The Bipedal Stem Crocodilian *Poposaurus gracilis*: Inferring Function in Fossils and Innovation in Archosaur Locomotion

Jacques A. Gauthier,[1] Sterling J. Nesbitt,[2] Emma R. Schachner,[3]
Gabe S. Bever[4] and Walter G. Joyce[5]

[1] *Corresponding author:* Department of Geology and Geophysics, Yale University,
P.O. Box 208109, New Haven CT 06520-8109 USA
and Division of Vertebrate Paleontology, Peabody Museum of Natural History,
Yale University, New Haven CT 06520-8109 USA
—*email:* jacques.gauthier@yale.edu

[2] American Museum of Natural History, New York NY 10024 USA
and Jackson School of Geosciences, University of Texas at Austin, Austin TX 78712 USA

[3] Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia PA 19104 USA
and Department of Biology, The University of Utah, Salt Lake City UT 84112 USA

[4] Department of Geology and Geophysics, Yale University, P.O. Box 208109, New Haven CT 06520-8109 USA

[5] Institut für Geowissenschaften, University of Tübingen, 72074 Tübingen, Germany
and Division of Vertebrate Paleontology, Peabody Museum of Natural History,
Yale University, New Haven CT 06520-8109 USA

Abstract

We introduce a spectacular new specimen of a Late Triassic stem crocodilian identified as *Poposaurus gracilis*. It is part of a poorly known group, Poposauroidea, that, because of its striking similarities with contemporaneous stem avians ("dinosaurs"), has long puzzled archosaur paleontologists. Observed vertebrate locomotor behaviors, together with exceptional preservation of distinctive anatomical clues in this fossil, enable us to examine locomotor evolution in light of new advances in phylogenetic relationships among Triassic archosaurs. Because this stem crocodilian is unambiguously an archosaur, a diapsid, a tetrapod and a choanate sarcopterygian, we can safely infer major components of its locomotor behavior. These inferences, together with form-function constraints, suggest that *P. gracilis* was a fleet-footed, obligately erect-postured, striding biped. That behavior seems to have been superimposed on the ancestral archosaur's innovative locomotor repertoire, which includes the capacity to "high walk." These novelties persist in a recognizable form in archosaurs for at least 245 million years and are widely distributed across Earth's surface in diverse ecological settings. They thus qualify as evolutionary innovations regardless of significant differences in diversification rates among extant diapsid reptiles.

Keywords

Archosauria, Poposauroidea, Crocodylia, Aves, phylogeny, locomotion, bipedality, evolution, innovation

Introduction

Researchers have made enormous strides in the past two decades in sorting the perplexing diversity of Triassic stem crocodilians and stem avians using important new fossils combined with explicitly phylogenetic methods (Gauthier 1986; Benton and Clark 1988; Sereno 1991; Parrish 1993; Juul 1994; Novas 1996; Benton 1999; Rauhut 2003; Irmis et al. 2007; Langer et al. 2009; Nesbitt 2009, in press; Brusatte et al. 2010). Nevertheless, most Triassic species remain too fragmentary to allow us to draw firm conclusions about evolutionary trends at the root of Archosauria, even in the well-studied locomotor system (Cruickshank and Benton 1985; Gauthier and Padian 1985; Parrish 1986, 1987; Novas 1989; Gatesy 1991; Sereno 1991; Hutchinson 2006). The

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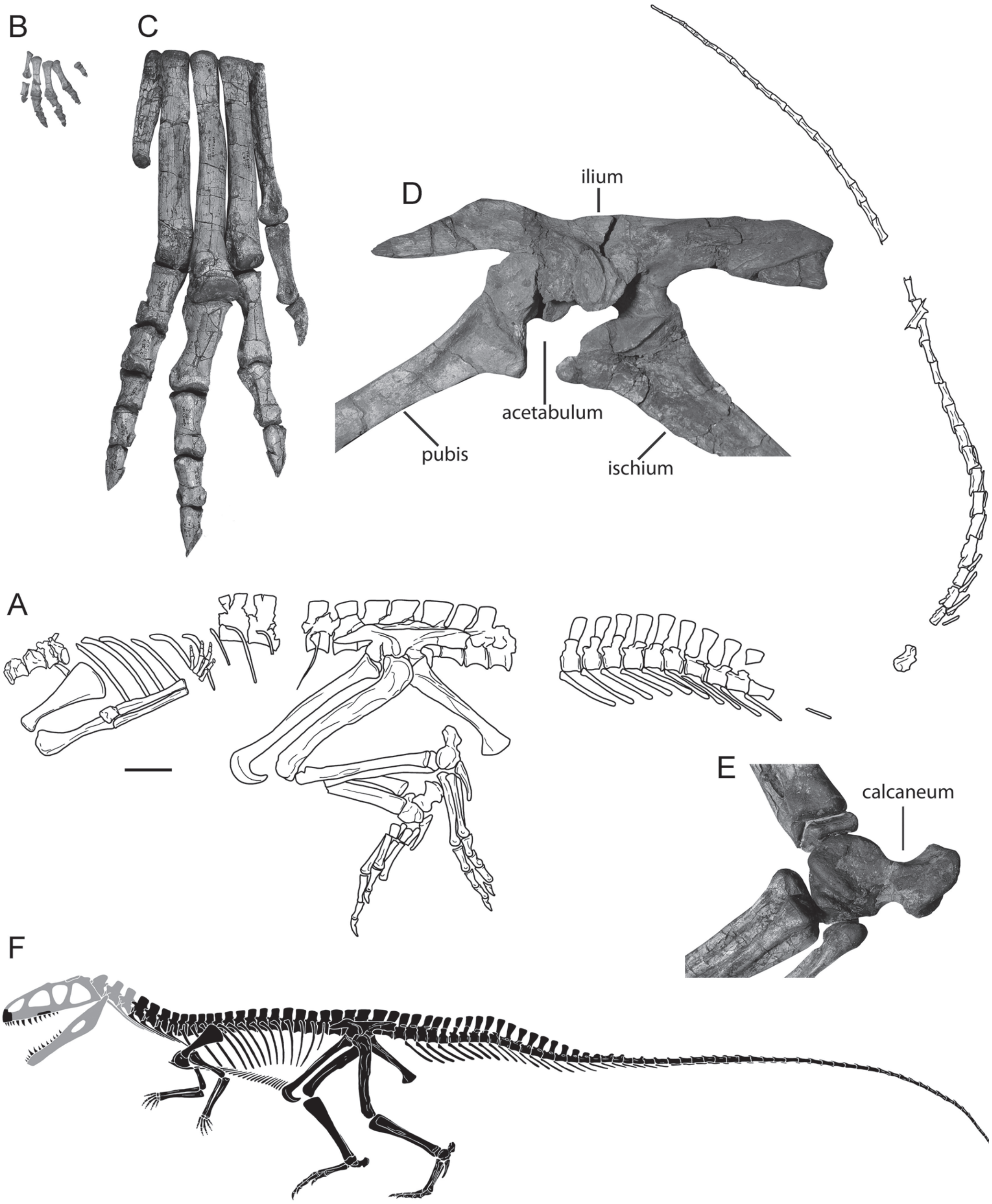

