontal ridge and prefrontal depressions are absent in this specimen, but elongate interorbital depressions and paired foramina (as in UA 10605) are present. Few teeth are preserved on the main skull element: the roots of the right I3 and I4, both canines, and the crowns of the right PC1 and PC2. The left maxillary fragment (Fig. 6) preserves PC1–7 (PC2 only as an alveolus, all others as crowns). The labial margins of these postcanines are all in-line with each other. These teeth are heavily worn, with the labial cusps worn down to their bases. The right maxillary fragment preserves a posterior portion of the postcanine tooth row, as indicated by the greater tooth size relative to those in the other fragment. A single intact postcanine and two alveoli are present in the right fragment. Unusually, the posteriormost alveolus is smaller than the one preceding it.

FMNH **PR 3036** is a very small partial lower jaw and associated thoracic rib (distance from base of first preserved incisor to fourth preserved incisor is 20 mm, although this figure is somewhat uncertain because the symphysis is reconstructed). The lower jaw (Fig. 7) preserves the anterior portions of both mandibular rami, two incisors, and the right canine. The incisors are spatulate and partially denticulated on their distal margins. The canine is weakly recurved with a smooth posterior keel. Four postcanine crowns are preserved on each mandibular ramus. These teeth are remarkably narrow compared to the lower postcanines of larger specimens (e.g., FMNH PR 3038) and do not increase in size posteriorly (all preserved postcanines are ~1 mm wide labiolingually, ~2 mm long mesiodistally). Although these teeth are clearly gomphodont, they differ in cusp pattern from those in larger specimens. Only two cusps are present: a tall anterior cusp and a lower posterior cusp. The anterior cusp appears to be homologous with the lingual cusp and the posterior cusp with the posterior accessory lingual cusp in larger specimens' lower postcanines. All postcanines in this specimen are heavily worn, with large wear facets covering most of the labial surface of the teeth. It is probable that this wear accounts for the apparent absence in FMNH PR 3036 of the labial cusps that are observed in larger specimens.

FMNH **PR 3037** is a very small partial skull (Fig. 8) preserving the anterior interorbital region and the postcanine portion of the snout (preserved portion of skull 22-mm dorsal

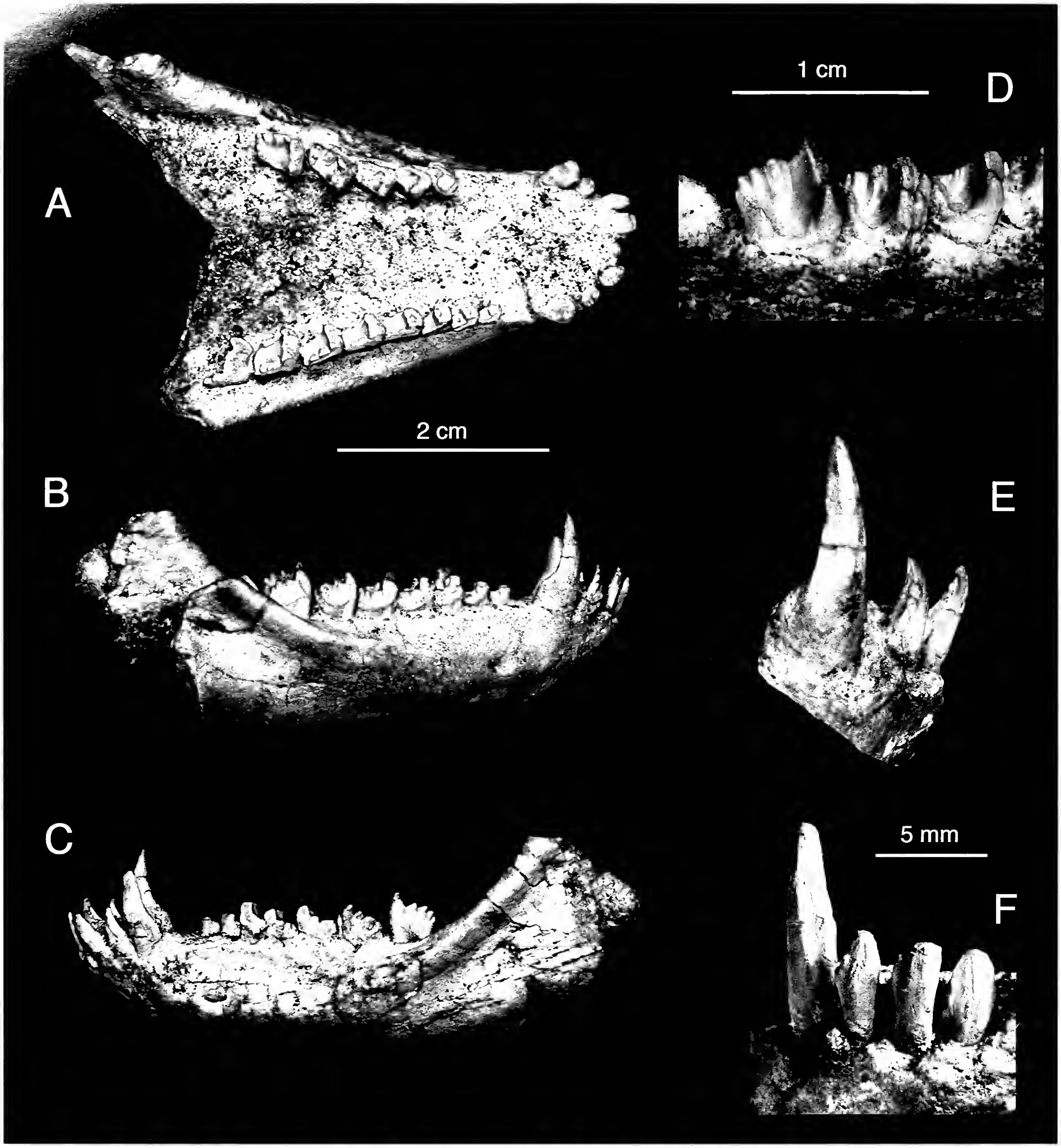

Fig. 4. FMNH PR 3035, a partial lower jaw of *Dadadon isaloi*, in (**A**) occlusal; (**B**) right lateral; and (**C**) left lateral views. Close-ups of dentition: (**D**) last three left lower postcanines in lingual view; (**E**) the right i2, i3, and lower canine in lingual view; and (**F**) the lower right incisors and canine in anterior view. Note the presence of denticulated distal edges of the incisors in **E**, **F** (© American Museum of Natural History, 2012).

length, preorbital portion 12 mm long, right postcanine tooth row 16 mm long). This specimen is dorsoventrally crushed but otherwise well preserved, with the upper postcanines preserved in excellent detail. Although the snout tip is not preserved, the intact portion of the skull indicates that this specimen had a relatively shorter and broader snout than larger specimens (e.g., FMNH PR 2232) of *D. isaloi*. The interorbital surface is flat, without any prominent depressions or ridges. A large lateral maxillary foramen is present at the lateral edge of the maxillary labial platform, anteroventral to the orbit. The maxillary-palatine suture is distinct, and shows that the palatine contribution to the secondary palate extends from the level of the third to the sixth (the penultimate) postcanine. Seven postcanines are present on both sides of the skull. These postcanines all exhibit the same cusp pattern, although they become relatively wider and absolutely larger anteroposteriorly.

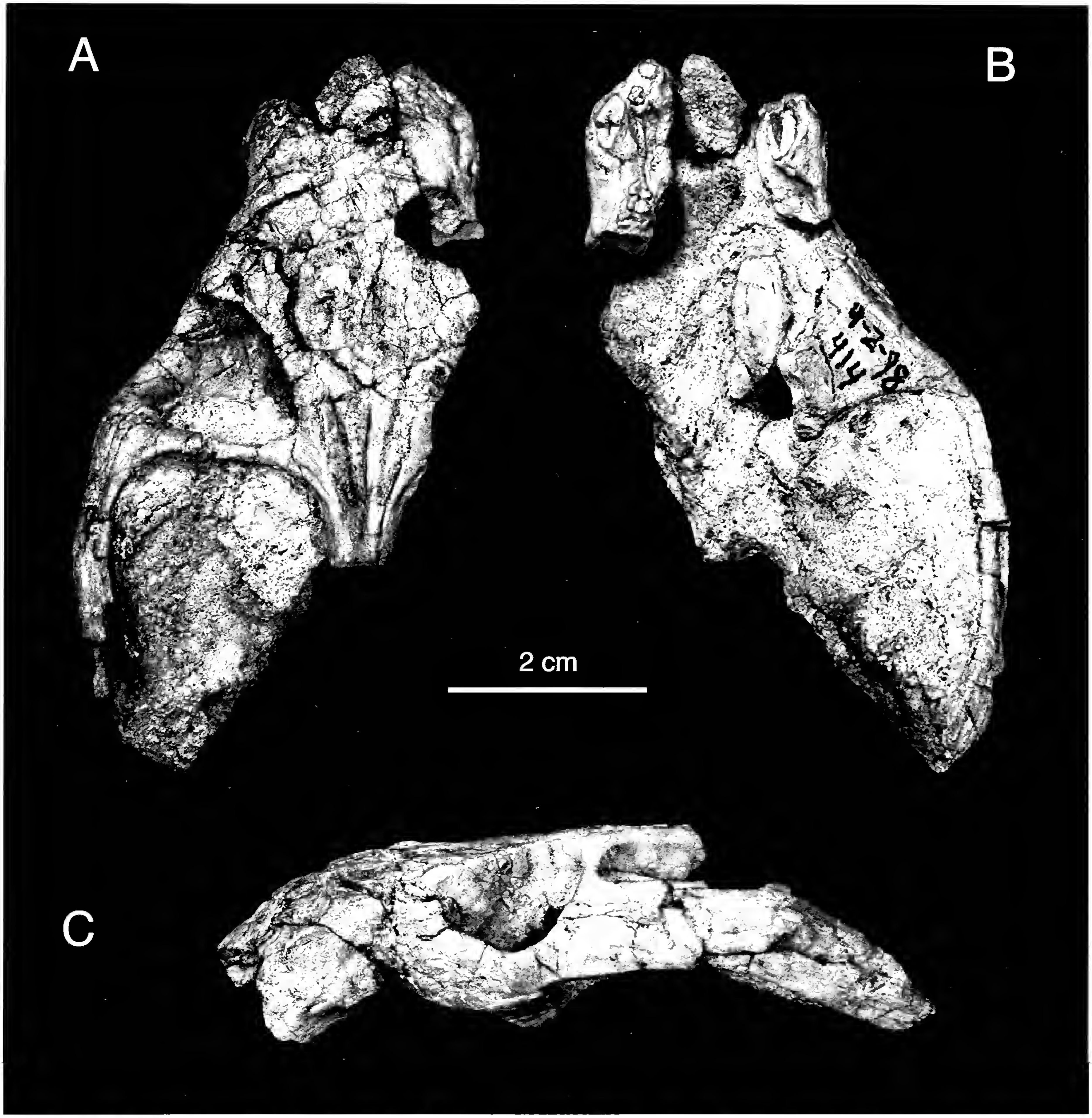

FIG. 5. Main fragment of UA 10615, a fragmentary skull of *Dadadon isaloi*, in (**A**) dorsal; (**B**) palatal; and (**C**) left lateral views. The postcanine dentition on the left maxilla of this individual is shown in Fig. 6. (© American Museum of Natural History, 2012)

The seventh postcanine on both sides was in the process of eruption when the animal died and would have been nonfunctional. The labial margin of PC1 is in line with those of the other postcanines, unlike in larger specimens where this tooth is angled anterolaterally. The postcanines of this specimen preserve fine cusp morphology usually obliterated by wear in larger specimens. Two anterior accessory labial cusps are present, located extremely close together and appearing to form a single cusp when worn. These cusps are nestled posteromedial to the main labial cusp of the preceding tooth, making the postcanines "shouldered." The anterior cingular crest is covered with three to five tiny cuspules. In the transverse crest, the main labial cusp and the lingual cusp are nearly equivalent in height on unworn teeth. Interestingly, the main labial cusp is lower and more heavily worn than the lingual cusp on worn teeth, the opposite condition from larger specimens. The lingual and central cusps are extremely close together, forming essentially a single cusp with a bifurcate tip opposite the main labial cusp. A thin posterior cingulum, lacking cuspules, is visible on some of the postcanines (most clearly on the right PC6 and PC7).

FIG. 6. Left maxillary fragment of UA 10615 (occlusal view), preserving six upper postcanines (PC1 and PC3–7) (© American Museum of Natural History, 2012).

UA **10612** was referred to *Dadadon isaloi* by Goswami et al. (2005; listed under its field number 9-11-98-553) and is described in greater detail here. This specimen is a partial left dentary (Fig. 9) preserving two intact postcanines and portions of four others (fragment is 37 mm long). This specimen represents the rear dentigerous region of the dentary, as the posteriormost preserved tooth is a partially erupted postcanine, the anterior edge of the masseteric fossa is preserved laterally, and the Meckelian groove is relatively tall medially. The anteriormost tooth is a partial postcanine preserved only as a root in section where the dentary is broken anteriorly. The following tooth has a mostly broken crown, but is clearly twice as long as wide. The third preserved postcanine is intact and much larger than the previous one, although it retains the longer-than-wide morphology. This tooth has a massive wear facet that covers nearly all of the labial face. The fourth postcanine is too badly broken to tell, but the fifth and intact sixth postcanines have a more squared-off profile—although they are still longer than wide. The labial wear facet in the fifth postcanine also covers the entire face of the tooth, but is restricted to the sides of the posterior accessory labial cuspules in the sixth, indicating that this was a relatively recently erupted tooth.

FMNH **PR 3038** is a right dentary fragment (Fig. 10) preserving the posterior part of the postcanine tooth row (fragment is 26 mm long, posteriormost postcanine is 5 mm long on labial side, 5 mm wide at anterior edge). Laterally the masseteric fossa is evident and the alveolar margin of the dentary is beginning to curve upwards into the coronoid process posteriorly. The ventral margin of the dentary is straight. Three postcanines (and part of the root of a fourth) are present. Although largely unworn (with only a small wear facet on the top half of the labial surface of the most anterior postcanine and faint wear facets on the labial surfaces of the labial and anterior two posterior accessory labial cusps of the middle postcanine), all of the cusps on these teeth are broken. The posterior cingula are well preserved, however, and demonstrate an increase in number of cingular cuspules with increasing postcanine width moving posteriorly through the tooth row. The posterior cingulum of the anteriormost preserved postcanine is made up of three cuspules roughly equivalent in size to the third (posteriormost) posterior accessory labial cusp. The posterior cingulum of the middle preserved postcanine is also composed of three cuspules, but the central and lingual cuspules are subdivided into finer cuspules (three and two, respectively) at their tips. In the posteriormost postcanine, the posterior cingulum is composed of seven cuspules, all of roughly equal size (showing no indication of being subdivided from larger cuspules as in the middle tooth), and smaller than the posteriormost posterior accessory labial cusp on that tooth.

UA **10616** is an isolated upper left postcanine tooth (not figured). The posterior lingual cusp has a small accessory cuspule medially.

FMNH **PR 3034** is a fragmentary, poorly preserved partial skull (Figs. 11, 12) preserving the snout and part of the right zygomatic arch (preorbital portion of fragment is ~43 mm long on the right side of the skull). The dorsal surface of the skull is not preserved. Proportionally, this specimen is similar to FMNH PR 2232 albeit broader across the palate, which may be an artifact of dorsoventral flattening. No intact incisors are preserved but both canines are present although broken. The root of the left canine is exposed for nearly all of its length and shows a distinct groove running down it at labial midlength. This groove is also observed in the left canine of FMNH PR 2232, giving it a "figure-8" shape in cross section (Ranivoharimanana et al., 2011). This canine morphology is autapomorphic for *Dadadon*; in *Massetognathus* and *Santacruzodon* the canine is ovoid in cross section with a smoothly rounded labial surface. Well-preserved paracanine fossae are located medial to the canines. Postcanine dentition is only preserved on the left side of the skull and includes PC1 followed by a break and then four larger postcanines. These postcanines are similar in relative size, orientation, and degree of wear to those of FMNH PR 2232.

UA **10617** is a partial mandible broken off behind the level of the coronoid process (not figured). The preserved portion of the left mandibular ramus is 40 mm in length. The mandibular rami of this specimen are splayed laterally to a greater degree than in FMNH PR 3035, possibly due to postmortem dorsoventral flattening. The three lower incisors and canine are preserved with their crowns broken off on both sides of the jaw. Seven postcanine positions are present on both jaws, with crowns preserved for the left pc6–7 and the right pc3–4. The postcanine morphology of this specimen is extremely similar to that of FMNH PR 3035.

Phylogenetic Analysis

The new material of *Dadadon* described here permits a reinvestigation of its phylogenetic position within Traversodon-

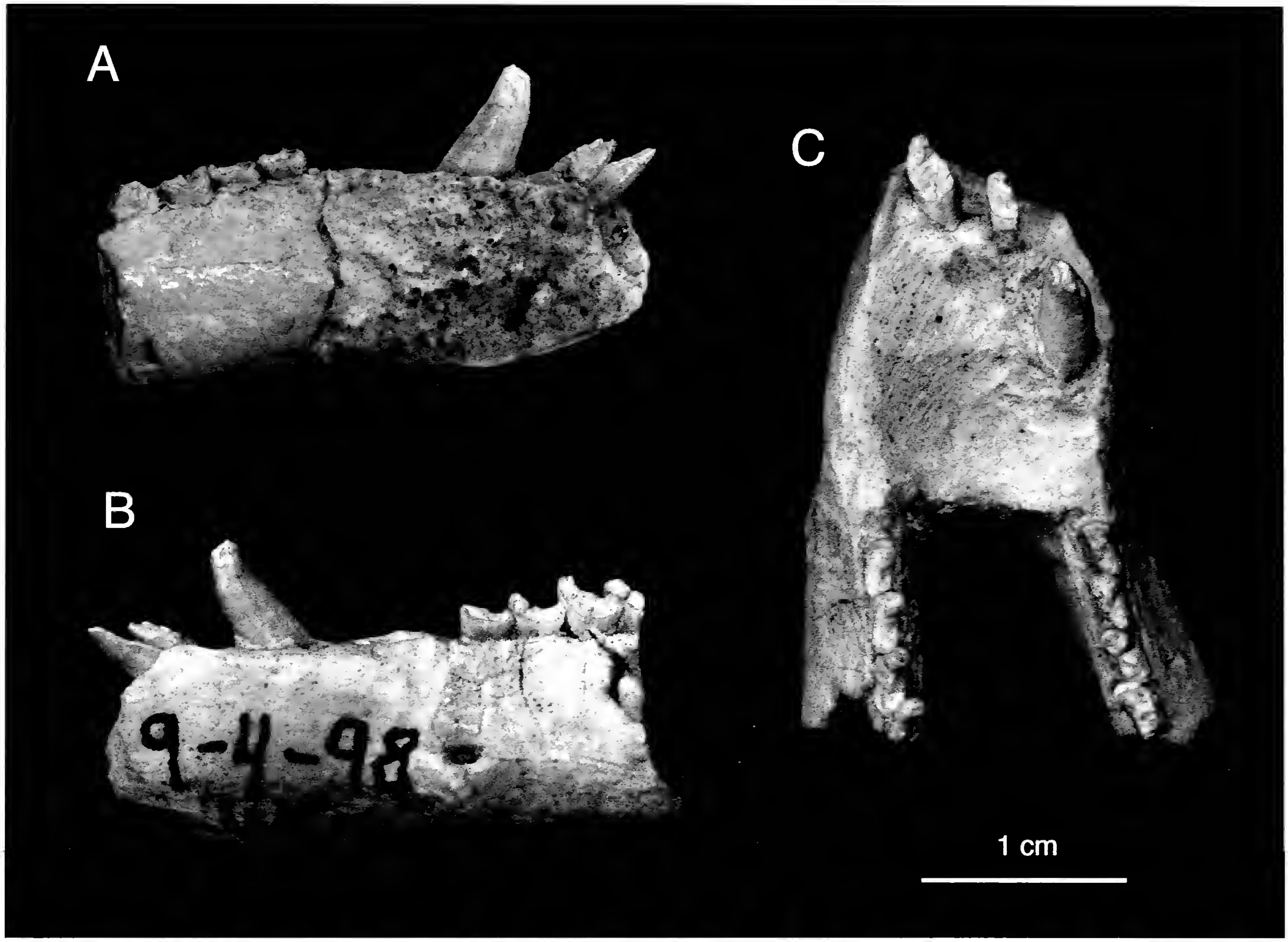

FIG. 7. FMNH PR 3036, a partial lower jaw of *Dadadon isaloi*, in (**A**) right lateral; (**B**) left lateral; and (**C**) occlusal views. Symphysis in this specimen is reconstructed; procumbent orientation of incisors may not have been present. Note that the postcanines in C are significantly narrower (relatively greater anteroposterior length relative to labiolingual width) than in larger specimens, e.g., FMNH PR 3038 (Fig. 10) (© American Museum of Natural History, 2012).

tidae. The position of *Dadadon* within "higher" traversodontids has fluctuated between analyses, with recovered positions including: sister-taxon of *Santacruzodon*, with this clade lying outside of (*Massetognathus* + Gomphodontosuchinae) (Abdala & Ribeiro, 2003); sister-taxon of (*Santacruzodon* + (*Massetognathus* + Gomphodontosuchinae)) (Abdala et al., 2006); unresolved polytomy with *Massetognathus* and *Santacruzodon* (Ranivoharimanana et al., 2011); and part of an unresolved polytomy with (*Massetognathus* + *Santacruzodon*) and Gomphodontosuchinae (Kammerer et al., 2008; Gao et al., 2010; Sues & Hopson, 2010, figure 12B). The unstable position of *Dadadon* has been due in part to missing data: until recently no lower jaw characters and few non-dental cranial characters could be coded for this taxon based on the literature. With the description of numerous new specimens, including well-preserved crania and lower jaws (Ranivoharimanana et al. [2011] and the present paper), *Dadadon* can be nearly completely coded in analyses addressing traversodontid interrelationships.

The current analysis (see Appendix I) expands on that of Ranivoharimanana et al. (2011), which was derived from previous analyses by Abdala and Ribeiro (2003), Abdala et al. (2006), and Kammerer et al. (2008). Additional characters from recent analyses of gomphodont relationships were added: characters 45–50 in the current analysis are characters 45–50 from Gao et al. (2010), who added new characters to the data set of Kammerer et al. (2008), and characters 51–57 are characters 29–31 and 33–36 from Sues and Hopson (2010). Taxa newly added to the data set include *Arctotraversodon plemmyridon*, *Boreogomphodon jeffersoni*, *Nanogomphodon wildi*, *Protuberum cabralense*, and *Scalenodon attridgei*. Codings for these taxa are based on personal examination of the material (except for *N. wildi*) by C.F.K. as well as information from Sues et al. (1992), Hopson and Sues (2006), Reichel et al. (2009), Liu and Sues (2010), and Sues and Hopson (2010). The supposed Chinese trirachodontids *Beishanodon* and *Sinognathus* (see Gao et al., 2010) have not been included in the current analysis, because the skulls of these taxa more closely resemble probainognathians than trirachodontids (C.F.K., pers. obs.), and their identification as gomphodonts must be tested in the larger context of eucynodont relationships, something beyond the scope of the current paper.