Figure 1. *Poposaurus gracilis*. **A,** Illustration of in situ *P. gracilis* (YPM VP 057100) from the base of the Chinle Formation, Circle Cliffs, Grand Staircase–Escalante National Monument, Utah, USA. Scale bar equals 10 cm. **B,** Dorsal view of left manus as found in situ. **C,** Dorsal view of left pes after extraction from the block. **D,** Left lateral view of acetabular portion of the pelvis. The femur has been removed to reveal the incompletely ossified acetabulum. **E,** Left lateral view of the left ankle in situ. **F,** Skeletal reconstruction of the bipedal stem crocodilian *P. gracilis* based on YPM VP 057100.

problem is only exacerbated by the dearth of anatomical correlates that clearly distinguish facultative from obligate behaviors (Lauder 1995). We introduce an exceptionally preserved specimen of a suchian stem crocodilian (Figure 1) from the Late Triassic (Norian) Chinle Formation of Utah, USA, which we assign to *Poposaurus gracilis* Mehl 1915. It is unique among specimens of fully terrestrial carnivorous Triassic stem crocodilians in that it consists of most of the postcranial skeleton of a single well-preserved individual in full articulation (the skull, unfortunately, is known only from the premaxillae and a few partial tooth fragments).

Assessing the stance and gait of extinct vertebrates such as *Poposaurus gracilis* has proven difficult because extant species provide few unambiguous morphological correlates applicable to fossils (Lauder 1995). Even with strong correlations, phylogenetic autocorrelation may leave little statistical power from which to evaluate their significance (Felsenstein 1985). This problem is especially acute in the case of rare evolutionary innovations; that is, synapomorphies bundled in evolutionarily stable configurations that enable organisms to confront the challenges of existence in striking new ways (Wagner and Schwenk 2000). Studying the origin of locomotor innovation is further complicated because organisms often display complex accumulations of adaptations that work in synchrony. As a result, it often remains unclear whether isolated morphological features found in incomplete fossils indicate compulsive (obligate), voluntary (facultative) or nonexpressed (potential) behaviors. Moreover, the presence in stem species of one (or more) of the features that in its descendant crown contributes to a highly integrated functional complex tightly coupled to a particular derived behavior does not necessarily support the presence of that behavior in this extinct stem species. Such characters might, after all, have appeared prior to their integration into a functional complex, and its associated behavioral capabilities, within which we observe them today (exaptation; Gould and Vrba 1982).

To avoid some of the potential pitfalls in putative form-function relations, we propose a tree-based method that predicts which locomotor capabilities *Poposaurus gracilis* should have had solely on the basis of its phylogenetic position—without even considering its morphology in a "functional" sense. In this method, described below, tree topology and justified inferences based on observed locomotor repertoires in extant species provide a null hypothesis about which behaviors should be present in an extinct species. That null hypothesis can then be tested in light of the anatomical details preserved in the fossil in question.