The phylogenetic analysis was run using TNT v1.1 (Goloboff et al., 2008) under the "Traditional Search" parameter and bootstrap resampling with 10,000 replicates. A single most-parsimonious tree of length 141 was recovered

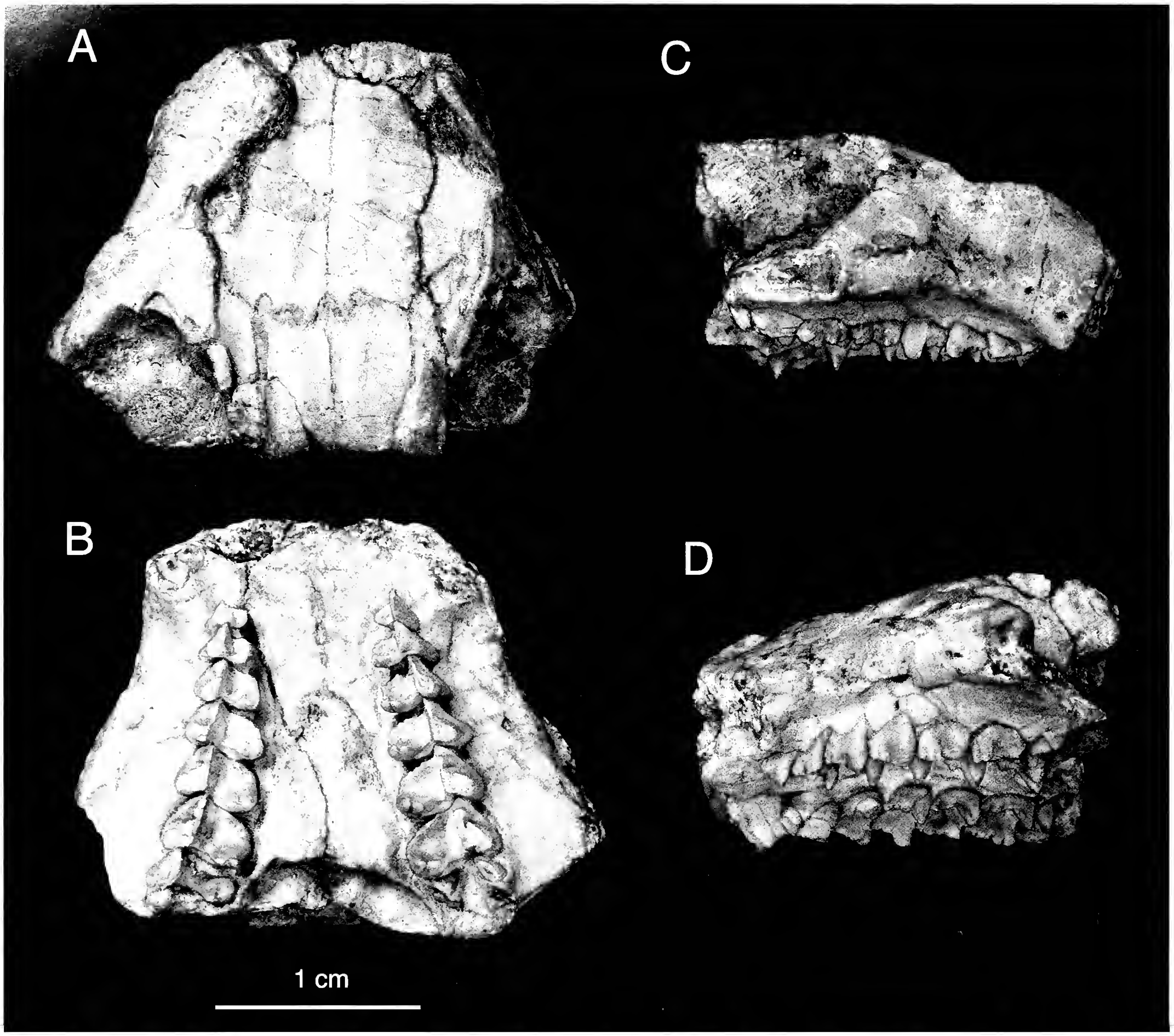

FIG. 8. FMNH PR 3037, a partial skull of *Dadadon isaloi*, in (**A**) dorsal; (**B**) palatal; (**C**) right lateral; and (**D**) left ventrolateral views. **D** is tilted slightly upwards to show labial morphology of left postcanine tooth row and lingual morphology of right postcanine tooth row. Note the presence of two anterior accessory labial cusps on the postcanine teeth; in larger individuals these cusps are heavily worn, giving the impression of a single cusp in this position (© American Museum of Natural History, 2012).

(consistency index = 0.526, retention index = 0.710) (Fig. 13). Monophyletic Trirachodontidae and Traversodontidae were recovered as sister-groups. The most basal clade of traversodontids contains (*Scalenodon angustifrons* + *Luangwa*). The next-diverging traversodontid clade is (*Traversodon* + (*Scalenodon attridgei* + *Scalenodon hirschsoni*)), successively followed by (*Andescynodon* + *Pascualgnathus*), (*Arctotraversodon* + (*Boreogomphodon* + *Nanogomphodon*)), (*Massetognathus* + (*Dadadon* + *Santacruzodon*)), and Gomphodontosuchinae. Of these clades, strong bootstrap support exists only for (*Massetognathus* + (*Dadadon* + *Santacruzodon*)) and Gomphodontosuchinae (Fig. 13). The recovery of *Protuberum* as a gomphodontosuchine is in agreement with the analysis of Reichel et al. (2009). The recovery of a clade containing the Laurasian traversodontids (*Arctotraversodon*, *Boreogomphodon*, and *Nanogomphodon*) is in agreement with the analysis of Sues and Hopson (2010), although the position of this group as the sister-taxon of the "*Massetognathus* group" + Gomphodontosuchinae is novel. Although *Andescynodon* and *Pascualgnathus* are recovered as sister-taxa as in all previous analyses of traversodontid interrelationships, the relatively late-diverging position of this clade (they usually form the most basal traversodontid group) is unusual. The Tanzanian traversodontids *Scalenodon hirschsoni* and *S. attridgei* are sister-taxa, but are not closely related to the type species *S. angustifrons*, instead they are recovered as the sister-group of *Traversodon*. Although the exact position of *Dadadon* relative to *Massetognathus* and *Santacruzodon* remains questionable (it is recovered as the sister-taxon of *Santacruzodon* here, but this pairing is weakly supported), the clade containing these three taxa is well supported and here formally recognized as Massetognathinae subfam. nov.

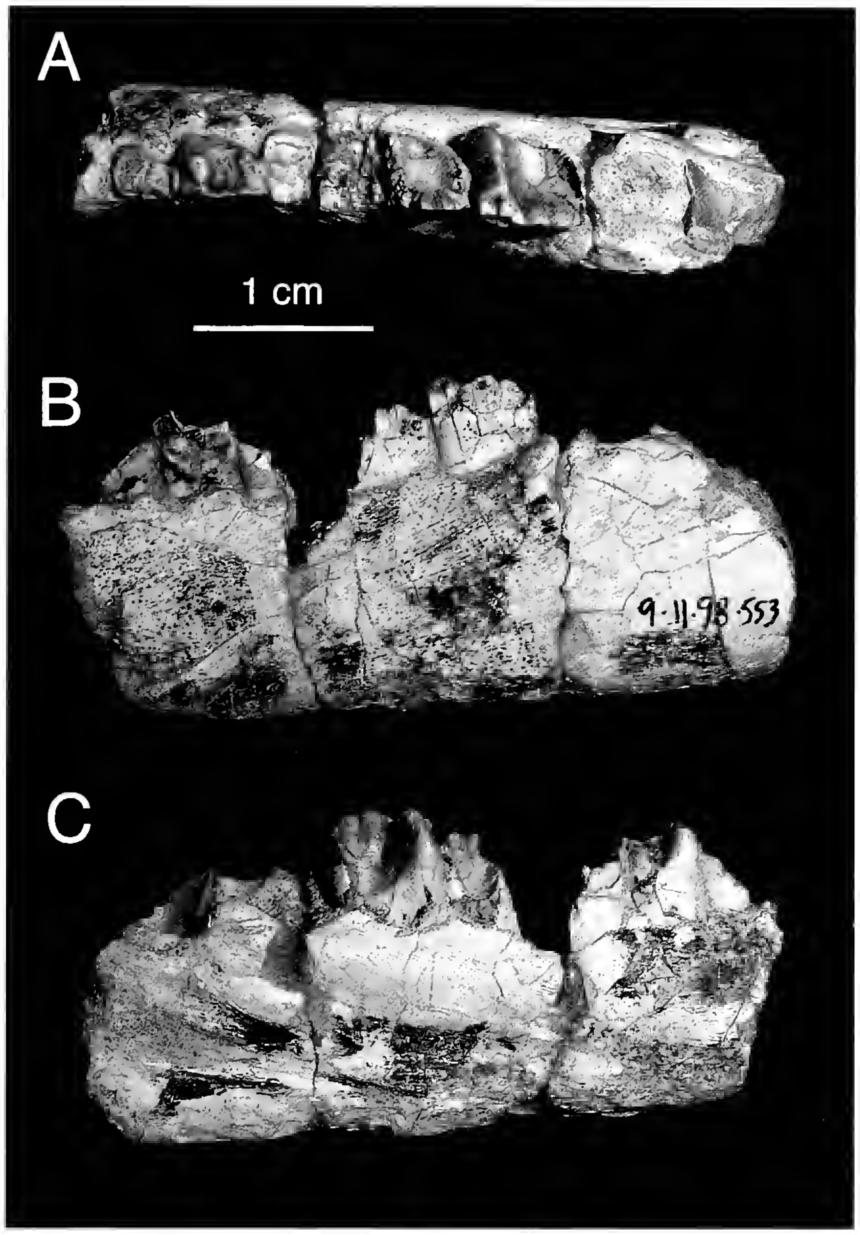

FIG. 9. UA 10612, a partial left dentary of *Dadadon isaloi*, in (**A**) occlusal; (**B**) left lateral; and (**C**) right medial views (© American Museum of Natural History, 2012).

Ontogenetic Changes in *Dadadon isaloi*

Among traversodontid taxa, extensive growth series have been described for *Massetognathus*, *Exaeretodon*, and *Andescynodon* (Abdala & Giannini, 2000; Abdala et al., 2002; Liu, 2007; Liu & Powell, 2009). A good growth series is also known for *Scalenodon angustifrons*, but thus far only the dental replacement pattern in these specimens has been described (Crompton, 1972). In several regards, *Dadadon* follows the usual pattern of traversodontid (and indeed, general therapsid) growth: larger specimens have relatively longer, narrower snouts, smaller orbits, and larger temporal fenestrae (Fig. 14). *Dadadon* is similar to *Massetognathus* in that larger specimens have higher postcanine counts (as opposed to *Exaeretodon* in which postcanine count decreases in larger specimens). The smallest *Dadadon* specimens described here (e.g., FMNH PR 3037) have 6 functional upper postcanines (with the seventh beginning to erupt) and the largest (e.g., FMNH PR 2232) have 10. In *Massetognathus*, by comparison, smaller individuals have 12 upper postcanines and the largest known specimen (the holotype of *Megagomphodon oligodens*) has 18 (although this may be aberrant, as several specimens of nearly equivalent size, such as MCZ 4138, have only 14 uppers) (Abdala & Giannini, 2000).

The size range of *Dadadon* specimens described herein elucidates the development of the unusual cranial ornamentation in this taxon. Although the autapomorphic frontal foramina are present in even the smallest specimens of *Dadadon* that preserve the skull roof, these specimens are otherwise similar to small specimens of *Massetognathus*, with a nearly flat, unornamented interorbital region. The interorbital depressions develop (as seen in UA 10615) prior to the midfrontal and frontal-postorbital ridges. This suggests that the concave appearance of the frontals in *Dadadon* is homologous with the interorbital depressions in other traversodontids, and is not just a side effect of the prominent interorbital ridges. It is the combination of these two growth features of *Dadadon* (raising of the interorbital sutures and depression of the main face of the frontal) that contribute to the great depth of interorbital depressions in this taxon. The prefrontal depressions are a separate and late-appearing concavity observed only in large specimens of *Dadadon*.

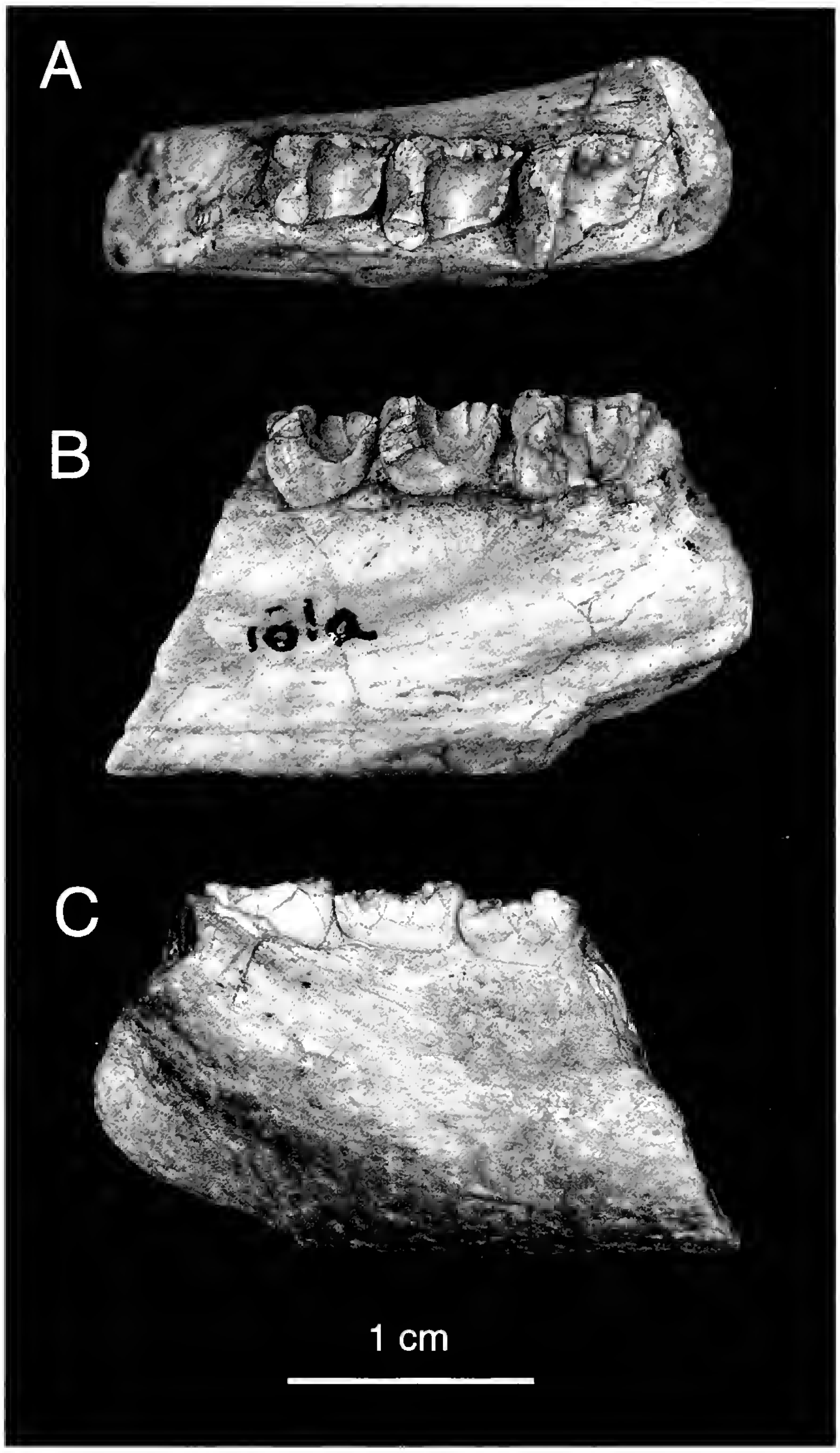

FIG. 10. FMNH PR 3038, a partial right dentary of *Dadadon isaloi*, in (**A**) occlusal; (**B**) left medial; and (**C**) right lateral views (© American Museum of Natural History, 2012).

Postcanine wear in *Dadadon* varies with size. In all upper postcanines, wear occurs on the internal side of a cusp (i.e., the labial side of the lingual cusp and lingual side of the labial cusp). However, in the smallest specimens (e.g., FMNH PR 3037), wear is greatest on the labial cusp, whereas in larger specimens it is greatest on the lingual cusp. In the lower postcanines of small specimens, the labial side of the postcanine is so badly worn as to obliterate the labial cusps

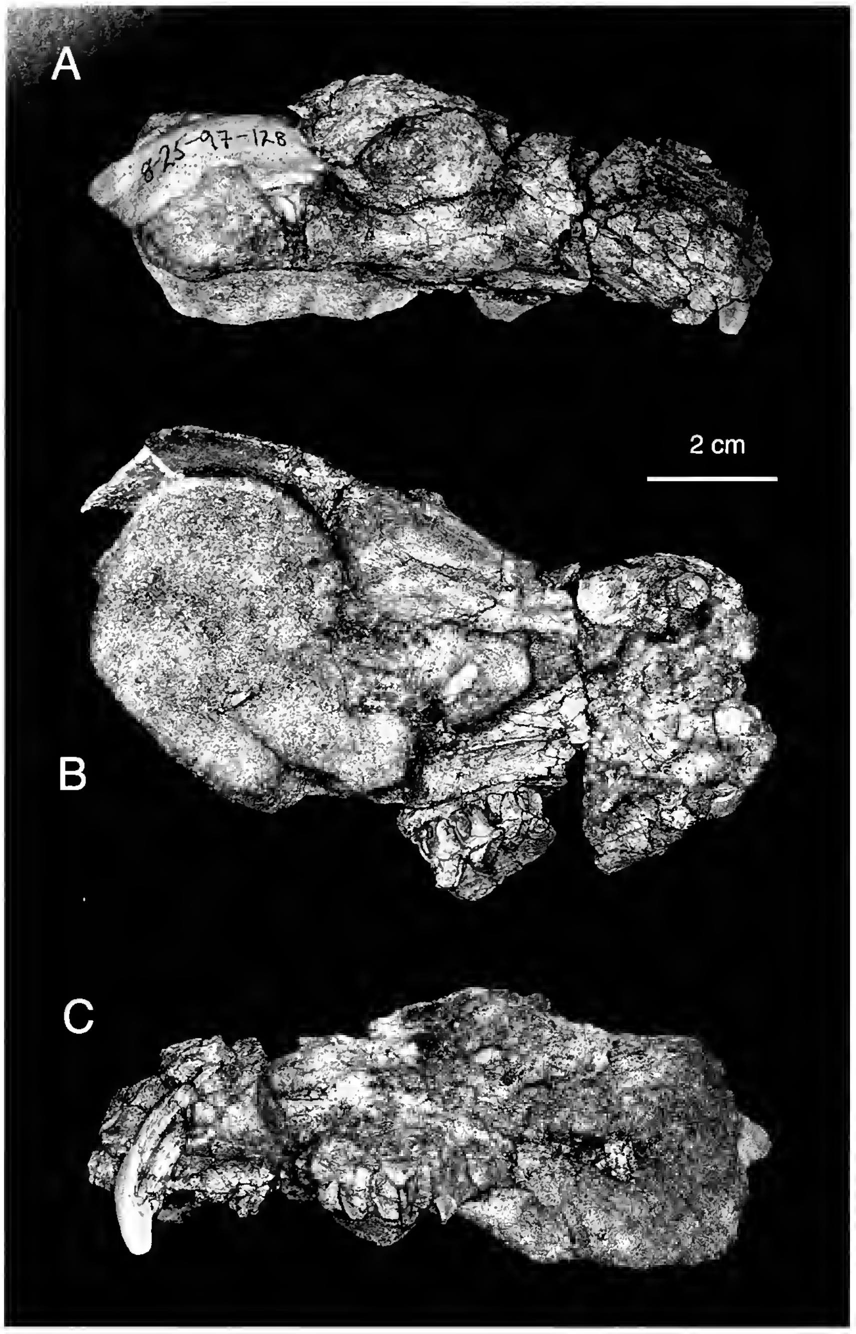

FIG. 11. FMNH PR 3034, a fragmentary skull of *Dadadon isaloi*, in (**A**) right lateral; (**B**) palatal (anterior is right); and (**C**) left lateral views. The dorsal surface of this skull is too poorly preserved to show any meaningful morphology (© American Museum of Natural History, 2012).

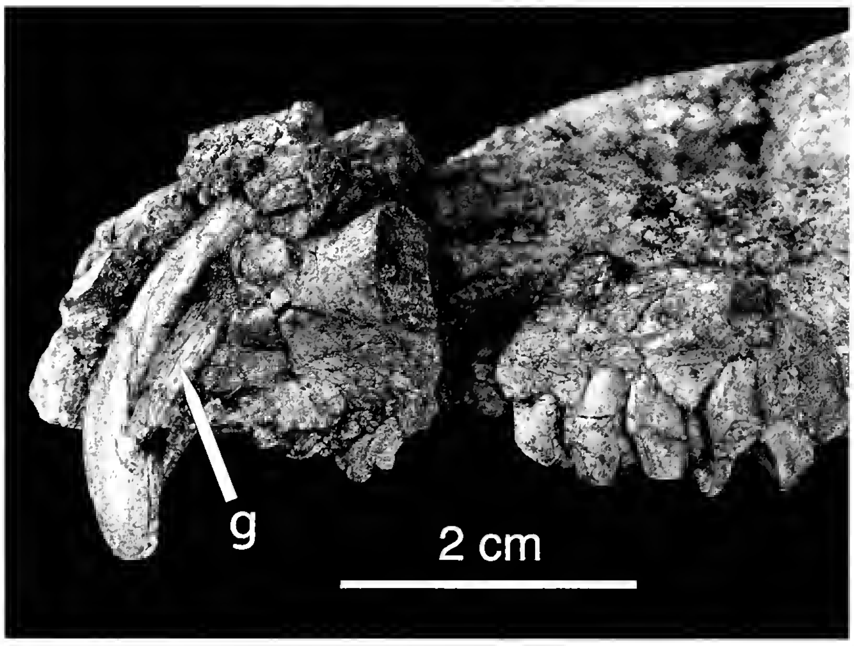

FIG. 12. Close-up of left tooth row of FMNH PR 3034 in lateral view, to illustrate midline groove (**g**) on left canine (indicated by arrow). (© American Museum of Natural History, 2012)

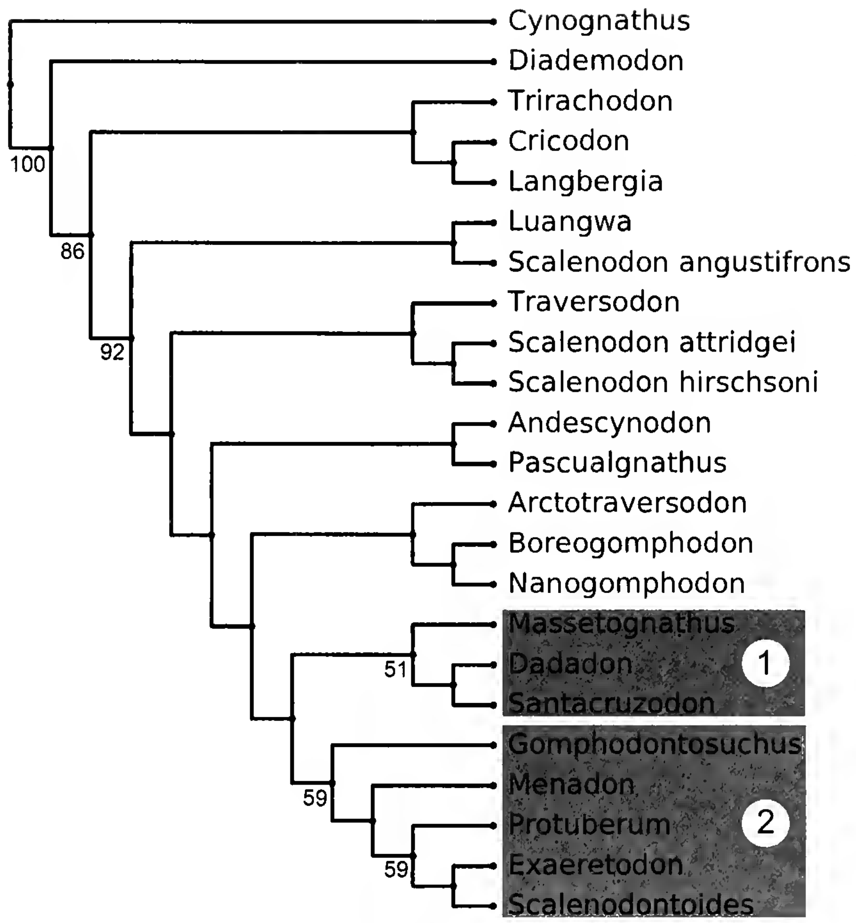

FIG. 13. Cladogram of traversodontid relationships derived from the current analysis. Numbers at nodes represent bootstrap values. The numbered clades are **1**, Massetognathinae and **2**, Gomphodontosuchinae.

completely, resulting in what is functionally half a tooth. In larger specimens the main labial cusp is present even when the tooth is badly worn. These changes in wear pattern can be attributed to changes in postcanine proportions during growth: In the smallest specimens the postcanines are anteroposteriorly elongate, twice as long as wide, whereas in larger specimens the postcanines become nearly as wide as long, with proportionally wider cusps occluding in slightly different positions than in the smaller teeth. The elongate anterior postcanines appear to have

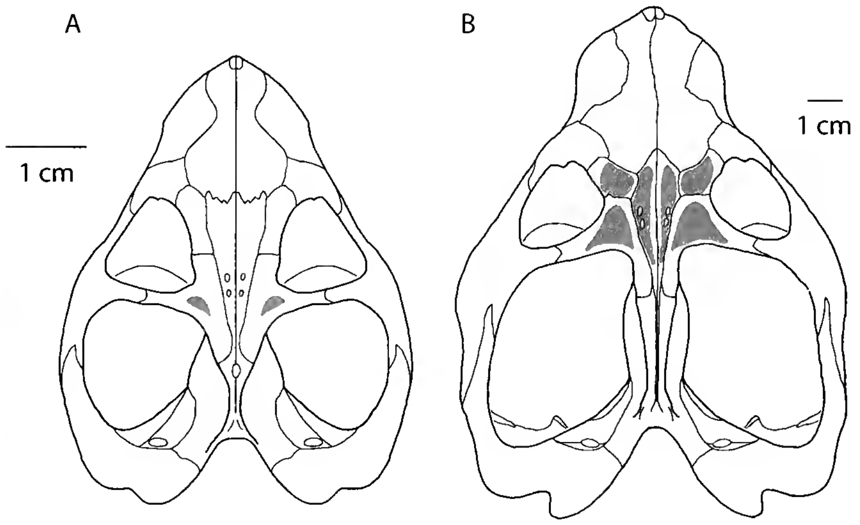

FIG. 14. Ontogenetic differences between (**A**) presumed juvenile and (**B**) adult individuals of *Dadadon isaloi*. Dark gray areas represent depressed portions of the interorbital region (prefrontal, frontal, and postorbital). Small postorbital depressions are present in juveniles, and this area enlarges with the expansion of the adductor musculature (indicated by the relatively larger temporal fenestrae at larger size). Interorbital depressions are present in specimens of intermediate size between those figured here (see Fig. 2) but become extremely deep in adults. Prefrontal depressions are only present in adults. Reconstruction of (**A**) based primarily on FMNH PR 3037 and UA 101615; reconstruction of (**B**) based on FMNH PR 2232 (modified from Ranivoharimanana et al., 2011). (© American Museum of Natural History, 2012).

been lost in larger specimens, and are replaced by wider postcanines from a posterior position in the tooth row.

Conclusions

The new craniodental material of *Dadadon isaloi* described here expands our knowledge of this taxon's morphology, including the first non-dental autapomorphies for this taxon. Although *Dadadon* has been a phylogenetically volatile taxon in the past because of missing data, it is now one of the most completely known traversodontids cranially and is well supported as a member of a clade including *Massetognathus* and *Santacruzodon*, here named Massetognathinae. This clade has a circum-Gondwanan distribution, with members known from South America and Madagascar (but not, as of yet, from mainland Africa).

Some of the smaller specimens described here were initially considered to represent a third taxon of traversodontid in the basal "Isalo II" beds (Flynn et al., 1999; Goswami et al., 2005). However, examination of the full range of non-*Menadon* traversodontid specimens from these localities reveals that the differences in postcanine morphology and cranial ornamentation between the small and large specimens grade into one another with size, and are best interpreted as ontogenetic variation. As such, we recognize only two species of traversodontid in this fauna (the gomphodontosuchine *Menadon besairiei* and the massetognathine *Dadadon isaloi*).

Denticles on the keeled edges of the incisors evolved at least two times in traversodontid history: in Massetognathinae and the Laurasian traversodontid *Arctotraversodon*. Leaf-shaped, roughly denticulated teeth are usually associated with slicing vegetation in tetrapods (Throckmorton, 1976). Massetognathines coexisted with gomphodontosuchine traversodontids, a group characterized by enlarged, procumbent incisors. Additionally, massetognathines had relatively smaller, less robust postcanines than gomphodontosuchines. The difference in dental morphology between these confaunal traversodontids suggests that different feeding strategies were being employed, possibly indicating niche partitioning. Goswami et al. (2005) suggested that niche partitioning would have been present between herbivores in this fauna; they analyzed postcanine microwear in *Dadadon* and the confaunal archosauromorph *Azendohsaurus* and concluded that *Dadadon* was consuming more resistant plant matter. The dentition of *Menadon* was not analyzed in that study, but its dental morphology (massive postcanines and grasping incisors) suggests that it may have been more of a rooter compared with the browsing/grazing *Dadadon*. Future research is necessary to support this hypothesis, such as determining whether the postcanines of *Menadon* exhibit pitting consistent with a diet of roots, seeds, or fruit.

In their review of alleged Triassic ornithischians, Irmis et al. (2007, p. 7) referred a number of taxa based on isolated teeth to Archosauriformes *incertae sedis*, because that group was thought to contain the "only Mesozoic vertebrates with teeth with sub-triangular crowns, enlarged denticles, and thecodont tooth implantation." Here we have demonstrated that this dental morphology is also typical of the incisors of certain traversodontid cynodonts (Figs. 4E, 7A), and as such, on a strict apomorphy basis for identification, the Triassic tooth taxa in question can only be assigned to Amniota *incertae sedis*. There are similarities in certain features between the incisors of *Dadadon isaloi* in particular and several tooth taxa from the Late Triassic of western North America: the lower incisors of *Dadadon* are similar to the teeth of *Tecovasaurus murryi* in having denticulation restricted to the lower half of one side, and the fourth upper incisor of *Dadadon* is similar to the teeth of *Lucianosaurus wildi* in having a single accessory cusp on an otherwise triangular tooth. This noted, based on dissimilarities in gross morphology and geographic separation, we consider it unlikely that any of the North American Triassic taxa reviewed by Irmis et al. (2007) represent traversodontid incisors; these taxa probably are indeed archosauriforms. However, we recommend that possible cynodont identification always be considered when dealing with isolated, "leaf-shaped" amniote teeth from the Triassic (especially in eastern North American basins, where traversodontids with denticulated incisors [e.g., *Arctotraversodon plemmyridon*] are known to be present).

Acknowledgments

We are delighted to include this contribution in a volume celebrating the life and research of John Bolt. We remain grateful for our collaboration with the Département de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo, Madagascar, the National Geographic Society for their extensive support of the fieldwork associated with this project, and support provided by our home institutions, The Field Museum, and the WWF (World Wide Fund for Nature, Madagascar). We thank Lorraine Meeker for photographing the specimens described herein and preparing the figures for publication.

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Appendix I

Data matrix used in the phylogenetic analysis. A =(0,1). B=(0,2).

Cynognathus	0000000? 0???? 0? 00???? 000000000000000000?? 00? 00000000000000
Diademodon	0000001000 0? 00? 0100? 000010A000000000001000100001001 0000000
Trirachodon	000000100B1A00? 2201? 001A10001000010012000110001000000000 0
Langbergia	00000010001000? 0201? 00001010100001101200011010000000000000
Cricodon	01000010001100? 0201? 001?? 010? 0? 0?? 0012000110 00??? 00000000
Andescynodon	0000002001 0? 10? 1310110112 0? 010??? 01123111100?????? 0000000
Massetognathus	0011112 1A21110003100201120001110112123001100101100001 0001

Exaeretodon	11101221120?101031012111110201111111231111011110000011111
Luangwa	000000100211010A3100101010010??0?100230011000?????0011110
Scalenodon angustifrons	000000100B11110231001010210?1??0?00023011100??????0011100
Scalenodon hirschsoni	1111?020?21100113100101??????01???1123001100??????0010000
Traversodon	0000002012110111310020101?0????0??1123?01100??????0011110
Gomphodontosuchus	01111121120?10?13101201???0????0??1123111100??????00111?0
Pascualgnathus	10000010000?0?0231????1100001??0?01123?011001?????0000000
Scalenodontoides	111??221?20?10?031012111?1021??1?21?23111101??????0011?11
Menadon	01111121120?1011310?201?210201?0??10231111011?????0011111
Dadadon	001111211211110031012011300?11101121230011001?????0010001
Santacruzodon	000??121121110003101201?3?00?????121230011001110110010001
Scalenodon attridgei	1000?02112110011??????1??????0?0??11?3?111?011?000??10???
Boreogomphodon	0000002002111001311100112002 1?1012012210110011?1011110000
Arctotraversodon	?1??0?2?0211100131112?????????????2????011?0??????111?0?0
Nanogomphodon	??????2?????????31110?????????????????1?11???????????????
Protuberum	1111?220120?0012?????11011??10?1?11?23?11101111?01??11?11

Chapter 11: The Role of Foraging Mode in the Origin of Therapsids: Implications for the Origin of Mammalian Endothermy

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Abstract

The question of the adaptive basis for the origin of mammalian endothermy remains unresolved despite a great deal of research effort. Controversy continues over which physiological adaptations were of greatest importance in starting ectothermic nonmammalian synapsids of the Late Paleozoic on the path that culminated in modern endothermic mammals. Models of the selective basis for the origin of endothermy fall into two main categories: "thermoregulation first" and "aerobic capacity first." Studies of lizards show a dichotomy between a low-energy "sit-and-wait" (SW) foraging mode in Iguania and a more energy-intensive "widely foraging" (WF) mode in Autarchoglossa. It is proposed that in the transition from basal synapsids ("pelycosaurs") to therapsids, a shift from the primitive SW mode to the WF mode put the ancestors of mammals on the path to increased aerobic capacity and the ability to sustain high levels of foraging activity. Selection for increased energy expenditure disproportionately increased the amount of food energy consumed, thus improving foraging efficiency. A shift from reliance on anaerobic muscle metabolism for short but rapid dashes to capture prey to a reliance on aerobic metabolism for active searching for prey necessitated improvements of the cardiovascular system and lungs for increased aerobic capacity and greater stamina. Over time, therapsids became locked into high food requirements, which selected for improvements in aerobic metabolism, locomotor and food-processing ability, and neurosensory/behavioral specializations. Evidence of a link between maximum activity metabolism and resting (basal) metabolism in anurans and rodents suggests that further increases in aerobic activity metabolism required an increased basal metabolic rate, which led to high body temperatures and, ultimately, homeothermy. Therapsids show adaptations for increased activity, greater food-getting and food-processing ability, and higher metabolic rates than basal synapsids ("pelycosaurs"). It is argued that the "foraging mode" model is preferable to the "parental care" model of Farmer and the "correlated progression" model of Kemp for understanding the origin of mammalian endothermy.

Introduction

A clear distinction can be drawn between mammals and birds on the one hand and all other vertebrates on the other in that the former are endotherms, capable of maintaining a high and constant body temperature by metabolic heat production, even under resting conditions (Bennett & Ruben, 1979), whereas the remaining vertebrates (nonavian reptiles, amphibians, and fishes) are ectotherms, in which metabolic rates are too low to raise body temperature by a significant amount. Ectotherms must rely on external sources of heat (such as solar radiation or a warm substrate) to raise body temperatures to optimum levels for activity. Although some primarily ectothermic vertebrates, such as tunas and brooding female pythons, are able to sustain high body temperatures by means of intense muscle activity, the endothermy of mammals and birds is unique in that metabolic heat is produced while at rest mainly by visceral organs and, to a modest extent, the brain rather than by muscles (Bennett, 1991; Hayes & Garland, 1995; Ruben, 1995).

Living endotherms also differ from living ectotherms in relying primarily on aerobic metabolism both to sustain high body temperatures and to fuel their high levels of activity. Ectotherms have low levels of aerobic metabolism and rely on anaerobic metabolism when intense activity, such as high-speed locomotion to capture a prey item or to escape a predator, is required. The habitually elevated metabolic rates of endotherms confer on them the ability to maintain a high degree of independence from environmental temperatures. As a result, mammals and birds have been able to occupy most terrestrial and many aquatic habitats on the planet, from the polar regions to the tropics. However, these abilities come at a great energetic cost. When energy expenditures at both resting and maximal levels are compared between endotherms and ectotherms, those of endotherms are about five- to tenfold higher, with perhaps 80 to 90 percent of total energy intake going to maintenance of a high resting body temperature (Bennett & Ruben, 1979). This energetic cost would be much higher if endotherms had not evolved surface insulation (hair, feathers) that lowers their thermal conductance and prevents rapid dissipation of body heat.

Ectotherms have preferred body temperatures very similar to those of endotherms, but they maintain these temperatures through behavioral rather than metabolic means. Their lack of external insulation permits rapid exchange of heat with the external environment. The energy savings conferred by low metabolic rates can, for example, be directed toward increased reproductive output and permit survival in resource-poor environments (see Pough, 1980). However, the low energy output of ectotherms has a significant negative consequence: it limits intense activity to short bursts that cannot be sustained aerobically. However, by using anaerobic metabolism, ectothermic lizards are able to match maximal running speeds of similar-sized mammals (Bennett & Ruben, 1979, p. 653; Garland, 1982), although, in the absence of the high aerobic capacity characteristic of mammals, they lack the stamina to sustain such speeds (or other vigorous activities) for more than a few minutes. This is because anaerobic glycolysis, which uses muscle glycogen as fuel, is only about one-tenth as efficient as aerobic muscle metabolism (and generates much less heat). Furthermore, its metabolic product, lactic acid, is associated with rapid exhaustion, with restoration to the preactivity physiological state (using aerobic metabolism) taking a long time, sometimes hours (Bennett & Ruben, 1979; Bennett, 1980).

How mammals and, to a lesser extent, birds evolved an endothermic physiology from ectothermic ancestors is controversial. Bennett and Ruben (1979: 649) note that "the selective factors influencing its evolution have been substantial and highly significant," but "there is no general agreement among vertebrate biologists as to what those selective factors were or what the sequence of events culminating in endothermy was." Hayes and Garland (1995) and Kemp (2006b) have reviewed the hypotheses on what traits were selected for in the origin of endothermy. These hypotheses fall into two main categories: those that emphasize the advantages of homeothermy, that is, the ability to maintain a constant high internal temperature regardless of environmental temperature, and those that emphasize the augmentation of aerobic capacity to increase sustainable levels of high activity (see Bennett & Ruben, 1979).

Related to the distinction between the low metabolic and activity levels of ectotherms and the high metabolic and activity levels of endotherms is the behavioral distinction between an ancestral foraging mode that relies on intermittent short bursts of activity for prey capture and a derived foraging mode that relies on more continuous movement to seek out widely distributed prey. The former is characterized as "sit-and-wait" (SW) predation and the latter as "widely foraging" (WF) predation (Huey & Pianka, 1981). There is a large literature on the morphological, physiological, and behavioral differences between these two foraging modes, especially in lizards (Huey & Pianka, 1981; Reilly et al., 2007) and, to a lesser extent, in anurans (Toft, 1980; Taigen, 1983; Taigen & Pough, 1983; Walton, 1993) and snakes (Beaupres & Montgomery, 2007). The purpose of this paper is to demonstrate the relevance of foraging mode for hypotheses on the origin of endothermy in mammals. I previously expressed this thesis in abbreviated and less developed form in an abstract (Hopson, 1987) and a short review of the origin of mammals (Hopson, 2001, p. 91).

The thesis of the present paper is that an evolutionary shift in foraging mode from that of an ancestral SW ambush predator to a descendant WF predator also led to a shift from an ancestor specialized for a very fast but relatively short dash fueled by anaerobic muscle metabolism to a descendant specialized for sustained activity fueled by aerobic muscle metabolism. A shift in foraging mode from basal synapsids to therapsids is hypothesized to be the critical factor that put the ancestors of mammals on the path to morphological, physiological, and neurological/behavioral specializations that led to an increased aerobic capacity and the ability to achieve and sustain high levels of activity. This foraging shift led to the very high levels of metabolic activity and, eventually, the maintenance of a constant high body temperature in the resting animal that are the hallmarks of true endothermy. Thus, the first steps toward an endothermic physiology were initiated by a behavioral shift to a more active food-getting mode in which a premium was placed on increased locomotor stamina. The acquisition of a stable high aerobic resting metabolism and enhanced thermoregulatory ability (i.e., homeothermy)—and all of the advantages that accrue to them—occurred later. As noted below, however, the linkage between increased activity metabolism and increased resting (basal) metabolism, whether physiological or otherwise, remains uncertain and controversial. As this linkage is an essential part of the aerobic capacity model of the origin of endothermy (Bennett & Ruben, 1979), I shall discuss the evidence for and against it later in this paper.

The point in the history of synapsids at which the shift in foraging mode and, I believe, a coincident shift toward a more aerobic activity metabolism is most likely to have occurred is during the transition between basal synapsids, informally termed "pelycosaurs" of the Late Pennsylvanian and Early Permian and the earliest therapsids of the Middle Permian (see Kemp, 2006a). Unfortunately, intermediate fossils representing this transition are not known with confidence from the geologic record (see Laurin & Reisz, 1996; Conrad & Sidor, 2001; Amson & Laurin, 2011).

In the next section, I shall comment briefly on earlier hypotheses on the origin of endothermy. Then I shall review the literature on foraging mode in lizards and the morphological, physiological, and behavioral changes that characterize each mode. As the distinction between major clades of lizards is relevant to the distribution of foraging types, I shall discuss phylogenetic aspects of squamate foraging mode. Special attention will be devoted to varanids, which are the most specialized of the WF lizards and are those that show the greatest modifications in a mammal-like direction. I shall then compare the morphological features characteristic of both SW and WF lizards with features of basal synapsids ("pelycosaurs") and early therapsids. Finally, I shall discuss the evidence supporting a physiological link between maximum activity metabolism and resting (basal) metabolism (which is an essential but controversial part of the Bennett and Ruben "aerobic capacity" model) and compare the relative merits of the foraging mode model presented in this paper to the "parental care" hypothesis of Farmer (2000, 2003) and the "correlated progression" model of Kemp (2006a,b, 2007a,b) in providing the most useful framework for understanding the origin of mammalian endothermy.

Previous Hypotheses on the Origin of Endothermy

Much disagreement exists concerning "what is hypothesized to have been the initial selective pressure promoting the evolutionary progress toward endothermy" (Kemp, 2006b: 475). Kemp notes that the proposed hypotheses fall into two categories: "the 'thermoregulation first' and the 'aerobic capacity first' views." Hayes and Garland (1995) list and discuss six models for "the selective origins of endothermy" and briefly critique them. All but one of these models emphasize selection for increased resting metabolic rate (RMR), which is hypothesized to (1) permit expansion of thermal niche, (2) increase metabolic efficiency, (3) shift inertial homeothermy to metabolism-based homeothermy as body size decreased in the evolution of therapsids, (4) provide a metabolic basis for increasing muscle tonus required for the acquisition of an erect stance, and (5) follow from selection for brain size increase, which would require a more active metabolism to support it. The exceptional model (6) is that of Bennett and Ruben (1979), which proposes that selection for sustainable activity based on an increase in aerobic metabolic rate was responsible for the subsequent elevation of RMR and the origin of mammalian endothermy. A similar view had previously been advanced by Gans and Dawson (1976).

Kemp (2006b) has reviewed several of the same hypotheses, plus more recently published ideas of Farmer (2000, 2003) and Koteja (2000). Farmer (2000, 2003) proposes that selection initially acted to increase RMR or basal metabolic rate (BMR; "thermoregulation first") to increase parental ability to maintain a high incubation temperature for developing young; only later was there selection for an increase in aerobic capacity to enhance the collection of food for the growing offspring. Koteja (2000), like Bennett and Ruben (1979), emphasizes an initial selection pressure for increased aerobic locomotor capacity, here to enhance parental provisioning of the young with food, eventually including maternal milk ("aerobic capacity first"); this leads to increase in metabolic activity of the viscera for processing the increased parental food intake and hence the subsequent development of high RMRs (i.e., homeothermy). These proposed links of increased RMR or BMR with the provision of heat and nourishment to developing young will be discussed in greater detail below.

In a recent series of papers, Kemp (2006a,b, 2007a,b) has proposed that the origin of mammalian endothermy resulted from a "correlated progression" of character evolution leading to higher levels of metabolic activity and homeostatic regulation. Although he does not explicitly state whether thermoregulation or increased aerobic activity was the primary function selected for in the origin of mammalian endothermy, he continues to support his earlier view (Kemp, 1982, 1985) that "the overarching attribute manifested in the origin of the mammals is increasing homeostatic ability: the maintenance of a constant internal environment in the face of a fluctuating external environment, by means of high-energy regulatory processes" (Kemp, 2007b: 18). I would categorize this as a preference for the "thermoregulation first" model.