Institutional abbreviations used in this paper include: AMNH, American Museum of Natural History, New York, New York, USA; BMNH, Natural History Museum, London, United Kingdom; BPI, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; IGM, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico; MNHN, Muséum national d'Histoire naturelle, Paris, France; OUM, Oxford University Museum, Oxford, United Kingdom; SAM, South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, Texas, USA; TTUM, Texas Tech University Museum, Lubbock, Texas, USA; YPM HERR, Division of Vertebrate Zoology Herpetology Reptile Collection, YPM VP, Division of Vertebrate Paleontology Collection, and YPM VPPU, Division of Vertebrate Paleontology Princeton University Collection, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Systematic Paleontology

Archosauria Cope 1869,
sensu Gauthier and Padian, 1985
Suchia Krebs 1974,
sensu Benton and Clark, 1988
Poposauroidea Nopcsa 1923,
sensu Nesbitt, in press
Poposaurus gracilis Mehl, 1915

Holotype. FMNH 357, two dorsal vertebrae, one caudal vertebra, a left ilium, the proximal portion of a left femur, a right femur, distal portion of the ischia.

Type locality and horizon. "[N]ear Lander" (Mehl 1915), Freemont County, Wyoming, USA; Popo Agie Formation, Late Triassic.

Temporal and spatial range of referred material. ?Carnian–early Norian, Late Triassic: Popo Agie Formation, Wyoming, USA; Blue Mesa Member, Chinle Formation, Arizona; Mesa Redondo Member, Chinle Formation, Arizona, USA; Tecovas Formation, Dockum Group, Texas, USA; Monitor Butte Member, Chinle Formation, southern Utah, USA.

Material referred here. YPM VP 057100, nearly complete skeleton lacking most of the skull, Monitor Butte Member, Chinle Formation, Late Triassic, Circle Cliffs, Grand Staircase–Escalante National Monument, Garfield County, Utah, USA. More detailed locality information is archived at the Yale Peabody Museum Division of Vertebrate Paleontology.

Remarks. All elements preserved in the holotype are directly comparable to those of YPM VP 057100. According to the revised diagnosis of *Poposaurus* and *P. gracilis* of Weinbaum and Hungerbühler (2007), the holotype and YPM VP 057100 share the following unique combination of character states: long, low iliac blade; blade-like preacetabular process; postacetabular process elongate and expanded into a wing-like process; a thick lateral ridge posterior to the acetabulum; and a pit on the proximal ischium for reception of the ischial process of the ilium (Figure 2).

Furthermore, both the holotype and YPM VP 057100 were scored independently in the phylogenetic analysis presented in Nesbitt (in press; see Figure 4). The holotype of *Poposaurus gracilis* was found to be the sister of YPM VP 057100, a position supported by one ambiguous synapomorphy: the presence of a ridge connecting the posterior portion of the supra-acetabular rim to the posterior portion of the ilium (character 272[1] in Nesbitt [in press]). This character state is essentially equivalent to “a thick lateral ridge posterior to acetabulum” of Weinbaum and Hungerbühler (2007).

Methods

To understand how *Poposaurus gracilis* walked, we apply a three-pronged approach to exploring the innovations in terrestrial locomotion that this species inherited from successively more distant ancestors within Osteichthyes (Figure 3). In the first step, we infer the phylogenetic placement of the taxon in question. In the second step, we then consider the distribution of observable locomotor behaviors to infer the sequence in which these arose during phylogeny. This builds on the logic of ancestral state reconstruction that de Queiroz and Gauthier (1992) referred to as “justified inferences” and Witmer (1995) termed the “extant phylogenetic bracket.” Both methods rely on parsimony-based character optimization sensu Farris (1983): the former maintains that the last ancestor of a crown clade can safely be inferred to have had any characters, including plesiomorphies and “ambiguous” characters unknown in stem fossils (such as a four-chambered heart), so long as those characters are observed in their living descendants; the latter method focuses mainly on inferring soft, unlikely-to-be-preserved characters in extinct organisms within crowns. The first two steps in this three-pronged approach are the basis for our null hypothesis; namely, we expect descendants—in this case *P. gracilis*—to retain the locomotor capacities of their ancestors. In the third step, we refine our hypothesis regarding locomotor behavior in extinct *P. gracilis* by focusing on mechanically limiting, or at least tightly coupled, morphofunctional relations observable in this fossil. The constraints so identified can then lead us to partially or fully reject our null hypothesis, that *P. gracilis* could perform all behaviors inferred to have been present in the ancestral archosaur.

The phylogenetic hypothesis used herein is taken from the analyses of Nesbitt (2009, in press), which contain 83 species and 412 characters and resulted in 360 most parsimonious trees of 1285 steps (consistency index 0.375, retention index 0.776).

Results

Phylogenetic Placement of Poposaurus gracilis

A parsimony-based phylogenetic analysis of early Archosauriformes performed in Nesbitt (2009, in press) largely supports the current consensus in basal archosaur phylogeny (Figure 4). For example, most species assigned previously to either bird-line (Pan-Aves) or crocodile-line (Pan-Crocodylia) archosaurs remain as such, and these two great branches of the archosaur tree seem to have diverged shortly after the Permian–Triassic mass extinction (Nesbitt 2009, in press). The recently described silesaurid *Asilisaurus kongwe* from the Anisian of Tanzania predicts that the basalmost divergences within Pan-Aves (for example, Pterosauria and possibly Dinosauria) occurred by at least the mid-Triassic (Nesbitt et al. 2010). Our focal species, *Poposaurus gracilis*, lies deep in the crocodilian stem clade in the branch Poposauroidea, a clade that also includes the bizarrely modified *Effigia okeeffeae* and *Arizonasaurus babbitti*.

Justified Inferences about Vertebrate Appendicular Locomotion

Walking on land may be the archetypal adaptation of crown Tetrapoda, even though important components of that behavior originally arose underwater. Ray-finned fish (Actinopterygii) and the coelacanth (*Latimeria chalumnae*), for example,

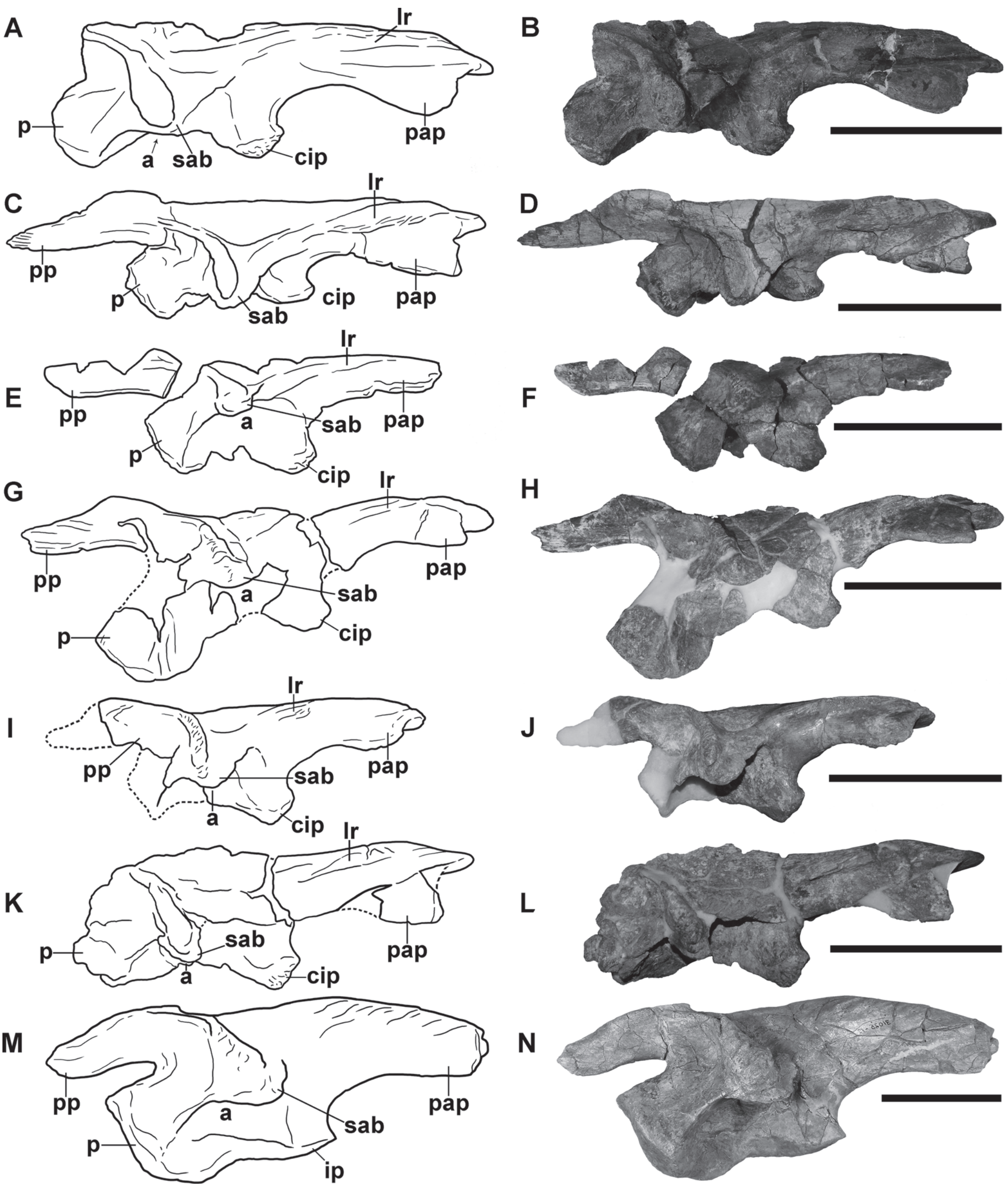

Figure 2. The ilia of specimens referable to *Poposaurus* in left lateral view (unless otherwise noted). **A, B,** Illustration and photograph of the ilium of the holotype of *Poposaurus gracilis* (FMNH UR357). **C, D,** Illustration and photograph of the ilium of *P. gracilis* (YPM VP 057100). **E, F,** Illustration and photograph of the ilium of *P. gracilis* (TMM 4368). **G, H,** Illustration and photograph of the right ilium of *P. gracilis* (TTUM 10419); image flipped horizontally. **I, J,** Illustration and photograph of the ilium of *P. gracilis* (TTUM 9243). **K, L,** Illustration and photograph of the ilium of *P. gracilis* (TTUM 11203). **M, N,** Illustration and photograph of the right ilium of *P. langstoni* (TMM 31025-12); image flipped horizontally. Scale bars equal 10 cm. *Abbreviations:* a, acetabulum; cip, concave ischial process; ip, ischial process; lr, lateral ridge; p, pubic process; pp, preacetabular process; pap, postacetabular process; sab, supraacetabular buttress.