Hypotheses proposing the development of metabolic homeothermy as the primary selective factor in the initiation of mammalian endothermy usually do not, in my opinion, provide a convincing selective advantage for the initial enhancement of body temperature. Bennett and Ruben (1979: 649–650) point out that "arguments for the evolution of endothermy based on thermoregulatory considerations alone tend to be ad hoc rather than a uniform explanation equally applicable to all groups." Hayes and Garland (1995: 837) argue that small increases in RMR would not enable animals to increase body temperature significantly above that of the environment, but they would nonetheless incur the cost of increased food intake, which would "outweigh any benefits to be gained, *at least in the early stages*" (emphasis added). For this reason, I do not support hypotheses that emphasize an increase in metabolic rate to increase body temperature, nor do I accept the ability to thermoregulate as the *primary* reason for the initiation of mammalian (or avian) endothermy. Rather, I believe that increased aerobic activity and consequent increase in food intake must precede significant increase in resting metabolism. Following Bennett and Ruben (1979), I believe that aerobically mediated metabolic rates and associated supporting changes (e.g., increase in pulmonary/cardiovascular function and in mitochondrial activity) were initially selected for to increase locomotor stamina. Enhancement of RMRs followed as a necessary consequence of providing the physiological basis for supporting greatly increased activity metabolic rates. However, once resting or basal rates reached a level where they yielded enough internally generated heat to sustain high resting body temperatures, then selection acted to expand thermal niches and increase thermal stability and metabolic (including digestive) efficiency and eventually facilitated a great increase in brain size, attainment of fully upright posture, and the capacity to incubate eggs using internally generated heat. At this stage, a premium would have been put on the evolution of effective surface insulation, which would have greatly decreased the metabolic cost of maintaining a high body temperature.

A major problem with the hypothesis that a metabolic linkage exists between maximal levels of oxygen consumption during activity and resting metabolic levels is that support for such a linkage is equivocal. The "aerobic capacity" hypothesis of Bennett and Ruben (1979) supposes that a correlation does exist in both ectotherms and endotherms, but, as Hayes and Garland (1995: 843) note, "the idea that resting and maximal aerobic metabolic rates have evolved in a positively correlated fashion" has mixed support from interspecific comparisons. For example, Koteja (1987) found no correlation between residual RMR and maximum rate of oxygen consumption during exercise for 18 species of mammals, though Hayes and Garland (1995) and Bozinovic (1992) suggest that using literature data that were collected by different methods may create problems. Furthermore, though increase in oxygen consumption during activity in WF lizards may be twice that of sedentary lizards, RMRs are similar in both groups (Bennett, 1972).

On the other hand, a significant positive rank correlation between resting and exercise rates of oxygen consumption has been reported in anurans by Taigen (1983), Taigen and Pough (1983), and Walton (1993), and in rodents by Hinds and Rice-Warner (1992) and Bozinovic (1992). In the Taigen and Walton studies of anurans and in both of the rodent studies, the authors state that this correlation supports the aerobic capacity model for the origin of endothermy. Also, in an experiment in which BMR and aerobic capacity during swimming exercise (AC_S) and cold exposure (AC_C) were measured in bank voles (*Clethrionomys glareolus*), Sadowska et al. (2005) found that mass-independent BMR is genetically highly correlated with AC_S and not at all correlated with AC_C. These authors conclude that selection for increased thermogenic capacity in voles "would not result in increased BMR," whereas "selection for increased exercise-related aerobic capacity should result in increased BMR." Thus, evolution of extensive aerobic locomotor activity "could indeed trigger the evolution of endothermy, as proposed by the aerobic capacity model" (Sadowska et al., 2005: 679).

Discussion of the correlation or lack of correlation between resting (basal) and maximal rates of oxygen consumption and its relevance for the aerobic capacity model and other models (e.g., the "parental care" model of Farmer [2000, 2003] and the "correlated progression" model of Kemp [2006a,b,

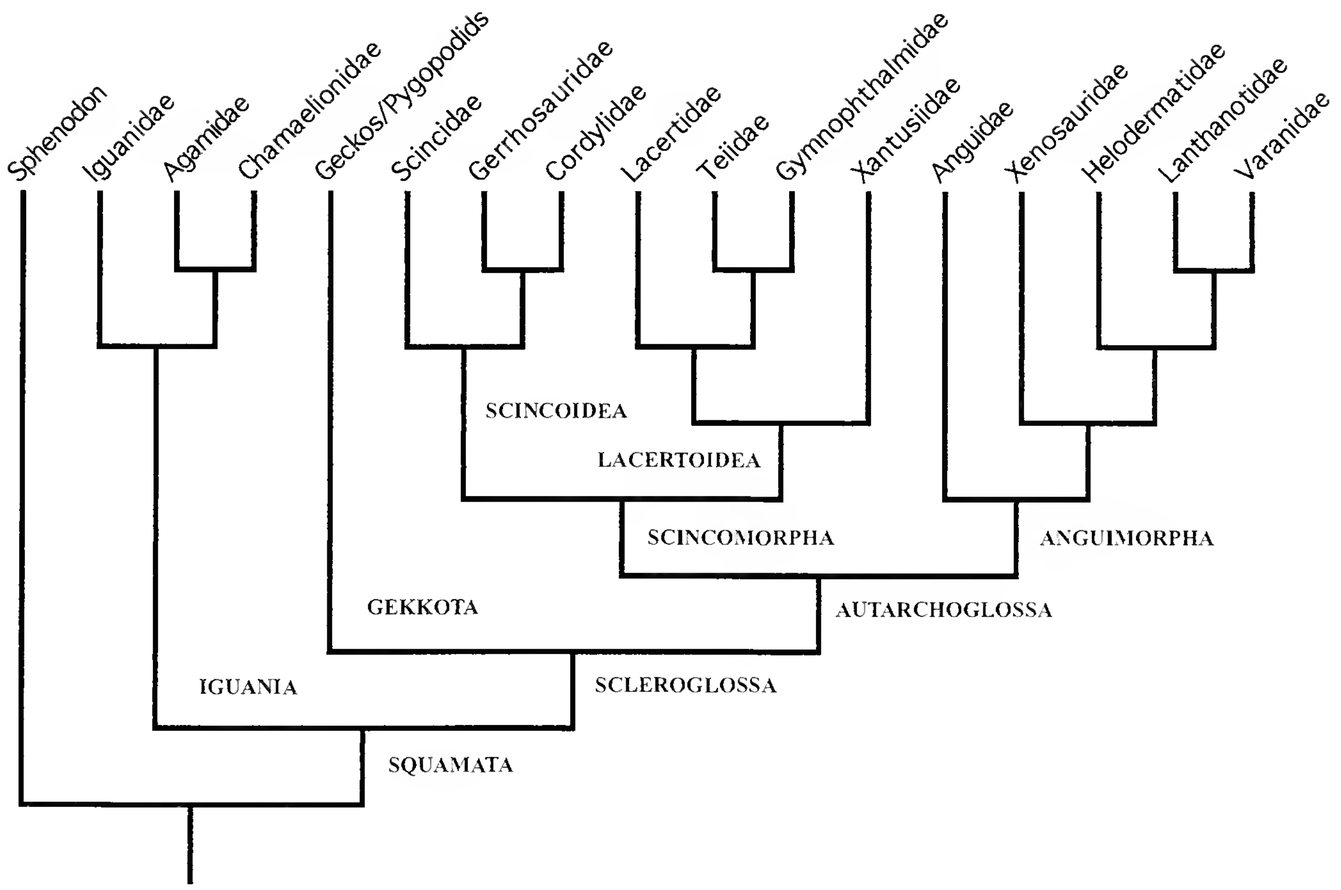

FIG. 1. Cladogram of lizard relationships (modified from Pianka & Vitt, 2003). *Sphenodon* is the living out-group of squamates. Most limbless groups of squamates (e.g., snakes and amphisbaenians) are omitted.

2007a,b]) for the origin of mammalian endothermy will be taken up again in the final section of this paper.

Foraging Behavior in Lizards and Its Morphological, Physiological, and Behavioral Correlates

Living Squamata (lizards and snakes) are divided into two great subgroups, Iguania and Scleroglossa, with the latter group further divided into Gekkota and Autarchoglossa (Fig. 1). Iguanians (iguanids, agamids, and chameleons) are almost exclusively SW predators, and autarchoglossans (a diverse assemblage that includes, among other groups, lacertids, teiids, skinks, gerrhosaurs, anguids, varanids, and snakes) tend to be active, WF predators though with some reversals to the more sedentary SW mode (cordylids, some scincids and lacertids, and many snakes). Gekkotans (geckos and pygopodids) are usually intermediate in specialization of foraging mode, being more active than iguanians but less so than autarchoglossans.

Table 1 (modified from Pianka & Vitt, 2003, fig. 3.2) shows contrasting biological attributes of Iguania and Autarchoglossa in relation to foraging mode and physiological, behavioral, and neurological differences that appear to be consequences of foraging mode. Gekkotans, which are intermediate in foraging mode between iguanians and autarchoglossans, are omitted. According to Pianka and Vitt (2003, p. 52), iguanians, as SW foragers (except for the herbivorous iguanines), feed on mobile prey that they detect visually. Scleroglossans, notably autarchoglossans, as more active foragers, rely on both vision and keen chemosensory systems so that they are able to locate and feed on both mobile and nonmobile, often hidden prey. These differences in foraging mode have had a profound effect on the directions of evolution of the two major squamate clades, influencing other important aspects of their biology (not all of which have been listed in Table 1). There is a large phylogenetic component to these differences, with iguanians more closely resembling the living out-group of squamates, *Sphenodon*, and therefore possessing more ancestral squamate traits in addition to iguanian specializations. Scleroglossans are derived within Squamata, with autarchoglossans being the most highly derived.

Huey and Pianka (1981), in a classic paper on ecological consequences of foraging mode in lizards, present a table listing postulated correlates of foraging mode; their table 8, slightly modified, is presented here as Table 2. When compared with the contrasting attributes of iguanians and autarchoglossans listed in Table 1, it is clear that the former possess the major characteristics of SW predators and the latter those of WF predators.

The attributes of SW vs. WF predators listed by Huey and Pianka (1981) and those listed for iguanians vs. autarchoglossans by Pianka and Vitt (2003) show significant commonalities, the essential thrust of which is that activity levels in the two clades are correlated with contrasting foraging modes and that the differences in activity levels are correlated with major physiological and sensory specializations in the more derived clade that are absent in the more primitive clade.

TABLE 1. Attributes of Iguania and Autarchoglossa related to foraging mode (modified from Pianka & Vitt, 2003).

	Iguania	Autarchoglossa
Foraging model	sit-and-wait	active
Prey	high mobility	low mobility
Prey detection	visual	visual and vomerolfaction
Daily energy intake	low	high
Sprint speed	high	low
Aerobic capacity	low	high
Rate of exercise recovery	low	high
Daily activity	intermittent	sustained
Use of space	territorial	nonterritorial

TABLE 2. Postulated correlates of foraging mode (modified from Huey & Pianka, 1981).

	Sit and Wait	Widely Foraging
Prey type	mobile prey	sedentary and unpredictable (but clumped or large) prey
Volume prey captured per day	generally low	generally high
Daily metabolic expense	low	high
Types of predators	vulnerable to widely foraging predators	vulnerable to both sit-and wait and widely foraging predators
Rate of encounters with predators	probably low	probably high
Mode of escape from predators	camouflage, speed, saltation	camouflage, speed, aposematism (poisonous)
Morphology	stocky	streamlined
Probable physiological correlates	limited endurance	high endurance capacity
Sensory mode	primarily visual	visual or chemoreceptory
Learning ability	limited	enhanced learning and memory, larger brains

Below, I discuss what appear to be biological consequences of the evolutionary shift in one clade of early squamates from the primitive SW ambush strategy for capturing prey to a derived strategy of seeking out prey by actively ranging over a wide geographic area. My thesis in this paper is that basal synapsids ("pelycosaurs") and therapsids showed the same divergence in foraging behavior, with therapsids evolving consequent morphological, physiological, and neurological adaptations to a more active way of life.

Characteristics of Iguanians as SW Predators

As discussed above, iguanians, as exemplified by the mainly New World Iguanidae and the Old World Agamidae, are ambush predators that usually sit motionless until a potential prey item comes within range, at which time the predator dashes at high speed from its lookout post to seize it. (Chameleons are iguanians that rely on a very long projectile sticky tongue rather than a physical dash to close the gap between predator and prey; thus, according to Pianka and Vitt [2003, p. 53], they could be considered the ultimate SW predators because they continue to sit even during prey capture.) In studies comparing percent of time moving (PTM) in lizards, iguanians have very low values (under 10%), demonstrating that very little movement occurs during food-getting activities (Miles et al., 2007). Therefore, iguanians expend very little energy in the hunt for food. Data on the North American desert iguanid *Callisaurus draconoides* (Anderson & Karasov, 1981) show that it may spend up to 10 hours a day in this low-energy food-getting activity, compared with half that in WF predators (Table 3). Levels of aerobic metabolism in such SW predators, both resting and active, are low (Fig. 2). Thus, when a high-speed dash is required in prey capture, they rely on anaerobic sources of energy to fuel their muscles.

Anaerobic muscle metabolism has the advantage of permitting rapid acceleration to high speeds because it is not subject to an inherent lag time in transport of increasing amounts of oxygen to the tissues (Bennett, 1973). In addition, running lizards must suspend breathing because hypaxial trunk muscles, which are usually active *bilaterally* during breathing, are used *alternately* during locomotion to create alternate lateral bending of the trunk; such bending contributes importantly to stride length, but at higher speeds it precludes normal breathing (Carrier, 1987a, 1987b, 1991). The main disadvantages of anaerobiosis are that it is much less efficient than aerobiosis, yielding about one-tenth the amount of energy from its fuel, and it produces lactic acid as a metabolic by-product, which, as it builds up in the muscles, causes rapid fatigue. Consequently, the brief period of intense activity is necessarily followed by a long aerobically mediated recovery time for the muscles to regain their former activity capacity. For these reasons, anaerobic metabolism, though facilitating high sprint ability, cannot be sustained for long and so greatly limits endurance.

Consistent with specialization for sprinting, iguanians usually have relatively long limbs, with the hind limbs often much longer than the forelimbs, and elongated distal limb elements (i.e., the epipodials and feet), including a very long fourth toe (Miles et al., 2007). They also tend to have stocky trunks and relatively short tails compared with autarchoglossans. A number of iguanids and agamids with very long hind limbs have adopted bipedal running (Snyder, 1952).

The SW foraging mode of iguanians is correlated with many other aspects of their biology (Huey & Pianka, 1981). Of necessity, iguanians rely on moving, conspicuous prey that they can sense visually. Like the squamate out-group, *Sphenodon*, classified as a SW forager by Vitt et al. (2003), they have a fleshy sticky protrusile tongue that is used to capture small to medium-sized prey, mainly invertebrate (commonly ants, other hymenoptera, and beetles) though sometimes vertebrate, and they usually process their food by "palatal crushing" between the tongue and the palate (which often bears teeth), though the jaws may also be used (Reilly et

TABLE 3. Daily energy intake and expenditure (in J day^{-1}) in a SW iguanid lizard (*Callisaurus draconoides*) and a WF teiid lizard (*Apsidoscelis tigris*). Data from Anderson and Karasov (1981).

Taxon	Body mass (g)	Hours of activity	Energy ingested	Energy expended	Foraging efficiency*
Callisaurus draconoides	9	10	900	810	1.1
*Apsidoscelis tigris***	16	5	3,700	1,800	2.0

* Equals metabolizable energy intake/energy expended.

** Formerly *Cnemidophorus tigris*.

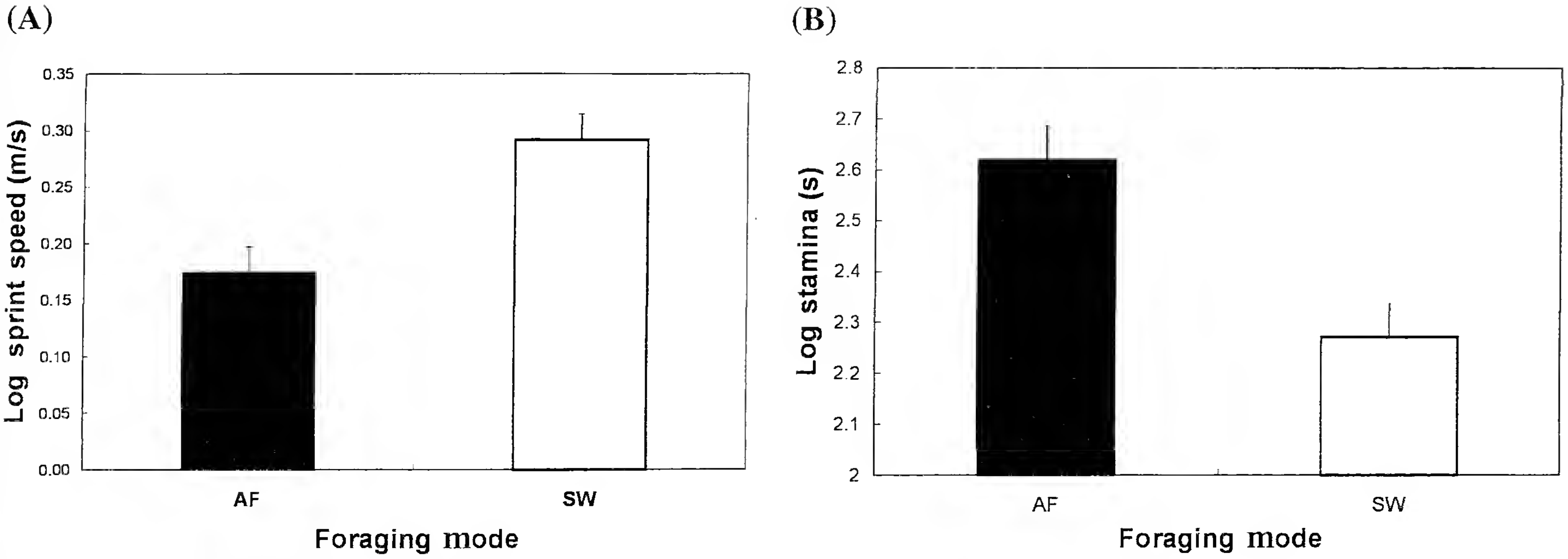

FIG. 2. Differences in (A) sprint speed (m s^{-1}) and (B) endurance (s) in relation to foraging mode for actively (i.e., widely) foraging (AF) and sit-and-wait (SW) lizards (from Miles et al., 2007).

al., 2001; Reilly & McBrayer, 2007). Iguanians, like other diurnal ambush foragers, rely almost exclusively on visual cues for locating prey (which usually is moving) and do not use chemical (olfactory, vomeronasal) cues (Cooper, 2007) to sense prey at a distance. Regal (1978: 196) points out that "the sit-and-wait predator primarily needs to occupy a suitable perch until a stimulus appears." As a result, iguanians lack the behavioral flexibility of more WF lizards that actively search for a greater variety of prey.

Characteristics of Autarchoglossans as WF Predators

WF lizards are those that "actively search out and pursue their prey" (Pianka & Vitt, 2003: 53). Autarchoglossans characteristically fit this definition, with PTM values well above 10% (with teiids over 60%), although one family (Cordylidae) and members of two additional families (Scincidae and Lacertidae) have secondarily reverted to SW predation, with reacquisition of behavioral and physiological features of this ancestral foraging mode (Miles et al., 2007). Species in the families Gerrhosauridae, Gymnophthalmidae, Teiidae, Helodermatidae, and Varanidae, however, are categorized as strict active foragers by Miles et al. (2007, p. 66), although some varanids appear to be SW predators (see below).

WF autarchoglossans are much more active than SW foragers, ranging over large territories in the search for food and, therefore, expending large amounts of energy in movement. Their foraging speeds are usually moderate and are fueled by aerobic metabolism, which has the advantage of permitting sustained locomotion without fatiguing. Prey types are more varied than those encountered by SW predators and are usually inactive, often hidden, and widely dispersed (such as termites, spiders, cryptic insects, and some vertebrates), which has consequences for search mode and sensory specialization (see below). The fact that WF lizards are able to exploit a food source (hidden or nonmoving prey) that visually hunting SW predators are not able to detect means that a previously unexploited food source became available because of a shift to a more active search mode. Adopting an underexploited food resource presumably compensated for the increased exposure of the hunter to predators as compared with hunting from a single, safer spot.

Active foragers may expend more than twice the energy per day as SW foragers, but they find and ingest perhaps four times as much food. Anderson and Karasov (1981) compared activity level and physiology in a WF lizard, the teiid *Aspidoscelis* (formerly *Cnemidophorus*) *tigris*, and a SW lizard, the iguanid *Callisaurus draconoides* (Table 3). They determined that *A. tigris* spent 91% of its five-hour daily activity period in movement, whereas *C. draconoides* spent about 1.5% of its 10-hour activity period in movement. Measurements of daily energy metabolism and water flux measured with doubly labeled water in free-living animals showed that *A. tigris* had significantly higher rates of field metabolic expenditure (210 J g^{-1} day^{-1}) than *C. draconoides* (136 J g^{-1} day^{-1}; Anderson & Karasov, 1981, table 2). Feeding rates, calculated from water influx data were 13.3 mg g^{-1} day^{-1} (metabolizable energy = 229 J g^{-1} day^{-1}) for *A. tigris* and 5.8 mg g^{-1} day^{-1} (metabolizable energy = 100 J g^{-1} day^{-1}) for *C. draconoides*. Although the actively foraging predator *A. tigris* had a much higher daily rate of energy expenditure, its foraging efficiency (metabolizable energy intake/energy expended) was twice that of the more sedentary ambush predator *C. draconoides* (Table 3). This is especially notable in that active foraging time per day for the former was half that of the latter (5 vs. 10 hours).

In a series of studies of a pair of closely related Kalahari Desert lacertids with differing foraging modes, Huey and coauthors (Huey & Pianka, 1981; Huey et al., 1984; see also Bennett et al., 1984; Nagy et al., 1984) compared their physiological and morphological traits as they relate to foraging behavior. (These species were formerly placed in the genus *Eremias* but are now placed in separate genera.) *Pedioplanis lineoocellata* is a SW predator, and *Heliobolus lugubris* is a WF predator. As expected for an active forager (see Table 4), laboratory studies show that *H. lugubris* has a much higher maximum rate of oxygen consumption (aerobic capacity) than *P. lineoocellata*, whereas the latter, as a SW forager, has a much higher anaerobic capacity than *H. lugubris* (Bennett et al., 1984). Furthermore, although the WF species expends about 1.3 to 1.4 times more energy in food acquisition

TABLE 4. Morphological and physiological factors relating to activity metabolism in two closely related species of African lacertid lizards differing in foraging pattern. Data from Bennett et al. (1984) and Huey and Pianka (1981).

	Pedioplanis lineoocellata	*Heliobolus lugubris*
Foraging mode	sit-and-wait	widely foraging
Maximum O_2 consumption at 37°C (ml O_2 $g^{-1}h^{-1}$)	2.49	3.22
Anaerobic scope and capacity at 37° C (mg lactate $g^{-1}min^{-1}$)	2.56	1.81
Relative heart mass (% body mass)	0.24	0.28
Hematocrit (% red blood cells in whole blood)	24.4	30.1
Field activity	expends less energy on locomotor activities; greater capacity for burst activity	sustains higher levels of field activity; greater stamina, less capacity for burst activity
Relationship of energy expenditure to energy capture	*Heliobolus lugubris* expends ~1.41 to 1.32 times more energy than *P. lineoocellata. Heliobolus lugubris* captures 2.1 times more food than *P. lineoocellata*. Therefore, *H. lugubris* has a net energy gain of 0.69 to 0.78 times that of *P. lineoocellata*.	

than the SW species, it captures more than twice as much food; thus, it has a net energy gain of 0.69 to 0.78 times that of the SW species (Huey & Pianka, 1981). During the course of their study of field energetics of these lacertid species, "the wide forager grew faster and had a somewhat larger body mass" (Nagy et al., 1984: 595).

As indicated above, levels of aerobic muscle metabolism during foraging activity are much higher in WF lizards than in SW lizards (see also Miles et al., 2007). As a consequence, WF lizards have high endurance (stamina). However, their levels of anaerobic metabolism tend to be lower than in SW lizards, and maximal running speeds are usually moderate at best. Although a negative correlation between speed and endurance has been demonstrated in some lizard families, Miles et al. (2007, p. 84) note that teiids have a positive correlation between speed and endurance; these authors suggest that this is because teiids often feed in open habitats where encounters with predators may be more common and high sprint capacities may be required.

In addition to laboratory studies of aerobic and anaerobic capacity in *P. lineoocellata* and *H. lugubris*, Bennett et al. (1984) also determined heart mass and hematocrit (percent red blood cell volume to whole blood volume) in eight individuals of each species (Table 4). Heart mass, expressed as a percentage of body mass, was significantly larger in *H. lugubris* (0.28%) than in *P. lineoocellata* (0.24%). Hematocrit was significantly greater in *H. lugubris* (30.1) than in *P. lineoocellata* (24.4). As noted by Bennett et al. (1984), the greater maximal oxygen consumption of *H. lugubris* correlates with its larger heart mass and hematocrit. They also note that "our findings provide indirect comparative evidence that the cardiovascular system may be the first aspect of physiology to respond to an evolutionary change in activity level" (Bennett et al., 1984: 117).

Miles et al. (2007) show that morphological characteristics of WF autarchoglossans include narrow bodies, long tails, and relatively short limbs with proportionally shorter distal elements, including the toes. This contrasts with the broad bodies, short tails, and long limbs with longer distal elements, including a very long fourth toe, in SW iguanians. Active foragers are built for sustained locomotion at moderate speeds, not for high sprint speed, so total limb length and distal limb length tend to be proportionally shorter than those of SW predators, especially the length and distal proportions of the hind limbs (see Miles et al., 2007).

Because the prey of WF autarchoglossans is usually patchily distributed and often not active, it is difficult to locate by vision alone. As a consequence, chemosensory systems, particularly the vomeronasal organ, but also the olfactory system are well developed in autarchoglossans and are used to sense prey that may be hidden from sight. Chemosensory specializations are common in WF predators and in herbivores (such as the desert iguana, *Dipsosaurus*, and other iguanines; see below) but not in SW predators (Cooper, 2007, p. 238). Olfaction may be important in food getting in geckos, which have the most highly developed olfactory system among lizards (Cooper, 2007). The tongue in more derived autarchoglossans has a forked tip that is specialized to carry airborne chemical cues to the vomeronasal organ. As the tongue became more specialized as a sensory structure, it was no longer used for prey apprehension as in iguanians. The jaws of autarchoglossans are the main means of prehension and processing of food items. Palatal teeth are often lost, and the skull becomes increasingly kinetic. The anterior part of the tongue is increasingly specialized for a chemosensory function in lacertoids (lacertids and especially teiids) and anguoids (especially varanids), with only the hind tongue retaining a food transport function (Reilly & McBrayer, 2007). Varanids and teiids independently developed inertial intraoral transport of prey in which the tongue is not used at all.

Iguanians have simple oral processing of prey items, crushing them against the palate before swallowing. More derived autarchoglossans (lacertoids and anguoids) use the jaws and marginal teeth for puncture crushing of prey and use more chewing cycles to reduce the prey before swallowing (Reilly et al., 2001). Reilly and McBrayer (2007: 328) suggest that more processing of food "may indicate (as in mammals) that the prey are actually being better reduced and punctured prior to swallowing to increase digestive efficiency, which has been proposed to be related to higher metabolic needs of wide foraging."

In an intriguing paper that foresaw many of the issues raised later concerning the consequences of different foraging modes in lizards, Regal (1978: 195) asked, "What differences might we expect in mental functions between active foragers and sit-and-wait predator lizards?" He rejected the assumption that large brains are "somehow dependent upon endothermy" but argued that "development of a four-chambered heart [in the ancestors of mammals] allowed extreme specialization in active foraging and that, for this way of food gathering, there are great selective advantages to be derived from the development of enlarged memory capacities and enlarged and advanced information-processing capacities and systems." He considered endothermy to be "simply another adaptation for this same way of life," being related to brain enlargement only because it [endothermy] would lock individuals into high food requirements and hence select for "behaviors and mental capacities" that improve success in active foraging. This would include the ability to efficiently exploit widely and heterogeneously distributed food resources by gaining a detailed familiarity with their surroundings and evolving appropriate behaviors, such as spontaneous exploration, and mental capacities, such as a sense of curiosity. The forager not only will form a search image for recognizing prey but also would develop a search strategy for effectively locating the prey.

From his ideas cited above, Regal (1978: 197) asked a second question: "Will some degree of curiosity and exploration be found among the intensive-foraging lizards?" He predicted that if it does, it is likely to be among varanids and teiids. He cited evidence of group foraging in the teiid *Cnemidophorus* and in young Komodo monitors as well as cooperative behavior in *Varanus niloticus*. Pianka (1968), in describing the behavior of the small Australian desert varanid, *Varanus eremias*, emphasizes its curiosity and exploratory behavior, such as being attracted to fresh diggings as well as its ability to remember the exact positions of burrows previously visited and in an emergency running directly to the closest one.

A Digression on Herbivory and Omnivory in Lizards

The ecological and morphological/physiological distinctions between SW and WF lizards that have been discussed to this point do not necessarily apply to lizards that are specialized for a diet that includes plants, regardless of the foraging mode of their ancestral clade. According to Cooper (2007), about 11% of living lizards are omnivores, and only 1% are strict herbivores. Of all lizards considered to be strictly herbivorous, 60% are iguanians, including all eight genera of the subfamily Iguaninae (Herrel, 2007) and two genera of the agamid subfamily Leiolepidinae (Pianka & Vitt, 2003). Although predominantly herbivorous taxa are less common among scleroglossans (including the skinks *Corucia* and *Tiliqua* and a few species from other families), Cooper and Vitt (2002) suggest that omnivory may be more widespread among scleroglossans than among iguanians.

Herrel (2007, table 7.1) lists ecological and morphological characteristics of SW predators, WF predators, and herbivores, indicating that some features of herbivores are shared with SW predators and others with WF predators, while still other features are unique specializations.

As noted by Herrel (2007: 209), herbivores "are active foragers by definition (waiting motionless for plants to pass by is an unviable evolutionary strategy)," but, paradoxically, the majority of herbivores are found among the Iguania, the clade most constrained to SW foraging. Like SW predators on animals, herbivores do not have an increased endurance capacity and so have relatively low energy needs. This is presumably because they maintain low foraging speeds and have home ranges that are relatively small (compared with WF predators), befitting a forager on nonlocomoting "prey." However, because plants often occur in unpredictable, widely spaced clusters, all herbivores, whether they belong to SW or WF foraging clades, are like WF predators in having a well-developed chemosensory apparatus for both detecting and assessing the suitability of potential food items. In this feature, they differ from most nonherbivorous iguanians, which rely almost exclusively on visual cues to detect their prey.

Tough, fibrous plant food is inferred to require greater bite force than animal food to be broken down, and, indeed, experimental evidence indicates that herbivores and omnivores bite significantly harder than insectivores (Herrel, 2007, p. 218). Herbivores have wide heads (like SW predators) and also uniquely tall heads, presumably to accommodate larger jaw muscles. Their teeth are usually specialized for cutting up plant material, and like WF lizards, they engage in active prolonged chewing to break down their food (Herrel, 2007). Herbivores tend to be larger than their nonherbivore relatives and tend to have large heads and stocky bodies (features of SW foragers generally). The colon of herbivores/omnivores is more elongate than in animal-eating lizards and is often specialized to form a cecum, with ridges and valves that serve to slow passage of food (Herrel, 2007).

Herrel (2007) points out that herbivores arose independently in Iguania and Scleroglossa (most in Autarchoglossa and very few in Gekkota) and have converged on one another in a number of features. Iguanian herbivores all possess a chemosensory prey detection system (unlike other iguanians but like scleroglossan WF predators), and scleroglossan (i.e., autarchoglossan) herbivores have large heads and stocky bodies (like iguanian SW predators but unlike autarchoglossan WF predators, which have smaller, narrower heads and more slender bodies).

In summary, herbivorous and omnivorous lizards resemble WF predators in actively searching for their "prey" and in using a well-developed chemosensory apparatus to locate it as well as extensive intraoral processing to break it down. They resemble SW predators in having large heads and stocky bodies. Because they "prey" on immobile food sources, they are like SW predators in having low aerobic capacity and, therefore, relatively low energy needs. In this respect, lizard herbivores do not appear to fit the model for the highly active, high-endurance, aerobically dependent organisms that I envision as the ancestral endotherm. Nonetheless, the obligate active foraging behavior of early synapsid herbivores/omnivores may have preadapted them to a path toward an increasingly aerobically based locomotor metabolism, a path that was not taken by typical SW synapsid meat eaters.

Features of Varanids as the Most Mammal-Like of Lizards

The lizard families that are undoubtedly the closest living analogs of early therapsids are the Varanidae and Teiidae, both containing very active predators that include large vertebrates in their diet. The energetics of WF varanids have been more thoroughly studied than are those of the larger teiids, and they will be used here as early therapsid analogs as I review morphological, physiological, and neural correlates that might be expected in the early ancestors of endothermic mammals.

Varanids range in body length from 0.28 m to more than 3.0 m, occupy a variety of habitats, and are ecologically very diverse (Losos & Greene, 1988). Although they are widely believed to specialize in large vertebrate prey, Losos and Greene point out that most species, regardless of size, are primarily insectivorous, only occasionally taking large vertebrates. They note, however, that vertebrates are the most

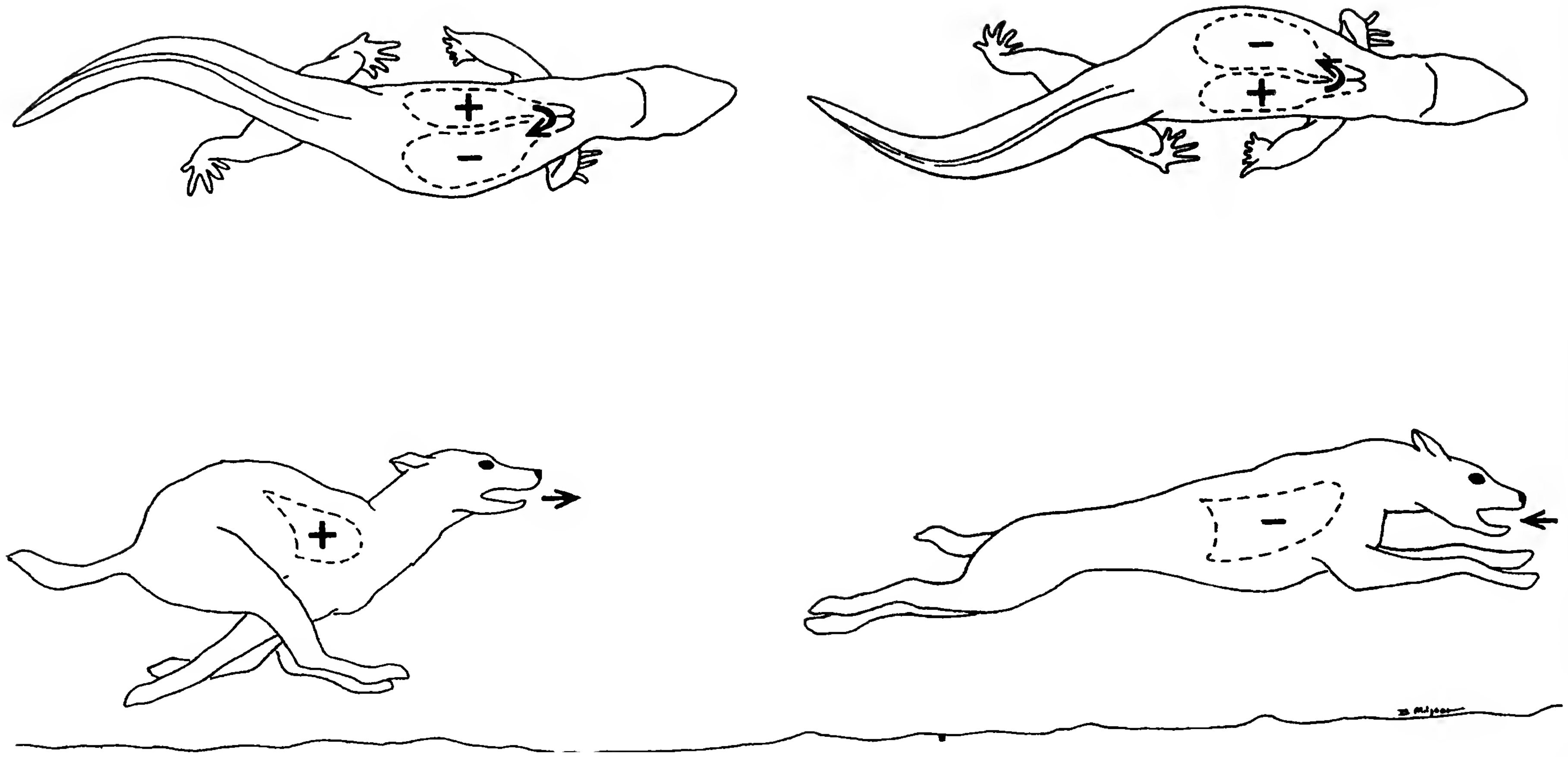

Fig. 3. Comparison of the effect of axial bending on lung volume in a running lizard and a galloping dog. In the lizard (top), the bending axis of the thorax is situated between the right and left lungs, so as the lizard bends laterally to one side, the lung on that side experiences a reduction in volume while the other expands. Air is pumped back and forth between the lungs, but little, if any, moves in and out of the animal. In contrast, the bending axis of a galloping mammal is dorsal to the thoracic cavity, so sagittal bending changes the thoracic volume and actively pumps air in and out of the lungs during each locomotor cycle (from Carrier, 1987a).

energetically important prey for most large varanids, such as *V. griseus*, *V. giganteus*, and *V. komodoensis*, and for some smaller ones, such as *V. eremias* and *V. gilleni*, which prey mainly on other lizards (Pianka, 1968; Losos & Greene, 1988). It is also the case that not all varanids are wide foragers, nor do all have an unusually high aerobic capacity. Christian and Conley (1994) found that although some species of *Varanus* (e.g., *V. rosenbergi*, *V. gouldii*, *V. panoptes*, and *V. exanthematicus*) have aerobic capacities higher than those of other lizards, some (e.g., *V. mertensi* and *V. salvator*) have much lower aerobic capacities, comparable to those of iguanids. The species in the former group are terrestrial and apparently wide foragers, whereas those in the latter group are semiaquatic and not widely ranging. A few varanid species are sedentary and appear to be SW predators (Christian & Conley, 1994).

Although resting or standard metabolic rates of varanids are comparable to those of other lizards, more active species, such as *V. gouldii*, consume nearly twice the amount of oxygen during peak activity than does a similar-sized iguanid, such as the chuckwalla, *Sauromalus hispidus* (Bennett, 1972). As already described, SW predators such as iguanids rely on anaerobic metabolism to supply the energy for rapid locomotion. Because they have extensive production of lactic acid that causes them to fatigue quickly, they must rest for a long period to recover standard metabolic levels. *Varanus gouldii* relies much more on aerobic metabolism during extreme activity and experiences only moderate anaerobiosis (only two-thirds that of *Sauromalus*), from which it recovers more than three times as quickly as the iguanid (Bennett, 1972).

Morphological specializations of the pulmonary and cardiovascular systems of varanids support their unusually high aerobic capacity. The lungs of varanids are far more complex than those of other squamates, in which the lungs are relatively simple sacs lacking intrapulmonary bronchi. Varanid lungs "possess cartilage-lined intrapulmonary bronchi and extensive spongy, alveolar-like air cells throughout the lung" (Bennett, 1972: 260). The heart shows several specializations that reduce peak blood pressure in the pulmonary artery and increase it in the systemic arches (Fig. 4; see below).

The fully divided ventricles of the mammalian and avian heart completely separate the deoxygenated blood returning from the systemic circulation from the fully oxygenated blood returning to the heart from the lungs. This permits the systemic part of the heart to exert a higher blood pressure required to overcome the higher resistance of the body's vasculature and the pulmonary part of the heart to exert a lower blood pressure to match the lower resistance of the lung's vasculature.

Ectothermic tetrapods have incomplete division of the heart and incomplete separation of oxygenated from deoxygenated blood. Most reptiles have a tripartite ventricular portion of the heart, consisting of the cavum arteriosum on the left side, into which oxygenated blood enters from the left atrium, and the cavum venosum and cavum pulmonale on the right side, into which deoxygenated blood enters from the right atrium (see Fig. 4). The left and right systemic (aortic) arches carrying oxygenated blood to the body tissues exit from the cavum venosum, and the pulmonary artery carrying deoxygenated blood to the lungs exits from the cavum pulmonale. The cava arteriosum and venosum are partially separated by an incomplete septum that allows oxygenated blood to pass from the cavum arteriosum into the cavum venosum and thence to the systemic arches (Fig. 4, right). Deoxygenated blood from the systemic circulation also enters the cavum venosum via the right atrium and passes into the cavum pulmonale to enter the pulmonary artery (Fig. 4, left). Thus, both oxygenated blood from the cavum arteriosum and deoxygenated blood from the

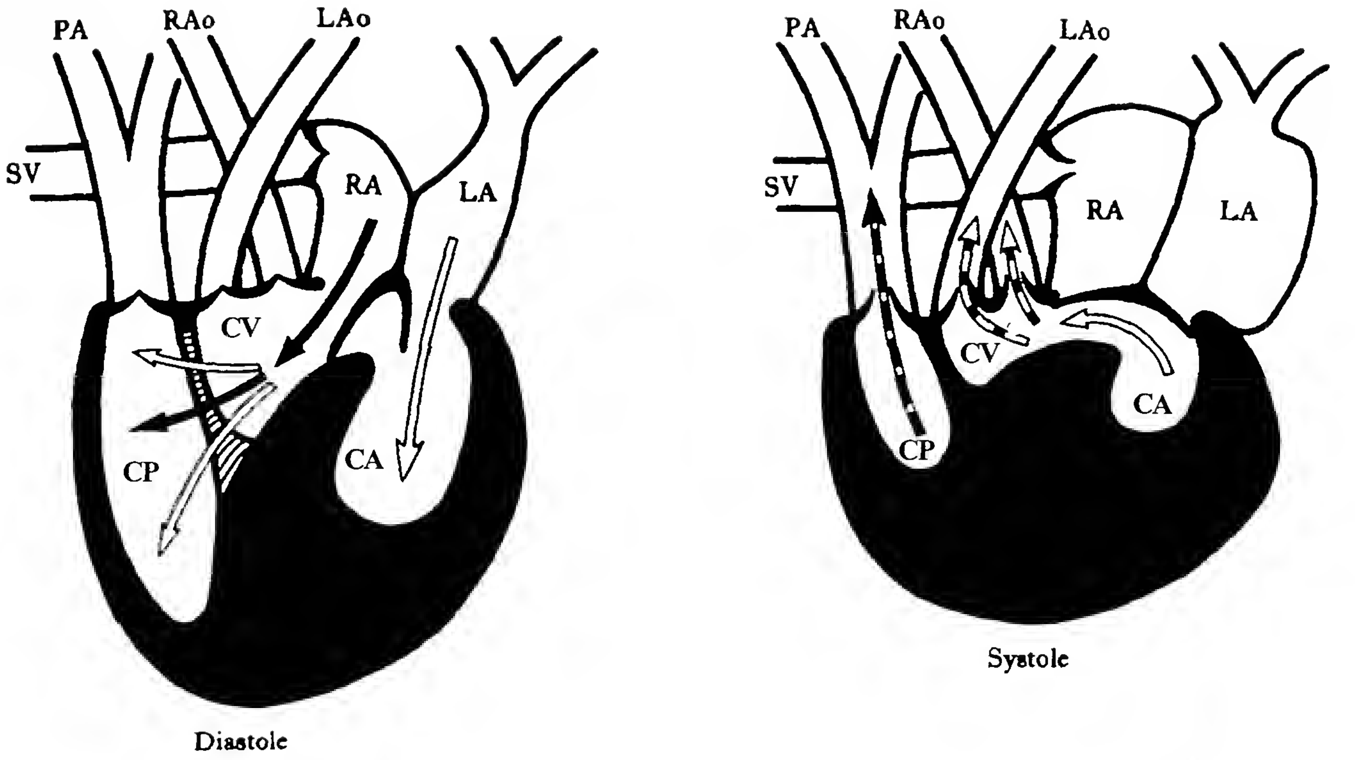

FIG. 4. Schematic two-dimensional representation of the heart chamber and vessel arrangement in *Varanus exanthematicus* during ventricular diastole (passive intake of blood due to atrial contraction) on the left and ventricular systole (contraction and ejection of blood) on the right. The muscular ridge (striped area on left, solid black on right) between the cavum venosum (CV) and the cavum pulmonare (CP) is projected onto the outer heart wall for clarity. Open arrows represent the path of oxygenated blood and solid arrows the path of deoxygenated blood. Some mixing of oxygenated and deoxygenated blood occurs in the CV, so the CP and pulmonary artery (PA) receive some oxygenated blood, and the right and left aortic arches (RAo and LAo) receive some deoxygenated blood. Other abbreviations: CA, cavum arteriosum; SV, sinus venosus; RA, right atrium; LA, left atrium (modified from Heisler et al., 1983, with permission of the *Journal of Experimental Biology*).

right atrium enter the cavum venosum, where some mixing of the two streams occurs. Intraventricular blood pressures in turtles and most squamates show that pressures in all three cava and in the systemic and pulmonary circuits are essentially identical, although some nonvaranid lizards, such as *Iguana iguana*, are able to increase peak pressure in the systemic arches to about 50% above that in the pulmonary artery (Heisler et al., 1983).

The heart of varanids is specialized in having a much better separation of the systemic and pulmonary portions of the ventricles and, consequently, less mixing of deoxygenated and oxygenated blood. Pressure separation in the heart is much greater than in other squamates, with at least a twofold higher aortic than pulmonary blood pressure (Heisler et al., 1983; Burggren, 1985). This means that blood pressures in the systemic circulation can be much higher than in typical reptiles. According to Burggren (1987), varanids show cardiovascular adaptations that fall on a physiological continuum between the single pressure ventricle of most reptiles and the completely divided, dual pressure circulation of mammals and birds.