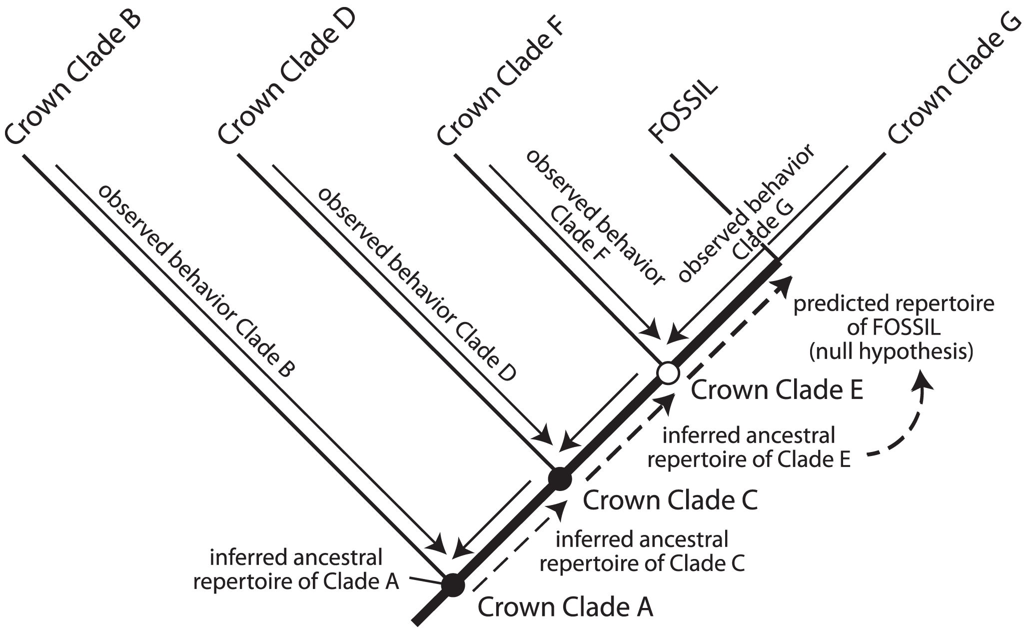

FIGURE 3. Diagrammatic representation of the three-pronged approach (dashed-line arrows) used to study the locomotor ability of *Poposaurus gracilis*. Step 1 involves determining the phylogenetic relationship of the fossil taxon of interest. A null hypothesis of that fossil's behavioral repertoire is then established (Step 2) by reconstructing the ancestral repertoire of the least inclusive crown clade containing that fossil (Crown Clade E). This repertoire is inferred from behavioral observations of the extant representatives of this, and successively more inclusive, crown clades and serves as the null hypothesis of what that extinct taxon should be doing behaviorally based solely on its position on the tree. Step 3 is the testing of this hypothesis by determining which of these predicted behaviors are precluded, or elaborated, based on the morphology of the fossil.

are like tetrapods in that they can use their mobile pectoral appendages (Mckenzie et al. 2007)—and in *Latimeria* muscular pelvic appendages as well (Fricke and Hissmann 1992)—to propel themselves while swimming at low speeds. It thus seems reasonable to suppose that the ancestor of crown Sarcopterygii could do likewise. And because living lungfish (Dipnoi) also have the alternating step cycle characteristic of Tetrapoda (Greenwood 1986; Kemp 1986), the ancestral choanate (Choanata) likely could forage by dragging itself, primarily with its forelimbs, across a submerged, and perhaps even subaerial, substrate. On land, however, tetrapods normally hold themselves off the ground on all four limbs while walking and, indeed, most of the metabolic costs of terrestrial locomotion derive from simply supporting body weight (Teunissen et al. 2007). Moreover, their robust hindlimbs assumed a far greater role in locomotion than was the case in the ancestral choanate (Clack 2002); while the forelimbs could still be said to be "pulling" the body along, the hindlimbs were now "pushing" the body forward during terrestrial locomotion in crown tetrapods.

Hindlimb Locomotion in Diapsid Reptiles

The role of the hindlimbs in lizard locomotion has received considerable attention, particularly in relation to facultative bipedality (the ability to achieve a bipedal stance while sprinting; Snyder 1954, 1962; Huey and Hertz 1984; Snell et al. 1988; Losos 1990; Sinervo and Losos 1991; Sinervo et al. 1991; Garland and Losos 1994; Bauwens et al. 1995; Irschick and Jayne 1998, 1999; van Damme and Vanhooydonck 2001; Aerts et al. 2003; Husak and Fox 2006; Husak et al. 2006; Peterson and Husak 2006; Goodman 2007; Clemente et al. 2008). There is surprisingly little gain in either speed or efficiency to running bipedally, as opposed to quadrupedally, in a sprawling posture, and the energetic advantages of bipedal locomotion remain obscure (Clemente