Specializations of the varanid heart (Fig. 4) include reduced size of the cavum venosum so that it forms a narrow "interventricular" channel connecting the cavum arteriosum on the left and the cavum pulmonale on the right (Burggren, 1987). Furthermore, a muscular ridge partially separates the cavum venosum and cavum pulmonale. Early in the contraction of the ventricles, deoxygenated blood flows under fairly low pressure from the cavum venosum over the muscular ridge into the cavum pulmonale (Fig. 4, left). Continued contraction of the ventricles presses the muscular ridge against the dorsal wall of the right ventricle, preventing further inflow of deoxygenated blood into the cavum pulmonale (Fig. 4, right). Under the higher contraction pressure, most of the oxygenated blood flowing from the cavum arteriosum into the cavum venosum is directed to the systemic arteries (Fig. 4, right). Thus, the varanid heart has a functional division into a low-pressure pulmonary pump (cavum pulmonale) and a high-pressure systemic pump (cavum arteriosum), unlike conditions in other squamates. Some mixing of blood does occur in the small cavum venosum, but only about 30% of deoxygenated blood returns to the body, and only 10% of oxygenated blood is returned to the lungs (King & Green, 1999), a much lower level of mixing than seen in other lizards.

Standard metabolic rates at their preferred body temperature are nearly equal in the iguanid *Sauromalus* and *Varanus gouldii*, but at peak activity, consumption of oxygen in the varanid is twice that of the iguanid (Bennett, 1972). *Varanus* possesses an aerobic scope superior to that of other reptiles of comparable size. Bennett (1972: 272) contrasts the pattern of maximal activity in the iguanid and the varanid as "low aerobic scope, high lactate production and exhaustion in *Sauromalus*; high scope and moderate anaerobiosis in *Varanus*." It is clear that *Varanus* has the ability to meet the oxygen demands of high activity, whereas *Sauromalus* does not.

Bennett (1972, p. 275) points out that the amount of oxygen consumed must be equal to blood flow (which equals heart rate × stroke volume) multiplied by the difference in oxygen content of the blood entering and leaving the metabolizing tissue (known as the A-V difference). Oxygen pulse, the amount of oxygen transported per heartbeat, equals stroke volume times the A-V difference. Bennett notes that oxygen pulse declines during activity in both taxa but much more so in *Sauromalus* than in *Varanus*, where it remains much higher. According to Bennett, stroke volume is not greatly modified during activity or change in body temperature; therefore, declining pulse values must reflect a decrease in A-V differences, most likely in the oxygen saturation of arterial blood, with increasing metabolic demands (Bennett, 1972, p. 276). *Sauromalus* is capable of greatly increasing heart rate yet is unable to increase oxygen consumption during activity,

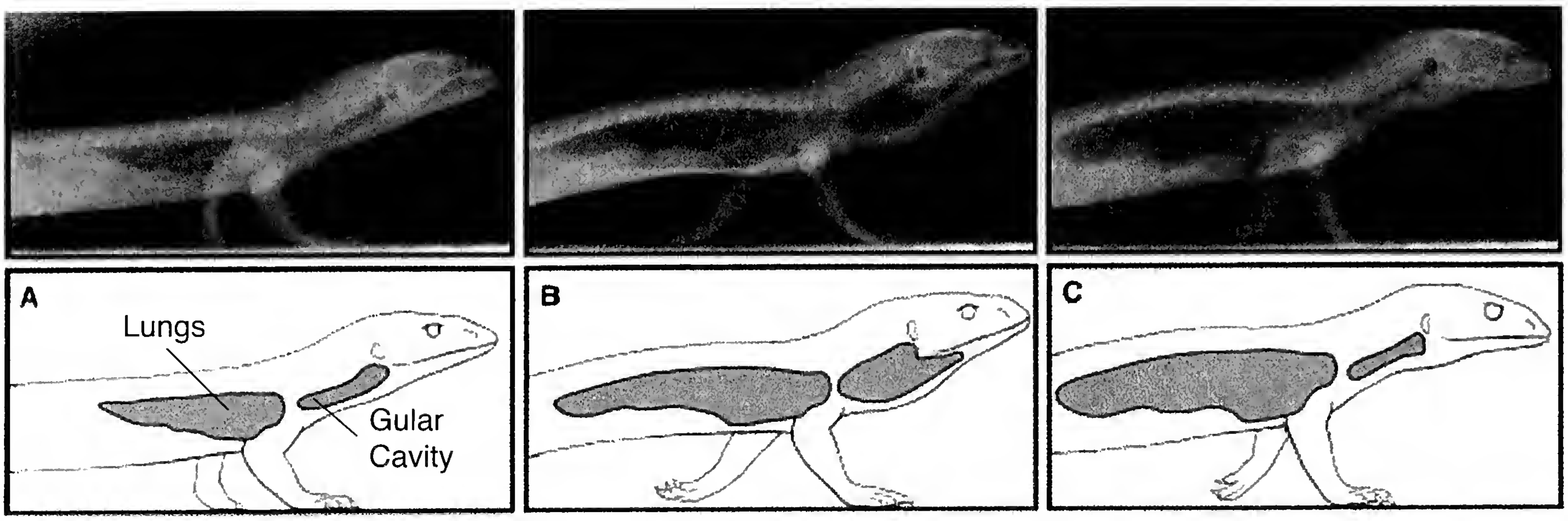

FIG. 5. X-ray negative video images of a savannah monitor (*Varanus exanthematicus*) walking on a treadmill at 1 km h^{-1}, with corresponding drawings of the body, lungs, and gular cavity. The lizard is shown at three different stages of a single breath cycle: (**A**) end of exhalation, (**B**) end of costal and gular inspiration, and (**C**) end of gular pump (modified from Owerkowicz et al., 1999).

hence its reliance on anaerobiosis. *Varanus*, on the other hand, has apparently "evolved mechanisms to sustain high levels of oxygen delivery to its tissues even during the most strenuous activity" (Bennett, 1972: 277). Part of the explanation for these differences is related to a morphological constraint placed on sprawling tetrapods, including lizards, and on how varanids have overcome this constraint (see below).

Since Bennett's early studies of activity metabolism in lizards, Carrier (1987a,b, 1989, 1991) and Wang et al. (1997) have shown that most reptiles suspend breathing when moving at high speeds because of the conflict between use of hypaxial trunk muscles (1) during respiration, when they expand the thorax and aspirate air into the lungs, and (2) during locomotion, when they bend the trunk from side to side to increase stride length (Fig. 3). Carrier (1987b) measured lung ventilation during locomotion in lizards and showed that at low speeds they increased ventilation, but as speed increased, ventilation (tidal volume) decreased "dramatically" and breathing became more difficult. Carrier (1989) used electromyography to show that hypaxial muscles that were used bilaterally during breathing would alternate contraction on the left and right sides during locomotion. The hypaxial muscles flex the trunk from side to side and also stabilize the trunk against horizontal and torsional forces as supporting limbs are lifted from the substrate. It is this conflict between the two functions of the hypaxial muscles that explains the reduced ventilation at higher speeds of a typical lizard, such as *Iguana* or *Sauromalus*.

Varanids differ from other lizards in that during locomotion ventilation, and oxygen uptake rates increase with increasing speed (Wang et al., 1997), indicating no axial bending constraint. This apparently conflicts with the "biomechanical constraint" hypothesis of Carrier (1987a). Varanids are highly derived among lizards, and it appears that their ability to effectively breathe despite lateral undulation of the trunk is due to a specialization that facilitates simultaneous running and breathing not present in other lizards. Owerkowicz et al. (1999) demonstrate that *V. exanthematicus* (and presumably all other varanids) possesses a unique breathing mechanism, accessory to that of the bilateral action of hypaxial muscles, to cause thorax expansion and inflation of the lungs during locomotion. When the costal inspiratory phase partially inflates the lungs, the gular (throat) cavity is depressed by the hyobranchial apparatus, drawing air into the throat, and then raised, pumping additional air into the lungs (Fig. 5).

Experimental impairment of the gular pump caused significant decrease of ventilatory volume and oxygen consumption at higher speeds (Owerkowicz et al., 1999, fig. 4). This indicates that although varanids are indeed subject to the same speed-dependent axial constraint on increased oxygen consumption with increased running speed as are other lizards, they have been able to circumvent this constraint by means of the gular pump. Thus, they can sustain aerobically supported speeds between 2 and 3 km h^{-1} without fatiguing.

As with mammals and birds, varanids have overcome the ancestral amniote constraint on respiration created by sprawling locomotion and the need for lateral bending of the trunk to increase stride length (Carrier, 1987a). Where mammals and birds, with their upright parasagittal limbs, have removed the respiratory-locomotor constraint by eliminating the need for lateral bending of the trunk, varanids have retained the primitive locomotor mode but have overridden its negative effect on respiratory sufficiency by supplementing the primitive respiratory mechanism with the gular pump.

To summarize, the physiological and morphological specializations that permit varanids to be much more active than other lizards (with the possible exception of teiids), the complex lungs, and greater separation and differences in pressure of the pulmonary and systemic circulations mean that greater amounts of oxygen are delivered to the tissues and that active metabolic rates are higher. This explains the high A-V difference in *Varanus* that is absent in iguanids.

As noted above, whereas iguanians have reduced or lost the vomeronasal system, it is well developed in scleroglossans and hypertrophied in varanids and teiids (Northcutt, 1978; Cooper, 2007). Both of these families of highly active foragers have more abundant vomerolfactory receptors than do other lizards, and their forked tongues are very elongated and have few or no taste buds. Cooper (2007, p. 259) suggests that evolution of progressively active foraging led to increased vomeronasal receptor abundance, permitting increased discriminatory powers in the search for prey.

Brain size in varanids and teiids is larger than in other lizard groups (see Hopson, 1980, where these taxa lie at the very top edge of the polygon for reptile brain/body size). King and

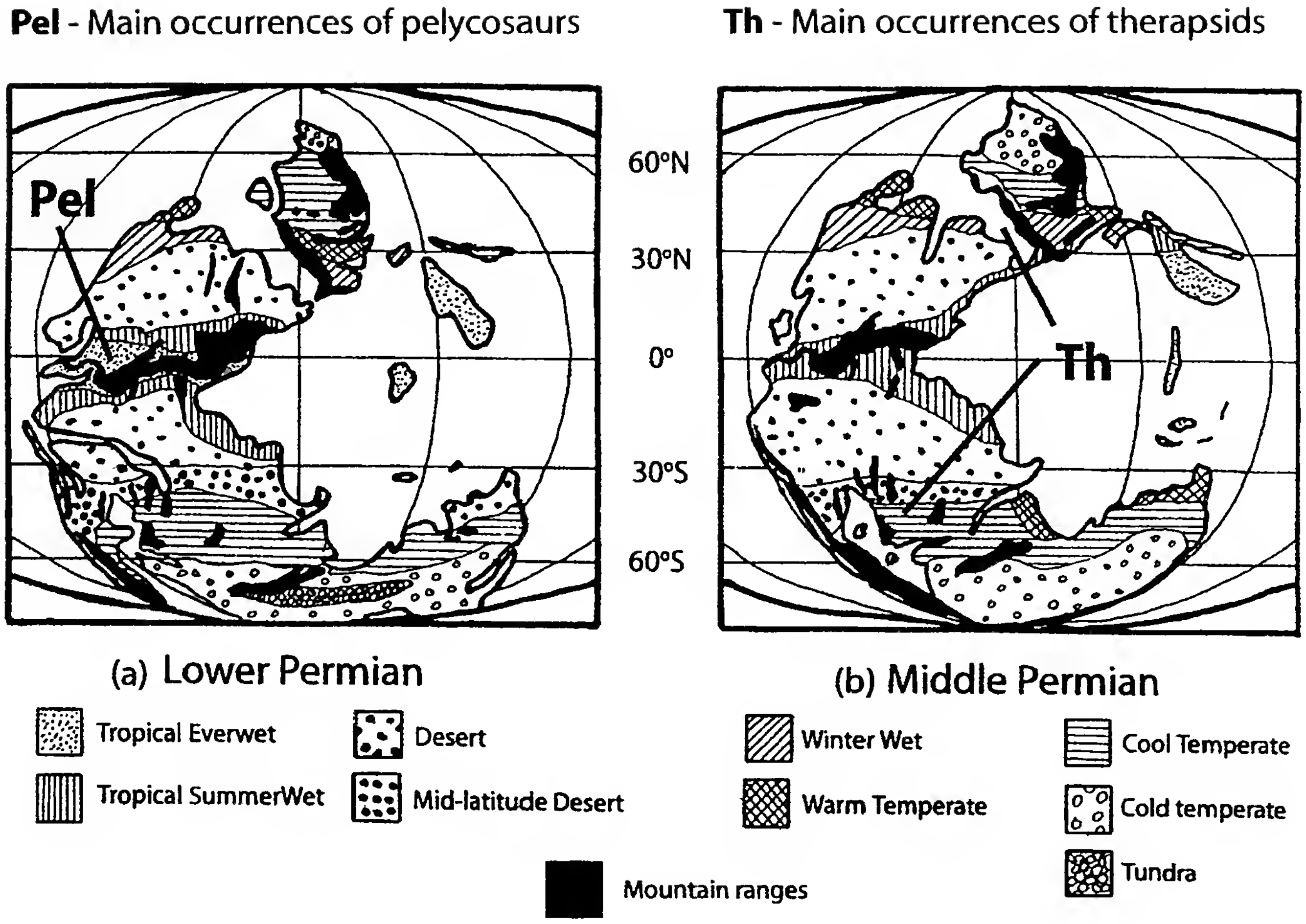

FIG. 6. Paleoclimatic reconstructions for (A) Lower Permian (Sakmarian Stage) and (B) Middle Permian (Wordian Stage), showing the biomes and major occurrences of "pelycosaurs" and therapsids (from Kemp, 2006a, after Rees et al., 2002).

Green (1999: 43) characterize varanids as having acute sensory capabilities, a highly developed mental capacity, and the ability to use complex strategies to select particularly desirable prey items. They state that varanids appear to have very good memories and learn many of the features within their home ranges. As already noted, Pianka (1968) characterized the small, very active, and widely ranging Desert Goanna, *Varanus eremius*, as exhibiting curiosity and exploration behavior and also of remembering the locations of safe burrows along its hunting route. In experiments in which captive *V. albigularis* were fed a fixed number of snails at a time, they could determine when one snail was missing from groups of up to six snails (King & Green, 1999: 43). Thus, varanids have the mental capacity to count to six. In the view of Pianka and Vitt (2003: 274), "varanids, more than any other lizards, have developed a neurophysiology that makes them seem nearly mammal-like."

In summary, varanids are the most mammal-like of living reptiles in terms of morphological and physiological adaptations for high aerobic metabolism during activity, WF behavior, chemosensory specialization, and mental capacity. Yet they appear to be identical to other lizards in resting or standard metabolic rate. As such, they are still ectotherms, although in their activity metabolism they are pushing the envelope of ectothermy in the direction of endothermy (but see below for a contrary view). As Regal (1978) has pointed out, the reptilian heart structure of varanids, in which the ventricles are incompletely divided, prevents full separation of oxygenated and deoxygenated blood and thus imposes a constraint that prevented achievement of endothermic levels of aerobic metabolism. Perhaps this same constraint has caused varanids to retain low RMRs, which appear not to differ from those of other lizards, as a general ectothermic strategy for conserving energy when high activity is not called for (see below).

Therapsids as WF Predators: Morphological and Physiological Correlates

The paraphyletic "pelycosaurs" were the dominant synapsids of the Pennsylvanian and Early Permian in North America and Western Europe, with only two basal lineages (caseids and varanopids) extending their ranges into the Middle Permian. Replacing "pelycosaurs" as dominant synapsids were the therapsids, descendants of sphenacodont "pelycosaurs" that in the Middle and Late Permian successfully dominated terrestrial environments until the extinction at the end of the Permian. Subsequently, the therapsids shared dominance of the Triassic landscape with the archosaurs and, in the Late Triassic or Early Jurassic, gave rise to the common ancestor of living mammals. As stated in the Introduction, my contention is that therapsids, in their transition from the "pelycosaur" structural grade, shifted from an ancestral SW foraging mode to become WF predators and that this shift caused them to evolve from a low-energy to a much-higher-energy existence.

Basal synapsids of the Late Carboniferous and Early Permian and early therapsids of the Middle Permian sequentially occupied very different geographic and climatic regions of the supercontinental landmass of Pangaea. Kemp (2006a) provides an excellent summary of the environmental conditions of the Early Permian, during which "pelycosaur" communities thrived, and of the Middle Permian, when therapsids had almost completely supplanted them (Fig. 6). In the Late Carboniferous and Early Permian, "pelycosaurs" were restricted to North America and Europe in an east–west "Tropical Everwet Biome," which Kemp likens to a modern tropical rain forest, that extended about 10 degrees north and south of the paleoequator. To the north and south of this zone was a narrow band of "Tropical Summer Wet Biome,"

Table 5. Contrasting features of the skeletons of "pelycosaurs" and primitive therapsids. Data from Sidor and Hopson (1998) and Kemp (2006b).

Feature	Pelycosaur	Therapsid
Shape of glenoid	a-p elongate, screw-shaped	rounded, facing posterolaterally
Scapular blade	broad above glenoid	constricted
Humeral head	broad, straplike	elongate oval
Ulna olecranon	long, well-ossified	short, not well-ossified
Acetabulum	shallow	deep
Femoral head	on proximal end of shaft	offset medially from shaft
Carpus/tarsus	many small elements, joint spread over carpus/tarsus	fewer elements, hinge joint between epipodials and proximal carpals/tarsals
Metacarpal/metatarsal lengths	moderate increase from I to IV	moderate to no increase from I to IV
Length of digits	toes long; strong increase from I to IV	toes shorter; less length disparity from I to IV
Phalangeal formula	2-3-4-5-3 (4 in pes)	some phalanges reduced or lost from digits 3 and 4 (5 in pes)
Bone histology	many annual growth rings, few haversian canals, little remodeling of bone	few or no growth rings, many haversian canals, extensive remodeling
Tooth differentiation	homodont, small upper canines, except in sphenacodontids	differentiation into incisors, canines (often large), and postcanines of distinct form
Size of temporal fenestra	usually small	usually enlarged

analogous to today's tropical deciduous forest and savannah. Beyond this zone lay a wide "Hot Desert Biome" between north and south latitudes 10 and 30 degrees. Farther north and south was a "Cool Temperate Biome" and beyond that a "Cold Temperate" zone. In the Middle Permian, the "Tropical Everwet Biome" had disappeared, being replaced by the expanding "Tropical Summer Wet Biome." The north and south Hot Desert Biomes separated the summer wet zones from the cool temperate areas, except along a narrow strip on the east coast of Pangaea. Therapsid faunas were concentrated in cool temperate zones of southern Africa and Russia. The large amount of taxonomic similarity between the vertebrate faunas of the two regions indicates that a migration route must have existed along the east coast of the supercontinent (see Rees et al., 2002, fig. 6).

The Early Permian vertebrate fauna had few terrestrial herbivores, so the terrestrial carnivores, largely "pelycosaurs," were tied to an aquatically based food chain that included abundant fishes and aquatic and semiterrestrial amphibians (Olson, 1966). The Middle Permian therapsid fauna, on the other hand, contained abundant herbivores (dinocephalians, dicynodonts, and pareiasaurs) that for the first time created a terrestrially based ecosystem.

The important point made by Kemp (2006a) is that whereas "pelycosaurs" were restricted to a predictable year-round wet equatorial environment, therapsids invaded a cooler, dryer, more seasonal environment some 30 to 40 degrees north and 60 degrees south. Thus, they had to adapt to a habitat in which rainfall and warm temperatures were restricted to certain parts of the year, and they had to cope with colder and dryer seasons as well. It is in this context that we must examine the initial stages in the evolution of mammalian endothermy.

In Table 5, differences between "pelycosaurs" and therapsids are contrasted. Limb proportions in basal tetrapods, including early synapsids ("pelycosaurs"), are such that the proximal limb elements (humerus and femur) are longer than the distal elements (radius/ulna and tibia/fibula). This is to be expected in sprawling tetrapods because the horizontally oriented proximal elements contribute more to stride length than do the more vertically oriented distal elements (Romer, 1956, p. 339).

Lateral undulation of the trunk is integral to the type of sprawling locomotion seen in living salamanders, *Sphenodon*, squamates, and crocodilians and is inferred to have occurred in basal amniotes, including synapsids. The principal reason for maintaining alternate bending of the trunk appears to be that it serves to increase stride length (Sukhanov, 1974, p. 90; Ritter, 1992, p. 8). However, as noted above (Fig. 3), alternate horizontal bending of the trunk involves *alternate* contraction of the hypaxial muscles, an action that interferes with effective functioning of the lungs, which requires simultaneous *bilateral* contraction of the hypaxial musculature (Carrier, 1987a, 1991). Thus, lateral bending of the trunk necessarily restricts bilateral constriction and expansion of the lungs so that during locomotion, breathing is necessarily greatly reduced or even completely suspended. When high speeds are necessary, either for capturing prey or for escaping from predators, anaerobic muscle activity is used. Therefore, like many living tetrapods with limited aerobic capacity, early amniotes had to be ambush predators, sitting still or moving slowly until a prey organism was spotted, then dashing at high speed to capture it. This pattern of SW predation characterizes many living amphibians and all predatory iguanian lizards and is considered to be the primitive foraging mode for early terrestrial tetrapods of the Late Paleozoic, including the early synapsid precursors of mammals (Carrier, 1991). The linkage between sprawling locomotion, lateral bending of the trunk, low aerobic activity metabolism, and reliance on anaerobic activity metabolism for high-speed locomotion would seem to be general among basal tetrapods of the Pennsylvanian and Early Permian (Carrier, 1987a). Correlated with their SW mode of foraging would be both low standard and low active metabolic rates (i.e., a low-energy existence).

The appendicular skeleton of "pelycosaurs" and other basal tetrapods has many features indicative of sprawling posture and limited mobility of the limbs. In his study of forelimb anatomy and function in the Early Permian basal amniote *Captorhinus aguti*, Holmes (1977) showed that the posture was sprawling and that the complex screw-shaped glenoid of the shoulder girdle strictly regulated degree of rotation of the humerus. This was also shown by Jenkins (1971, 1973) for the similar shoulder joint of the Early Permian synapsid *Dimetrodon*. The elbows of both are constructed to resist torsion as the humerus rotated at right angles to the lower limb. The hind limb of *Dimetrodon* was also clearly adapted for a sprawling posture (Romer, 1956; Jenkins, 1971). The articular head lies proximally on the femur and fits into a shallow acetabulum; the femur's orientation was essentially horizontal, and it extended laterally from the trunk. The range of anteroposterior motion of the humerus and femur of these early tetrapods was limited, though long-axis rotation of these bones would have contributed to stride length. However, lateral bending of the trunk would also have been important in increasing the forward extension of the distal ends of the radius/ulna and tibia/fibula and of the manus and pes.