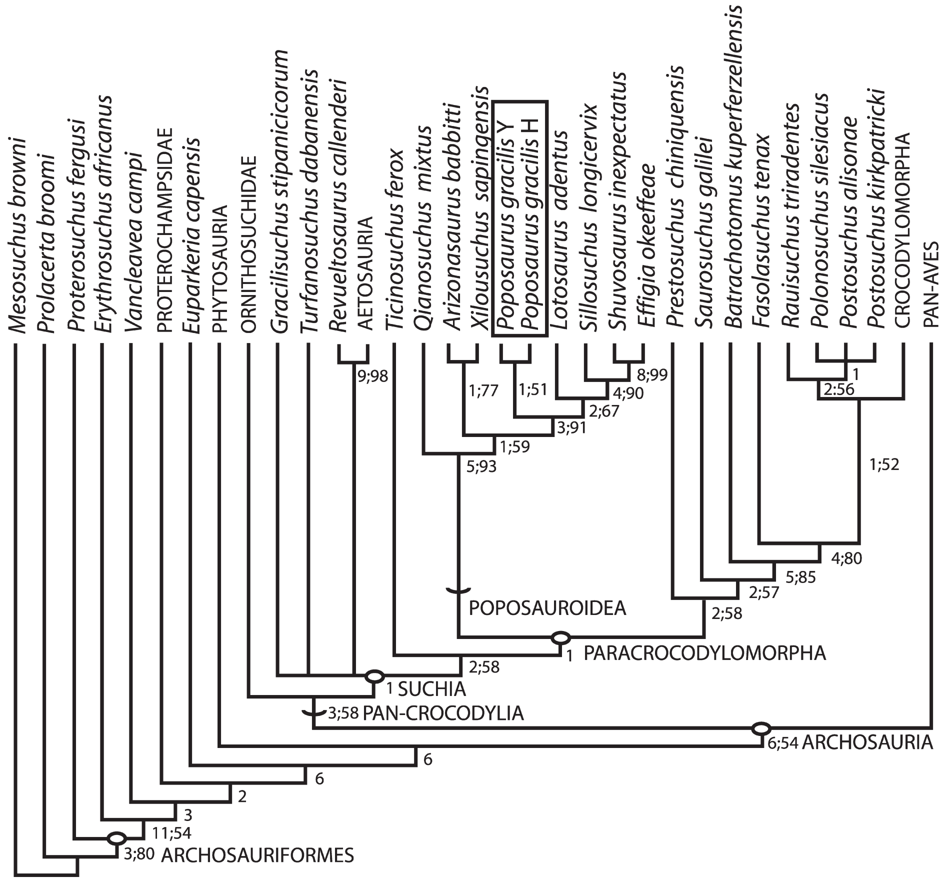

FIGURE 4. Phylogenetic placement of the holotype of *Poposaurus gracilis* (H) and that of the new specimen *P. gracilis*, YPM VP 057100 (Y) according to Nesbitt (2009, in press). Taxa in uppercase letters are collapsed for brevity, but were originally represented by at least two species (see Nesbitt, in press). Numbers below nodes refer to Bremer support (on left) and bootstrap partitions (if more than 50%; on right).

et al. 2008; Rocho-Barbosa et al. 2008). Potential advantages of seeing farther while running bipedally have not been explored, though being seen in this pose may have its rewards (Husak and Fox 2006; Clemente et al 2008). But note that a neck modified to elevate the head well above the body arose deep in the archosaur stem shortly after the origin of crown diapsids (Gauthier 1994). This would have further broadened the visual field available to this originally macropredatory clade, an adaptation that is particularly marked in exceptionally long-necked bipedal archosaurs such as poposauroids and dinosaurs.

Yet simply having exceptionally long hindlimbs whose enlarged muscles are the primary force producers during locomotion, especially at speed or while leaping or climbing, is diagnostic of crown Diapsida, and not just lizards. Indeed, Pennsylvanian stem diapsids such as *Petrolacosaurus kansensis* are like other Paleozoic amniotes, and like living turtles (Table 1), in retaining forelimbs and hindlimbs of roughly equal length (Reisz 1981). In contrast, the last ancestor of crown diapsids had shorter forelimbs that were only about two-thirds the length of its much longer hindlimbs (Gauthier 1994). This results in an even more caudal displacement in the center of mass in crown diapsids, and may underlie facultative bipedality in small diapsids while accelerating in a sprawling posture (Aerts et al. 2003; Clemente et al. 2008).

Limb proportions have varied considerably during the past 310+ million years of amniote history. Perfectly preserved specimens suitable for morphometric analyses are uncommon in the early

Table 1. Femur-to-humerus ratios among select representatives of Tetrapoda and the sources from which these values were derived.

Species	Ratio	Source
Stem amniote		
Limnoscelis paludis	0.92	YPM VPPU 000811
Stem mammals		
Caseidae		
Casea broilii	0.89	Olson 1968
Caseoides sanangloensis	0.92	Olson 1968
Cotylorhynchus romeri	0.91	Olson 1968
Varanopidae		
Varanops brevirostris	1.21	Langston and Reisz 1981
Aerosaurus wellesi	1.18	Langston and Reisz 1981
Ophiacodontidae		
Ophiacodon uniformis	1.12	Romer and Price 1940
Ophiacodon retroversus	1.15	Romer and Price 1940
Edaphosauridae		
Edaphosaurus boanerges	1.12	Hurlburt 1999
Sphenacodontidae		
Dimetrodon limbatus	1.13–1.23	Ontogenetic series, Romer and Price 1940
Haptodus garnettensis	1.06	Laurin 1993
Sphenacodon ferocier	1.11	YPM VP 000818
Stem turtles		
Milleretta rubidgei	1.26	Gow 1972
Odontochelys semitestacea	1.09	Li et al. 2008
Proganochelys quenstedti	1.08	SMNS 16980
Eudibamus cursorius	1.40	Berman et al. 2000
Nyctiphruretus acudens	1.21	Cisneros 2008
Barasuchus sp.	1.14	Cisneros 2008
Tichvinskia vjatkensis	1.06	Cisneros 2008
Procolophon trigoniceps	1.02	Cisneros 2008
Sclerosaurus armatus	1.06	Cisneros 2008