Distinct wrist and ankle joints are absent in basal amniotes and "pelycosaurs," with bending in these regions being spread proximodistally along the long carpus and tarsus (Romer, 1956). This suggests that the manus and pes did not generate much force against the ground as they extended (ventroflexed) at the end of a step. The digits tend to be long and increase regularly in length from first to fourth so that their clawed tips lie on a line that is strongly oblique to the long axis of the manus and pes. To align the toe tips so that they would grip the substrate perpendicular to the body axis, the manus and pes would have to be turned strongly outward. Such an outward orientation of the manus and pes is commonly seen in resting lizards (see Pianka & Vitt, 2003), although fossil footprints of walking "pelycosaurs" indicate that the feet were usually oriented parallel to the midline axis of the trackway.

The best evidence that the trunk of "pelycosaurs" contributes to stride length through lateral bending is seen in fossil trackways. Early Permian trackways from the Robledos Mountains in New Mexico, representing a likely sphenacodontid (probably the ichnotaxon *Dimetropus*), show left and right manus and pes much closer to the inferred midline axis than the describers expected in a sprawling animal (Hunt et al., 1993; MacDonald, 1994). MacDonald (1994, figs. on pp. 234–235) illustrates a standing *Dimetrodon* with a very wide sprawling stance (labeled "old stance") paired with a standing *Dimetrodon* in which the limbs are drawn in close to the animal's flank and the manus lies beneath the shoulder joint (labeled "new stance"). Hunt et al. (1993: 29) are also impressed by the narrowness of these trackways, which they observe are "narrower than is implied by most mounted skeletons of *Dimetrodon*." These observations illustrate a long-standing misinterpretation of trackways, that is, that a standing stance can be reconstructed from the tracks of a moving animal (and vice versa). A tetrapod usually places its feet farther apart when it is standing (in static equilibrium) than when it is walking (in dynamic equilibrium), at which time left and right feet are usually placed closer to the body midline axis. This is so for sprawling tetrapods, which use lateral undulation of the trunk, and for mammals, including elephants and humans, which shift from a stable standing stance with feet planted well apart to a moving one of dynamic stability with feet contacting the ground closer to the midline axis (thus minimizing lateral sway). In the case of sphenacodontids, with limb skeletons indicating a sprawling stance, lateral flexion of the trunk so that it is concave, say, on the right side causes the anterior end of the trunk on the left side and the rear end of the trunk on the right side to move closer to the longitudinal midline axis; this causes the forwardly extending left front foot and right hind foot to contact the substrate closer to the midline than would be possible in the absence of bending.

In the trackways of *Dimetropus* and other early tetrapods, the footprints show the digits pointing forward rather than to the side, as the foot skeleton suggests should occur. This was long ago noted by Romer (1956, p. 336). Presumably most trackways were made by slowly walking animals that placed their feet with the toes directed forward through the entire stride. It is likely, however, that the same animals running at higher speeds would evert their feet, especially the hind feet, toward the end of the stride, as high-speed films of a variety of fast-moving lizards attest (Shukanov, 1974, e.g., fig. 76, showing fast trot of *Eremias velox*). With the foot everted, the first four toes, of increasing length from I to IV, would presumably grip the substrate essentially simultaneously and exert a strong anteromedial force. Unfortunately, trackways of fast-moving sphenacodontids have yet to be recorded.

The trackway evidence strongly supports the anatomical evidence that basal synapsids were obligatory sprawlers and that they used lateral undulation of the trunk to increase stride length, as do modern sprawlers. This further supports the interpretation of these animals as having low aerobic capacity during locomotion and, therefore, of relying primarily on anaerobic activity metabolism at higher speeds, with the same negative effects on stamina and recovery as seen in living iguanians. Furthermore, reptile-grade bone histology of "pelycosaurs" (see Table 5), indicative of slow rates of growth and low levels of metabolic activity, supports the view that they had low metabolic rates and thus were ectotherms (Ricqlès, 1974, 1976).

When we look at early therapsids, we see a very different girdle and limb morphology (see Table 5): the pectoral glenoid and pelvic acetabulum are shorter and more concave, and the proximal limb bones have rounder articular surfaces. Furthermore, the femoral head is offset medially from the long axis of the bone so that when fitted into the acetabulum, the femur is oriented anteroventrally as well as somewhat outward (see Colbert, 1948). This suggests that the foot is habitually directed more anteriorly than in "pelycosaurs." This is also suggested by the shorter digits of more equal lengths, caused by reduction in the lengths of certain phalanges of the third and fourth and, in the pes, fifth digits or by loss of these phalanges (Fig. 7). In addition, therapsids show extension of the articular facets of the proximal tarsals (astragalus and calcaneum) increasingly on to the dorsal surfaces of these elements, indicating the concentration of ankle movement at a crurotarsal joint. Both carpus and tarsus of therapsids are more compact than in "pelycosaurs," and the manus and pes acted as levers to give a stronger push off the substrate at the end of the step. The hand and foot are still not completely symmetrical in early therapsids, as indicated mainly by disparity in metapodial length from digit I to IV (Hopson, 1995, figs. 1D, 2A–C, E–G). The lack of symmetry in the manus and pes of early therapsids suggests that a remnant of outward turning of the hand and foot and therefore of sprawling posture still occurred, probably at higher speeds. This also suggests that some lateral bending of the trunk continued to be important.

Evidence for retention of some lateral bending in therapsids is provided by Smith (1993, pp. 345–346, fig. 11), who described a large trackway of a presumed dinocephalian from the Middle Permian of South Africa in which the toes are slightly curved inward and the left and right tracks show that the medial sides of the footprints (especially digit I) lie on the longitudinal midline. This would happen only in a sprawling gait when the trunk is flexed from side to side, as illustrated by Smith in his reconstruction of the walking tracemaker. He believes that "the tracemaker had an elbows-out, 'rolling' gait

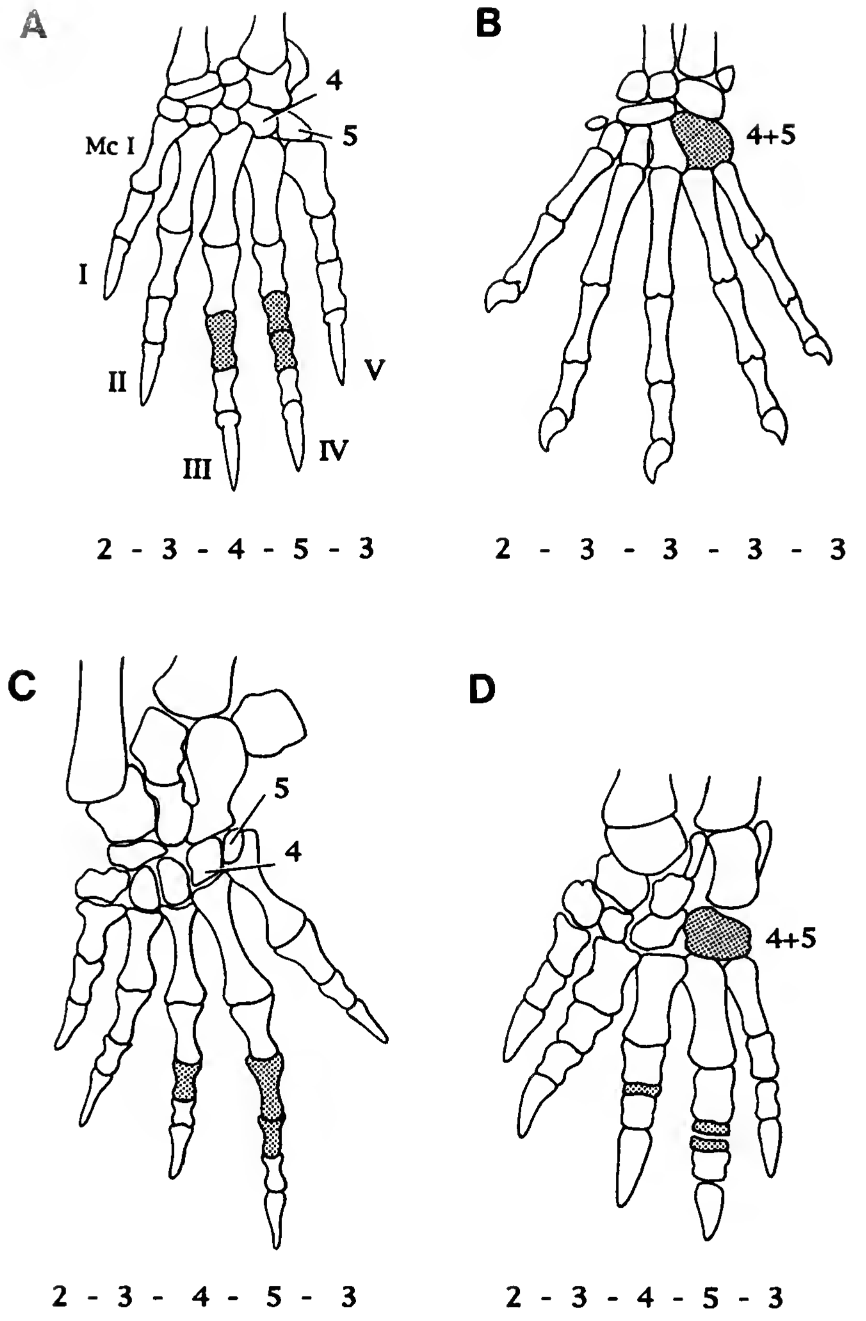

FIG. 7. The left manus of (**A**) *Sphenodon*, showing the primitive amniote phalangeal formula (but a modified, shortened digit IV); (**B**) *Didelphis*, showing the modified phalangeal formula and digital proportions of mammals; (**C**) the Early Permian sphenacodontid "pelycosaur" *Dimetrodon*, showing the primitive synapsid condition of the manus; and (**D**) the Late Permian gorgonopsian *Lycaenops*, showing an early therapsid condition of the manus. The phalangeal formula for each is given below the manus. The "extra" phalanges lost in mammals are indicated by stipple in **A**, **C**, and **D**. Abbreviations: Mc I, first metacarpal; 4, 5, separate fourth and fifth distal carpals; 4+5, fused fourth and fifth distal carpals; I–V, first through fifth digits (from Hopson, 1995).

with limited tarsal rotation … on both fore and hind limbs and *a certain amount of lateral flexure of the vertebral column*" (emphasis added). This resulted in a slight overlap of manus and pes prints and the inward curve on the toe prints." Smith's observations demonstrate that primitive therapsids retained some lateral flexion of the trunk as part of their locomotor activity, although the limbs were held in a more upright position than in primitive synapsids.

Bone histology of therapsids has been extensively studied (for summaries, see Ricqlès, 1974, 1976; Chinsamy-Turan, 2012), and it shows that the bone was metabolically very active, with heavy vascularization, extensive Haversian systems, and evidence of rapid growth during early ontogeny, with growth slowing as adult size was approached (as indicated by the appearance of incremental growth lines). This supports the view that therapsids, though not necessarily fully endothermic, possessed growth rates and metabolic activity that were greater than those of "pelycosaurs." RMRs were thus probably higher than those of ectothermic basal synapsids, suggesting an increase in resting aerobic metabolism.

The evidence of relatively rapid growth rates, active remodeling of the skeleton, and "improved" locomotion suggests that therapsids had high activity levels, similar to or exceeding those of varanids. The pattern of reduction of digit lengths in early therapsids resembles the pattern of digit shortening seen in WF autarchoglossans, including varanids. Whereas long toes of disparate lengths are characteristic of "pelycosaurs" and iguanians and thus of anaerobic sprinters, shorter toes of less disparate lengths are characteristic of autarchoglossan lizards, which engage in more sustained aerobic activity at more moderate speeds.

High aerobic capacity would seem to be a characteristic of therapsids, as it is of varanids. Early therapsids, like varanids, appear to have retained some lateral bending of the trunk as part of their locomotor repertoire. Therefore, the following question arises: how did therapsids overcome the biomechanical constraint that prevented primitive tetrapods, including basal synapsids, from developing a high aerobic capacity?

Mammals rely on the action of a muscular diaphragm to draw air bilaterally into the lungs. It is doubtful that early therapsids used gular pumping to force air into the lungs as varanids do. Therefore, I suggest that the diaphragm evolved during or shortly after the transition from sphenacodontid "pelycosaur" to basal therapsid. How it functioned with lateral bending alternately compressing and relaxing each lung is uncertain, although as limb posture became less sprawling, the amount of lateral bending and thus of alternate compression of the lungs should have decreased. A similar respiratory system operates in crocodilians, which have a diaphragm-like piston that moves the liver backward and forward, expanding and compressing the thoracic cavity and moving air into and out of the lungs (Carrier, 1987a).

The greater levels of aerobic metabolism proposed for therapsids required an efficient circulatory system. The heart of mammals appears never to have gone through a stage resembling that of chelonians and lepidosaurs, in which the ventricles were divided into three incompletely separated chambers. From an ancestor with a partially divided ventricle (as in lungfishes and presumably basal amphibians and amniotes), the Paleozoic ancestors of mammals completed the partition between pulmonary and systemic parts of the ventricles, thus separating the oxygenated blood destined for the body from the deoxygenated blood destined to pass through the lungs. I suggest that this complete separation of blood flow to the body and the lungs occurred either in the transition between sphenacodontids and basal therapsids or in early therapsids. With the complete separation of the two blood flows within the heart, the systemic circuit could develop much higher blood pressures than the pulmonary circuit, as in living endotherms. Not only could therapsids greatly increase aerobic capacity for food-getting activity, but they could increase RMRs as well. More rapid digestion of food requires greater metabolic activity of the digestive system (see Koteja, 2000), which may have provided enough metabolic heat to significantly warm the body. An evolutionary feedback loop would develop in which greater generation of metabolic energy would increase aerobie capacity, and this in turn would increase the ability to forage more widely and effectively to meet increasing energy needs. As discussed above, the expenditure of high levels of energy in searching for food by WF lizards leads to a proportionately larger amount of food energy being taken in.

Early therapsids carry on the trend seen in sphenacodontid "pelycosaurs" of specializing the enlarged canine teeth (and, in some subgroups, incisors) for the more effective capture, dispatching, and dismembering of prey. Marginal cheek teeth may be specialized in early therapsids for breaking down prey tissue, whereas palatal teeth tend to be reduced or lost. The temporal fenestra becomes increasingly enlarged in early therapsid history, indicating an increase in the mass of jaw-closing musculature (Barghusen, 1973). Thus, concomitant with improvements in the locomotor apparatus, presumably for more sustained foraging activity, were improvements in the prey-capturing and feeding apparatus for increased bite force and more efficient processing of food.

Mammals are highly olfactory and use the sense of smell to locate hidden prey, to track moving prey, and to sense and avoid predators. In this sense, they are similar to autarchoglossans, in which the vomeronasal organ rather than the olfactory system is used for chemical detection. It is likely that, early on, therapsids used olfaction for tracking and locating prey. Herbivorous therapsids, like dicynodonts, would also use their chemosensory abilities to locate dispersed food plants, as do herbivorous lizards (Herrel, 2007).

Among living lizards, the most actively foraging predators, the varanids and teiids, have the largest brains (Hopson, 1980) and appear to be most intelligent (Regal, 1978; Pianka & Vitt, 2003). Endocranial casts of Early and Middle Triassic cynodont therapsids (*Thrinaxodon* and *Trirachodon*) have brain-size-to-body-size relations similar to those of living varanids and teiids (Hopson, 1980), lying at the upper limit of the range of living reptiles. Under the interpretation of early therapsids as WF predators, increase in brain size and complexity occurred because they had to deal with a climatically and ecologically more complex world than their "pelycosaur"-grade ancestors (Kemp, 2006a), a world in which they had to search more widely and actively for food to meet the increased energy needs of a more demanding way of life.

Later therapsids, notably the Late Permian and Early Triassic baurioid therocephalians and cynodonts, evolved several features that suggest a higher, more mammal-like maintenance metabolic rate than occurred in more basal therapsids. A partial bony secondary palate formed by flat, medially extending laminae of the maxillary and palatine bones occur in baurioid therocephalians more derived than *Ictidosuchoides* of the early Late Permian (Mendrez, 1975; Hopson & Barghusen, 1986) and in primitive cynodonts (*Procynosuchus* and *Galesaurus*). In more derived baurioids, the maxillary plates either meet an expanded ventral plate on the fused median vomers (*Lycideops*, *Regisaurus*, and *Ericiolacerta*) or contact one another on the midline ventral to the vomers (Bauridae). In *Thrinaxodon* and all more derived cynodonts, both the maxillary plate and the palatine plate meet on the midline below the vomers. This fully developed bony secondary palate (and, possibly, a soft palate continuous with it posteriorly) would have separated the inspired air stream from the oral cavity, permitting continuous flow of oxygen to the lungs even if the mouth were filled with food (Hopson, 2001).

The morphology of the cheek teeth in bauriid therocephalians and all cynodonts is complex, usually with accessory cusps that created new puncturing and/or cutting components of the dentition, and sometimes with lingual expansions that created crushing surfaces. In addition, cynodonts (but not bauriids) show a great increase in size and differentiation of muscle attachment areas on the dentary bone of the lower jaw and on the temporal region of the skull (Barghusen, 1973; Crompton and Hylander, 1986), indicating an increase in mass and complexity of the muscles of mastication.

The specializations in cynodonts and, to a lesser extent, in baurioid therocephalians for breaking down food in the mouth (for rapid digestion and delivery of energy to the body) without interrupting the flow of oxygen to the lungs strongly suggest much higher energy and oxygen requirements in cynodonts than in more primitive therapsids (Hopson, 2001). Furthermore, they also suggest that RMRs, as well as maximum rates for activity, may have been significantly higher in cynodonts than in other therapsids. It is likely that cynodonts had evolved an insulating coat of hair to reduce heat loss and thus maintain higher body temperatures without extravagant expenditures of energy. In addition, some specimens of the Early Triassic cynodont *Thrinaxodon liorhinus* occur in a curled position (Brink, 1959; personal observation), possibly in burrows (Sidor et al., 2008), giving the impression that, like small mammals, they were conserving body heat. To what extent they regulated body temperature and were truly endothermic is at present impossible to determine, but the indirect evidence cited above suggests that they must have been significantly endothermic.

I would like to comment here on whether nonmammalian therapsids possessed respiratory turbinate bones, the homologs of the scroll-like maxilloturbinates of living mammals, within the nasal cavity. In living endotherms, the maxilloturbinates lie in the pathway of inspired/expired air and function to moisten and warm air coming to the lungs and reclaim water vapor and heat from exhaled air (Bennett & Ruben, 1986; Hillenius; 1992). Bennett and Ruben (1986: 211) pointed out that their presence would "provide the best anatomical evidence of endothermy in therapsids." Hillenius (1994, pp. 220–224, figs. 11, 13, 14) describes and figures bilateral longitudinal ridges on the dorsolateral walls of the nasal cavity in a primitive therocephalian and several cynodonts, which he interprets as the attachment areas for respiratory turbinates comparable to those of mammals. That they provide evidence of respiratory turbinates, and thus of elevated ventilation rates, in nonmammalian therapsids, has been generally accepted as "a clear sign that the evolution of endothermy had begun" (Hillenius, 1994: 224; see also Ruben, 1995; Ruben et al., 2012; for an alternate view, see Kemp, 2006a).

Hillenius (1994: 220) describes the ridge for a presumed respiratory turbinate in the therocephalian *Glanosuchus* as being "formed by the ventral edge of the nasal bone, which projects into the nasal cavity along its contact with the maxilla." In the cynodont *Massetognathus*, the ridge is also formed by the ventral edge of the nasal (Hillenius, 1994: 222). Hillenius argues that the ridges appear to be natural features and unlikely to be due to preservational distortion because neither specimen "has suffered any noticeable dorsoventral compression, and the bones surrounding the snout are essentially intact" (Hillenius, 1994: 222). In a serially sectioned specimen of *Massetognathus*, which does show some deformation, he notes that the nasals of both sides project inward symmetrically.

In my view, the ventral margins of the nasal bones project into the nasal cavity as a result of slight dorsoventral compression of the skulls. The thin nasal bones of therapsids are broadly overlapped laterally by thin dorsal lappets of the maxillae, with the contact surface between them being only slightly offset from the vertical. Thus, even a slight amount of diagenetic compression could push the nasal bones downward relative to the maxillae and cause their ventral margins to extend into the nasal cavity as free longitudinal ridges. This seems to me to be the more likely explanation for the projecting lower margins of the nasal bones. Observations should be made on additional therapsid specimens, including primitive taxa in which respiratory turbinates and, therefore, nasal ridges would not be expected. Ideal evidence for the presence of a turbinate attachment would be a ridge within the body of a bone, not at the contact between bones. In the meantime, however, I consider the evidence for respiratory turbinates in nonmammalian therapsids to be doubtful and their "almost Rosetta Stone-like significance" (Ruben, 1995: 85) greatly overstated.

In summary, the foraging model as developed primarily from the study of lizards (but with corroborating evidence from other groups) appears to explain a great deal about the early selective pressures leading to the development of endothermy in therapsids. My concern here is not to explain how mammalian endothermy, including a stable high body temperature, evolved. Rather, I have tried to formulate a hypothesis about the selective forces that acted on early synapsids to set in motion the chain of adaptive modifications that led to the evolution of high activity levels and that set the stage for the development of elevated levels of resting metabolism and true homeothermy. The first steps certainly involved an environmental change from a year-round hot, wet tropical, essentially constant and predictable climate to one in which seasonally dry, cool periods alternated with wetter, warmer periods and the environment became less predictable. In this more stressful environment, prey might be less abundant and more patchy in distribution, and it might take to burrowing to create a more constant microhabitat and hide from predators. Under these circumstances, the most successful strategy for a predator would be to forage widely and sharpen its chemosensory (vomeronasal) and auditory senses to supplement vision in locating hidden prey. In such circumstances, increases in resting or maintenance metabolic rates could have incrementally occurred, as advocated by Kemp (2006a,b, 2007a,b), but not before increases in aerobic activity metabolism laid the groundwork for increasing the food energy necessary to support increased maintenance rates.

Discussion

In developing the foraging mode hypothesis of the origin of therapsids, I have spent a great deal of this paper reviewing the morphological, physiological, and neurosensory features of lizards with contrasting foraging modes. From this study, I conclude that the feature that appears to be key to the origin of endothermy, the one that set in motion the chain of events that culminated in mammalian homeothermy, was an increase in aerobic capacity for sustaining high levels of activity for foraging. The underlying shift in lizard behavior that created the selection pressure for increased aerobic capacity was a change in foraging mode from that of a relatively inactive SW ambush predator, relying on anaerobic energy sources for short high-speed dashes, to that of an active WF predator, relying on aerobic energy sources for extended periods of movement over long distances. Selection for increased aerobic capacity would logically have led immediately to changes in the oxygen delivery system, for, as pointed out by Bennett et al. (1984: 117), "the cardiovascular system may be the first aspect of physiology to respond to an evolutionary change in activity level." Increase in lung complexity, heart size, and oxygen-carrying capacity of the blood, features seen in WF lizards, all promote the increase in aerobic capacity and thus in sustainable high activity levels. The resulting payoff of these changes is a significant increase in the amount of food energy taken in with respect to the amount of energy expended in acquiring it. Further selection to increase energy intake would involve changes in the musculoskeletal part of the locomotor system to increase its ability to move the predator longer distances at reduced cost. Also serving the same purpose are sensory and central nervous system changes that enhance the ability to locate and capture prey as well as changes in the food-processing system that enhance the speed of delivery of increased amounts of energy to the body. In anurans (Taigen, 1983; Walton, 1993) and snakes (Beaupres & Montgomery, 2007), the increase in activity metabolism for wide foraging is correlated with an increase in resting or standard metabolic rate (though the physiological link between the two is still controversial). Progressive increase in resting metabolism would lead to the internal generation of higher levels of body heat that could eventually be used to sustain high body temperatures and a homeothermic way of life. I endorse Regal's (1978: 195) characterization of endothermy as "simply another adaptation for [the actively foraging] way of life" that "would lock individuals into high food requirements and hence bias future evolution toward progressively refined active forager adaptations, including behaviors and mental capacities."