Continued

Table 1 continued

Species	Ratio	Source
Stem diapsids		
Captorhinus	1.10	Case 1911
Hylonomus lyelli	1.10	Carroll and Baird 1972
Paleothyris acadiana	1.08	Carroll and Baird 1972
Araeoscelis sp.	1.12	Reisz et al. 1984
Coelurosauravus elivensis	1.07	Carroll 1978
Claudiosaurus germaini	1.13	Type, MNHN 1978-6-1
Youngina capensis	1.48	Gow 1975
Crown diapsids		
Stem archosaurs		
Protorosaurus speneri	1.56	Gottmann-Quesada and Sander 2009
Prolacerta broomi	1.64	BPI 2676
Chasmatosaurus yuani	1.48	Young 1963
Euparkeria capensis	1.40	SAM 7696
Stem lepidosaurs		
Saurosternon bainii	1.41	Type, BMNH 1234
Icarosaurus siefkeri	1.73	Type, AMNH 2101
Stem squamate		
Huehuecuetzpalli mixtecus	1.56	Type, IGM 7389
Crown squamates		
Dipsosaurus dorsalis	1.40	YPM HERR 013364
Leiolepis triploida	1.42	YPM HERR 12864
Eichstaettisaurus schroederi	1.40	Type, BSPG 1937 I 1a
Aspidoscelis tigris	1.43	YPM HERR 013342
Stem sphenodons		
Kallimodon pulchellus	1.33	BSPG 1887 VI 1
Homeosaurus sp.	1.46	BSPG 1922 I 15
Crown sphenodon		
Sphenodon punctatus	1.20	YPM HERR 010646

amniote record, so paleontologists often rely on the femur–humerus ratio as a proxy for relative limb length. Even by that imperfect measure—for example, most of the added hindlimb length in the teiid lizard *Aspidoscelis tigris* is contributed by the foot—there is nonetheless some phylogenetically informative variation. Among the earliest Paleozoic amniotes, for example, there were apparently at least two transitions from a humerus that was longer than the femur (the original tetrapod condition) to one in which the femur was about 10% longer than the humerus (that is, once in early stem mammals and once in early stem reptiles; see Table 1). Surprisingly, *Eudibamus cursoris* (Berman et al. 2000), an aberrant stem turtle (Lyson et al. 2010; but see Rieppel and Reisz 1999 for an alternative view), rivals crown diapsids in the ratio of hindlimb to presacral vertebral column length. Snyder (1962) found this relation to be the most sensitive indicator of the capacity for facultative bipedality in sprawling lizards today. Nevertheless, with a femur that is about 40% longer than the humerus, crown diapsids are the only major reptilian clade whose ancestor was committed to locomotion on the basis of powerfully developed hindlimbs (see Table 1).

Upright Archosaurs

Locomotor systems in amphibious crocodilians and volant avians are wildly divergent, complicating inferences about the capabilities of their last common ancestor on the basis of behavioral observations of living species alone. Neither clade seems to have conserved the ancestral locomotor system fully intact (Gatesy and Middleton 1997; Reilly and Elias 1998). Avians are obligate bipeds unable to sprawl like other reptiles (although there are some conspicuous exceptions among the foot-propelled divers). Crocodilians remain quadrupedal, retain a long heavy tail, and can use the full range of hindlimb postures from sprawling to more upright poses (Reilly and Blob 2003). But crocodilians are no less remarkable among archosaurs for being slow-growing, low-energy ambush predators that rely mainly on the tail for propulsion while swimming (Willey et al. 2004) and they have relatively short limbs conspicuous for their negatively allometric pattern of growth (Dodson 1975).

As the largest living reptiles, most crocodilians are, moreover, simply too heavy to be effective runners. Many crocodilians surpass the 119 kg body mass optimal for erect-postured running in mammals and all far exceed the 48 g optimal for sprawling-postured running in lepidosaurs (van Damme and Vanhooydonck 2001). Indeed, 600 kg adult *Gavialis gangeticus* are ungainly at best on land, often merely belly sliding along the ground, and have never been reported to high walk, much less to gallop (C. Brochu to J. A. Gauthier, pers. comm. 2010). The controversial position of *Gavialis* in crocodilian phylogeny further complicates the matter; if that species is embedded within Crocodylia, as molecular data indicate (e.g., Willis et al. 2007), then poor performance of *Gavialis* on land would be autapomorphic; but if it is sister to all other crown crocodilians, as morphology suggests (e.g., Brochu 2003), that might compromise our ability to safely infer the locomotor behavior in the last ancestor of Archosauria. We must rely on anatomical correlation and broaden our phylogenetic scope for progress on this question.