What I find particularly appealing about this hypothesis is that it has a solid basis in observations on living species across a variety of taxa. Widely foraging species, especially those in which intense foraging activity can be sustained for long periods, show many adaptations that were selected to increase their stamina, that is, their ability to sustain such intense activity. As the most extreme active foragers among lizards, varanids and teiids show many such adaptations. Significantly, because they evolved on different branches of the autarchoglossan tree (Fig. 1), all of the adaptations unique to the two groups were acquired convergently. Thus, selection for highly active foraging acting independently on New World teiids and Old World varanids demonstrates the fundamental power of a way of life to select for near-identical solutions to meeting its challenges. Additionally, when some groups of lizards (cordylids and some skinks, lacertids, and, perhaps, varanids) abandoned the WF hunting mode for a more sedentary SW (ambush) hunting mode, they lost much of the high aerobic capacity of their close ancestors and came to rely more on anaerobic muscle metabolism in capturing prey. This indicates that along the ecological gradient or "ridge on an adaptive landscape" that bridges the extremes of ectothermy and endothermy (see Kemp, 2007b: 11), lineages can indeed track backward as well as forward.

Counterarguments to the Aerobic Capacity Model of the Origin of Endothermy

Very different perspectives on the origin of endothermy are offered by Farmer (2000, 2003) and Kemp (2006a,b, 2007a,b).

Before considering their arguments, however, I must deal with the potentially fatal charges leveled by a reviewer of an earlier version of this paper against the aerobic capacity model of Bennett and Ruben (1979). The reviewer cites several failures of the aerobic capacity model as presented by Bennett and Ruben (1979) and as advocated in this paper, stating, "The problem is that much of [Hopson's] discussion is based on the high activity metabolism hypothesis for evolution of endothermy and it seems clear that *there is not a physiological/ genetic linkage of standard and activity metabolism*" (emphasis added). As evidence against such a linkage, he points out that activity metabolism in mammals is quite variable, whereas basal metabolism may not vary much at all. He cites experiments in which mice that were run on exercise wheels for extended periods showed a great increase in aerobic capacity over that of control lines, but resting metabolism did not differ between the two groups (Vaanholt et al., 2007). Also, experimental evidence from active lizards indicates that they can greatly increase aerobic capacity during exercise but show no difference in RMR from sedentary species that have low aerobic capacities (Bennett, 1972).

The reviewer argues that if a physiological or other causal linkage cannot be demonstrated between active and resting metabolism, then "(1) the linkage does not exist and the hypothesis is not correct, or (2) each case in which the observed pattern is not consistent with the hypothesis represents a special evolutionary event in which a decoupling of the linkage has evolved." I shall argue that the latter alternative is more likely to be the correct one.

Bennett (1991: 16) acknowledges that "the physiological basis of this linkage [between maximal and maintenance aerobic metabolic rates] is unclear" and that the association between these factors "remains a generality, without a firm mechanistic explanation or intraspecific correlational basis." He concludes that both the thermoregulatory and the activity capacity explanations for evolution of the high metabolic rates associated with endothermy "have positive features and difficulties" and that "perhaps a combination of thermoregulatory and activity capacity factors were involved simultaneously or sequentially." I agree that, in the absence of knowledge of the ecology and physiology of the ancestors of modern endotherms, we cannot know which appeared first. However, an active foraging mode and a consequent shift from anaerobic to aerobic activity metabolism, which I believe provided the initial impetus for starting the ancestors of mammals on the path to endothermy, occurred in lizards in the apparent absence of an increase in resting or maintenance metabolism; therefore, it follows that increased activity capacity probably preceded increased thermoregulatory capacity in the origin of mammalian endothermy.

Evidence of a linkage between maximum metabolic rates (MMRs) and RMRs does exist in at least two tetrapod clades (anurans and rodents) and, with less certainty, a third (snakes). Anurans and rodents show a strong positive correlation between RMR/BMR and exercise metabolic rate and the authors of the relevant studies (see below) explicitly state that their results provide clear evidence in support of the aerobic capacity model of Bennett and Ruben (1979). In the case of snakes, active foragers, mainly colubrids, have higher standard metabolic rates and field metabolic rates than ambush foragers, mainly boids, pythons, and vipers, although these differences are also strongly correlated with family membership (Beaupre & Montgomery, 2007). What must be explained then are the cases where a correlation between resting and active metabolic rates is weak or nonexistent, that is, in lizards and many mammals. A great deal has been published on the relation between BMRs and MMRs in mammals, so I shall discuss the evidence for mammals before generalizing to lizards.

Koteja (1987), in a study of metabolic rate in 17 species of mammals, did not find a strong correlation between MMR and BMR. In some species, such as canids and bats, MMR is very high and BMR is either low or "normal," whereas in others, such as bovids, MMR is lower than expected and BMR is close to or higher than expected. He concluded that "the 'aerobic capacity" model is not supported by interspecific comparison within mammals" (Koteja, 1987: 206).

Weibel and Hoppeler (2005) argue that whereas BMR appears to depend essentially on body mass, MMR shows large interindividual and interspecies variability in mammals that is related to the work or exercise capacity of the species. Thus, although basal oxygen consumption in mammals scales to approximately the 0.75 power of body mass, maximum oxygen consumption scales to the 0.872 power of body mass. The data set for maximum oxygen consumption in mammals can be partitioned into a set of smaller, less athletic species in which oxygen consumption scales to the 0.849 power of body mass and a set of "athletic" species in which it scales to the 0.942 power of body mass. These authors suggest that the steeper allometric slope of maximum oxygen consumption in mammals indicates that larger mammals have a greater relative capacity to increase metabolic rate above the resting state than do smaller mammals. For "normal" species, the ratio of maximum oxygen consumption to BMR is on the order of 6 to 10, but for "athletic" species it is 10 to 60. Among the latter, dogs and horses increase their metabolic rate 30-fold from rest to maximal exercise, whereas race horses and pronghorns (*Antilocapra*) can raise it 50-fold (Weibel & Hoppeler, 2005: 1635).

The decoupling of MMR from BMR in many mammals suggests that ecological and behavioral factors, including foraging mode and escape from predators, may be as important as genetic correlations between MMR and BMR in contributing to the wide mass-independent variation in energy expenditure seen in mammals. Thus, although some smaller "nonathletic" mammals, such as rodents, show a close correlation between MMR and BMR (Bozinovic, 1992; Hinds & Rice-Warner, 1992), larger, more intensely active mammals have much higher MMR than predicted from the allometric equation for BMR (Weibel & Hoppeler, 2005). This leads to the conclusion that in mammals, natural selection for specific adaptations related to environmental factors has modified the presumably primitive (retained in rodents) high correlation between MMR and BMR so that any remaining correlation is low to nonexistent.

I believe that this is the explanation for the low correlation in mammals and that the same phenomenon probably applies to lizards, where selection has acted to make them model ectotherms in which resting or maintenance metabolic rates are kept very low because of a reliance on basking and efficient heat transfer from the periphery to body tissues. Retention of the left systemic arch has been suggested to increase thermal transport to the body because it diverts warmed venous blood returning from the periphery away from the lungs, where it would presumably cool, and back to the systemic circulation, presumably with little heat loss (Tucker, 1966; Baker & White, 1970). This and other anatomical and physiological mechanisms may have permitted resting lizards to keep metabolic costs low and still maintain an elevated body temperature. Although this is speculative, the departure from a close correlation between MMR and RMR in lizards may have an adaptive basis related to their ecology and food-getting or other behaviors. Note that this is closely comparable to Koteja's (1987: 206) point that "the instances of bats and canids indicate that natural selection pressure towards increased power with simultaneous economical use of energy during inactive or critical periods enables animals to achieve very high rates of aerobic metabolism without maintaining high values of basal metabolic rate." As noted by Hayes and Garland (1995: 844), "Additional comparative information on ecological, behavioral, or life history correlates of metabolic rate could provide additional insight concerning selective factors."

In summary, whether or not there is a cause-and-effect relation between high aerobic activity rates and high aerobic resting or maintenance rates, it would seem that there must be a physiological connection between the two, as suggested by Bennett and Ruben (1979). No living ectotherm has a high RMR or, by mammalian and avian standards, a high MMR. Likewise, no living (nonhibernating) endotherm has a low, ectotherm-level RMR or MMR. This certainly implies that the endothermic MMR could not be attained in animals with an ectothermic resting metabolism. Therefore, on a continuum between ectotherm and endotherm, there must have been a stage during which BMR had to increase to provide the physiological substrate for a variety of activities, including a very high aerobic capacity that would permit sustained high-speed locomotion, regulation of a high constant body temperature, and maintenance of the high energy demands of reproduction and parental care. It is clear that a great deal of leeway is involved in the gross correlation of low RMR and MMR in ectothermic amniotes and very high BMR and MMR in endotherms. The lack of a close correlation between RMR/BMR and MMR in lizards and many mammals probably has a great deal to do with selection for particular adaptive traits relating to environmental demands. This would be consistent with the great range of maximum oxygen consumption between more sedentary mammals and more "athletic" mammals, such as dog, horse, and pronghorn, all of which have a moderate BMR that scales to the 0.75 power of body mass (Weibel & Hoppeler, 2005, fig. 3). A strong correlation of RMR/BMR and MMR nevertheless does occur in a major group of ectotherms, anurans (Taigen, 1983; Walton, 1993), and of endotherms, rodents (Bozinovic, 1992; Hinds & Rice-Warner, 1992). This provides powerful evidence that the correlation is a real phenomenon. I believe that it may well be the primitive relationship of RMR to MMR among tetrapods. The conditions in lizards and nonrodent mammals, which show little correlation between the two metabolic states, is then a later adaptation, the acquisition of which was due either to selection for conservation of energy while inactive (lizards, bats, canids) or to more intensive use of energy while active ("athletic" mammals). Thus, I support the second explanation suggested by the reviewer for lack of a correlation between RMR/BMR and MMR rate in some amniotes: "each case in which the observed pattern is not consistent with the hypothesis represents a special evolutionary event in which a decoupling of the linkage has evolved."

Parental Care Models for the Origin of Endothermy—Koteja (2000) argued that the initial selection pressure on the ectothermic ancestors of endotherms was for increased aerobic locomotor capacity to enhance provisioning of the young with food. This later led to increase in metabolic rate of the viscera for processing the increased parental food intake and thus the subsequent development of high RMRs and homeothermy. Farmer (2000, 2003) has argued for the opposite sequence of events, whereby selection acted initially to increase resting or BMR to increase parental ability to maintain through thermogenesis a high incubation temperature for developing young and that only subsequently did selection cause an increase in aerobic capacity to enhance collection of food for the growing offspring.

Farmer (2000: 329) points out that "although in amniotes a broad correlation does exist between an endothermic physiology and an exceptional ability to sustain vigorous exercise, a [physiological] cause and effect relationship has never been established" (see also Bennett, 1991). She suggests that "another explanation for the 'correlation' between endothermy and the ability to sustain vigorous exercise is that they have a common cause: parental care." She proposes that endothermy may have evolved to permit a constant incubation temperature for developing embryos and that subsequently vigorous sustained exercise may have evolved so that parents could secure resources needed for warming and feeding developing young. Thus, instead of a physiological linkage, there is a behavioral linkage that accounts for the coexistence of a high basal metabolism with a high activity metabolism. Farmer (2003) provides many examples of the advantages to offspring of parental provisioning of food, but they are all from living endotherms—mammals and birds. She also provides examples of the enormous energy demands on parents to provide for their young, concluding that "it is not unreasonable to suggest that the extra energy expense incurred by this parental feeding of offspring is of sufficient magnitude to cause selection for an increased ability to sustain vigorous exercise" (Farmer, 2000: 330).

Farmer's arguments about the importance of intense parental care are certainly relevant to members of the clades Mammalia and Aves, which have been, presumably from their respective origins, very high energy endotherms with near-constant high body temperatures. A relationship between rearing of offspring and their high BMRs, high aerobic capacity, and efficient food-getting abilities certainly exists. However, the animals we should be considering to understand the origin of an endothermic metabolism are the early ancestors of mammals and birds when they were still at an ectothermic stage. These are the animals, in the context of their particular environments, that we should examine to test the hypotheses of the *origin* of endothermy. In this regard, I have used living lizards as models for the physiological state of the animals involved in the "pelycosaur" to therapsid transition, where I believe (as does Kemp, 2006a) the transition to mammalian endothermy began. Fossil evidence tells a great deal about the changes in locomotor and feeding anatomy in the ancestral therapsids but unfortunately nothing about their reproductive features. No fossil eggs attributable to synapsids are known, presumably because the eggshells were leathery and uncalcified. However, because the most primitive living mammals, the monotremes, are oviparous, it is most parsimonious to suppose that all nonmammalian synapsids also laid eggs.

Basal synapsids, or "pelycosaurs," were undoubtedly ectotherms, as the tree ring–like growth lines in their long bones indicate. In all likelihood, they deposited their eggs in the ground, where the warmth of the soil and perhaps of rotting vegetation would incubate them. At most, the mother might guard the nest against predators, as living crocodilians do, but it is highly unlikely that incubation was aided by her metabolic heat. No living reptile, with the exception of incubating females of some python species (in which muscle contractions generate heat), uses metabolically produced heat to incubate eggs or warm internally retained eggs or embryos. They all use behavioral mechanisms, such as basking, to increase body temperature, never increased resting metabolism.

All basal synapsids and most primitive therapsids lack dental specializations for breaking down animal prey into small pieces for rapid digestion. If they had increased resting metabolism at all, it would probably have been by a very small increment. Also, activity metabolism was probably very low in "pelycosaurs," and they would have relied on anaerobic energy sources for a quick ambush of prey. The changes in early therapsids producing a less sprawling stance of the limbs suggest that they probably foraged more widely than did "pelycosaurs" and that they used aerobic muscle metabolism, but they may not yet have increased RMR by very much if at all. When they did elevate resting rates, perhaps to cope with cooler environments, they could have used physiologically produced body heat to incubate eggs. However, I consider this to be an incidental consequence of increasing metabolic rates due to other selective factors, not because parental care was itself the selective factor for increasing RMRs.

We have no idea whether early therapsids incubated their eggs or brought food to their hatchling offspring. If living reptiles and amphibians are an indicator, feeding of offspring by the mother is unlikely. In carnivorous therapsids where the adults have large canines and pointed cheek teeth, presumably for grasping larger prey items, the small young have tricuspid teeth and no distinct canine (Hopson, 1971; personal observation), suggesting a diet of small invertebrates. I interpret this difference as suggestive of self-sufficient offspring living independently of their parents, as occurs in most living reptiles. Hence, I believe that a protective, nurturing relationship between parent and offspring did not evolve among therapsids until they were well along in the development of a high aerobic activity metabolism and an elevated basal metabolism, at which stage their excess body heat could have been put to good use in incubating eggs and warming poorly thermoregulating hatchlings.

I am doubtful that parental care was an important factor in the primarily ectothermic predecessors of modern mammals. Rather, I believe that an elevated capacity for aerobic activity preceded increase in RMR, although they may have been correlated at a later but still primarily ectothermic stage as they are in anurans and, apparently, in snakes. However, I doubt very much that increase in resting rate could have preceded increase in active rate, as proposed in the parental care model, because, as pointed out by Hayes and Garland (1995, p. 837), a small increase in RMR would not significantly increase body temperature above ambient temperature but would nonetheless incur the cost of increased food intake, thus outweighing any benefits to be gained. For this reason, I consider it untenable that a costly increase in BMR could have preceded an increase in active (aerobic) metabolic rate on which an increased food-getting capability would be based. However, once the presumed correlated increase in active and RMRs evolved, then increases in food-getting ability, physiological thermoregulation, and incubation of eggs as well as feeding and care of offspring could also have evolved.

THE CORRELATED PROGRESSION MODEL OF THE ORIGIN OF MAMMALIAN ENDOTHERMY—A very different perspective from the aerobic capacity model is offered by Kemp (2006a,b, 2007a,b), who proposes that endothermy resulted from a "correlated progression" of character evolution leading to higher levels of metabolic activity and homeostatic regulation in the transition from "pelycosaurs" to therapsids (Kemp, 2006a: 1244). "It was a response to the availability of a seasonally arid, savanna-like biome" where the carnivorous ancestral sphenacodontid began to acquire the characters needed for a higher energy mode of life. "Here, over time, species evolved with increasingly raised aerobic metabolic rates, the *fundamental ecological purpose* of which was to regulate body temperature and water content increasingly effectively in the seasonal climate" (Kemp, 2006a: 1244; emphasis added). Thus, as noted earlier, it appears that Kemp considers selection to have acted initially to increase internal homeostasis rather than aerobic capacity for locomotion, a conclusion with which I disagree.

In his general review of the origin of mammalian endothermy, Kemp (2006b) offers his own hypothesis on its origin within the framework of his "correlated progression" model of evolution. Kemp (2006b: 473) characterizes other workers as accepting "the tacit assumption that endothermy must have evolved in a stepwise pattern, with an initial adaptive function followed only later by the addition of further functions." He argues that "this assumption is unrealistic and that evolution of endothermy can be explained by the correlated progression model, [in which] each structure and function associated with endothermy evolved a small increment at a time, in loose linkage with all the others evolving similarly. The result is that the sequence of organisms maintained functional integration throughout, and no one of the functions of endothermy was ever paramount over the others."

To illustrate this concept as applied to the origin of endothermy, he hypothesized a mutation that increased mitochondria in cells by 10% and then considered the effects that this change might have. A series of small physiological and behavioral changes would occur so that "the hypothesized 10% increase in mitochondrial number would have had an instant incremental effect on all of the functions of endothermy at the same time." This could have led to a minor shift in several dimensions of an organism's niche simultaneously, which may have been of selective advantage. The main point of the correlated progression model is that new traits "consist of small changes in one trait at a time, *spread over the whole set of traits* (emphasis added). They evolve analogously to a line of people walking forward hand in hand: any one of them can be a single pace in front of or behind the next, but no more without breaking the line" (Kemp, 2007b: 1669). Elsewhere, he states that "the several functions of endothermy actually evolved together, increment by increment, in the pattern predicted by the correlated progression model, rather than any of the hypotheses which assumed that one particular function of endothermy must have been primary."

As noted above, my hypothesis for the origin of mammalian endothermy proposes a single predominant selection pressure for a more active mode of food getting than was possible in the "pelycosaurian" ancestor of therapsids. This behavioral shift set off a chain of subsequent modifications that led to a large increase in aerobic capacity, thus permitting a greatly increased level of sustainable foraging activity. Many additional morphological, physiological, and neurological modifications occurred in the early WF therapsids that further enhanced success in the acquisition of food energy. It is likely that the first adaptations for increasing delivery of oxygen to locomotor muscles would have occurred in the cardiovascular system (Bennett et al., 1984, p. 117). Subsequently, there may have been changes in the biomechanics of the locomotor and feeding systems, the acuity of the sensory systems, and complexity of the brain and behavior. The correlated progression model might be relevant to some aspects of these modifications. However, whereas Kemp sees all aspects of the organism related to endothermy progressing on a broad front, I see some of them becoming relevant for selection only after a certain level or threshold of evolution had been reached in certain other aspects. Physiological homeothermy would not become a significant goal of selection until production of body heat at resting metabolic levels was high enough to make a difference in sustainable body temperature. As noted by Hayes and Garland (1995, p. 837), small increases in RMR would not increase body temperature significantly but would nonetheless incur the cost of increasing food intake. Therefore, aerobic activity metabolism and resting metabolism may initially have been decoupled, as it appears to be in lizards though not in anurans and snakes, until it was no longer possible to increase the former without first increasing the latter (see Bennett & Ruben, 1979).

Kemp does not discuss selection pressures from the environment that, in retrospect, could have led to fundamental behavioral changes. Once such a new selection pressure set the therapsid ancestor on a novel evolutionary course, the same selection pressure might continue to determine the direction of evolution for the duration of the trend; in the origin of mammals, this would be for an energetically expensive way of life that permitted the evolution of activities impossible for low-energy organisms. Also, as demonstrated by the evolution of relatively high levels of aerobic activity and energy use in teiid and varanid lizards, increase in aerobic capacity is intimately tied to exercise metabolism and not to resting metabolism, which in these highly active lizards appears to be no higher than that of other lizards. Thus, the increase in resting (basal) metabolism and the origin of thermoregulation in the mammalian ancestor must have been entirely consequential to an adaptively significant increase in aerobic activity metabolism and was almost certainly a response to selection for increasingly higher levels of aerobiosis. As suggested by Bennett and Ruben (1979: 650), "thermoregulation was not the sole selective advantage behind the evolution of the endothermic condition and *was, perhaps, not even the initial factor that began its evolution*" (emphasis added). They consider that "this process [thermoregulation] was directly linked with the development of high activity that was sustained by aerobic metabolism" and conclude that "the increasing capacity for both activity and physiological thermoregulation ... were tightly related and that the latter would not have occurred without the former."

The foraging mode paradigm, I believe, fits better than does Kemp's correlated progression model as an explanation for the origin of mammalian endothermy. Kemp (2006a: 1244) sees the origin of endothermy as being initiated as a response to the invasion of a "seasonally dry, savanna-like, Tropical Summer Wet Biome" that excluded wet-adapted "pelycosaurs" (see Fig. 6). This new environment would have permitted early therapsids to take advantage of it if they were "capable of existing free of standing bodies of freshwater, of tolerating high ambient temperature fluctuation, and therefore of surviving during the dry season." This implies that internal physiological mechanisms were key to the exploitation of the new environment. I suggest that an equally or even more important selective pressure in such a seasonally dry, resource-poor environment would be finding enough food for survival. Those species capable of changing their behavior and taking up an energetically more expensive mode of actively searching for patchily and widely distributed food would outcompete those conservative species locked into waiting for food items to come to them. My thesis here is that the foraging mode model proposes a specific fundamental behavioral shift that research on living species demonstrates has the power to change the selective regime; this could then cause changes in metabolism and homeostatic regulation in an easily comprehensible way. In addition, I can envision applying the foraging model to interpreting many aspects of therapsid biology in a way that I do not believe possible with the much less focused, more diffuse correlated progression model that makes no specific predictions about selective factors except that functional integration of the organism must always be maintained.

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