Given the relatively large hindlimbs ubiquitous among diapsids and early archosaurs such as the near-crown stem archosaur *Euparkeria capensis* (Ewer 1965), early stem crocodilians such as *Gracilisuchus stipanicicorum* (Romer 1972; Nesbitt, in press) and early stem avians such as *Lagosuchus talampayensis* (Bonaparte 1975; Sereno and Arcucci 1994), it seems that the relatively very reduced limbs of adult *Gavialis* are autapomorphic regardless of uncertainty in its relationships among crown crocodilians. This suggests that it would be inappropriate to regard the inability of *Gavialis* to raise itself off the ground as somehow an evolutionary reversal to the ancestral condition for archosaurs. On the contrary, its poor performance on land is likely a consequence of adaptation in this specialized riverine piscivore to an even more profound commitment to aquatic habits than is generally the case among amphibious crown crocodilians.

It seems safe to infer that the capacity of the hindlimbs to assume an upright posture in a high-walking crocodilian is homologous with the fixed posture of the legs in an obligately bipedal avian (regardless of how many subsequent changes in hindlimb form and function occurred along the avian line after it diverged from the crocodilian line). The last ancestor of Archosauria could thus, at least at low speeds on land, perform a “high walk” in which the hindlimbs swung in a more parasagittal plane closer to the center of mass, with the knees and foreshortened toes pointing forward throughout the step cycle (Gatesy 1991; Hutchinson and Gatesy 2000; Reilly et al. 2005).

A suite of anatomical changes in the feet, legs and pelves thought to enable a more upright pose and parasagittal gait (Parrish 1986)—coupled with those strengthening the torso and enhancing dorsoventral flexion of the vertebral column (Frey 1984), as well as complex lungs with unidirectional airflow (Farmer and Sanders 2010) and mammal-like hearts that pumped oxygenated and deoxygenated blood from separate chambers (fully divided ventricles; Goodrich 1919)—are jointly thought to facilitate the ability to breathe while running in the ancestral archosaur (Carrier 1987; Farmer 1999; Carrier and Farmer 2000). The sequence of emergence of musculoskeletal characters anatomically correlated to this style of locomotion in the archosaur stem is reasonably well understood and seemingly this system was fully in place by the earliest appearance of archosaurs in the fossil record (early Triassic [Scythian]; Parrish 1987; Gatesy 1991; Sereno 1991; Gauthier 1994; Hutchison and Gatesy 2000).

A more upright pose likely antedated Archosauria, because evidence of such behavior is also preserved in fossil trackways attributed to the phytosaurian sister to crown Archosauria (Padian et al. 2009; Figures 4 and 5). This further confirms the hypothesis that the so-called "crocodile-normal" crurotarsal ankle joint, in which a rotatory calcaneum with a prominent heel that turned along with the foot on a slightly hemispherical "ball" on a fixed astragalus, antedates the origin of Archosauria. That is, only the convex distal portion of the diagnostic concavo-convex articular surface originally present on the astragalus of Archosauromorpha (Benton 1985) is involved in the crurotarsal joint ancestral for Archosauria (Gauthier 1994). The proximal portion of the original joint surface above the perforating artery (proximal to the ankle in crown archosaurs) was lost as the tibia and fibula shifted to nearly contact one another at their articulations on the ankle within Archosauriformes. In this model of character evolution, the "crocodile-reversed" joints of *Euparkeria capensis* and Ornithosuchidae are but variants of the "crocodile-normal" joint, rather than representing separate evolutions of intratarsal mobility within Archosauriformes from different parts of the ankle as originally conceived (Cruickshank 1979).

Nevertheless, the relatively primitive form of crurotarsal joint in phytosaurs is distinctly less modified compared to the fully elaborated crurotarsal system of stem crocodilians in general, and suchians in particular (Parrish 1987; Sereno 1991). In contrast, crurotarsal motion is reduced (*Lagosuchus talampayensis*), and then is lost entirely (*Silesaurus opolensis*), in the evolution of the simplified hinge-like ankle joint (Novas 1989) characteristic of striding bipedal, cursorial pan-avians (Gauthier and Padian 1985).

On the basis of the distribution of locomotor behaviors among ingroups and outgroups, we can safely infer that the ancestral archosaur could crawl (belly-slide) and run in a sprawling posture (but see Reilly and Elias [1998], for an alternative view). Its ability to high walk at slow speeds also seems a justifiable inference. But it remains unclear whether the ancestral archosaur could produce a gallop—with all four feet airborne during the step cycle—in this upright pose. The capacity to gallop is evidently widespread in Crocodylidae (Britton 1995–2009), but it has yet to be reported in Alligatoridae. Moreover, no cases of bipedality, facultative or otherwise, have been reported in any living crocodilian.

Crown avians are, of course, derived in that they are obligately bipedal, a mode of locomotion seemingly of great antiquity in the avian stem, as close-set, digitigrade, tridactyl trackways from the Triassic attest (Leonardi 1989). Avians are also able to produce a fully suspended phase in the step cycle at speed (e.g., Rubenson et al. 2007), albeit in a bipedal rather than a quadrupedal pose as in crocodylids. An apomorphic behavior could of course be conserved even if how it is achieved changes over time; sharks and snakes may ingest prey in very different ways, but it is no less clear that they inherited jaw-based prey prehension from their last gnathostome ancestor. Thus, the ability to take such a long stride as to produce a fully suspended phase in the step cycle at speed could be conserved from the locomotor repertory present in the last common ancestor shared by extant crocodilians and avians.

Note that juveniles of the smaller and more terrestrial living crocodylids display elaborate neuromuscular control while running (e.g., Renous et al. 2002) and can even produce a bounding symmetrical gallop at high speed (e.g.,

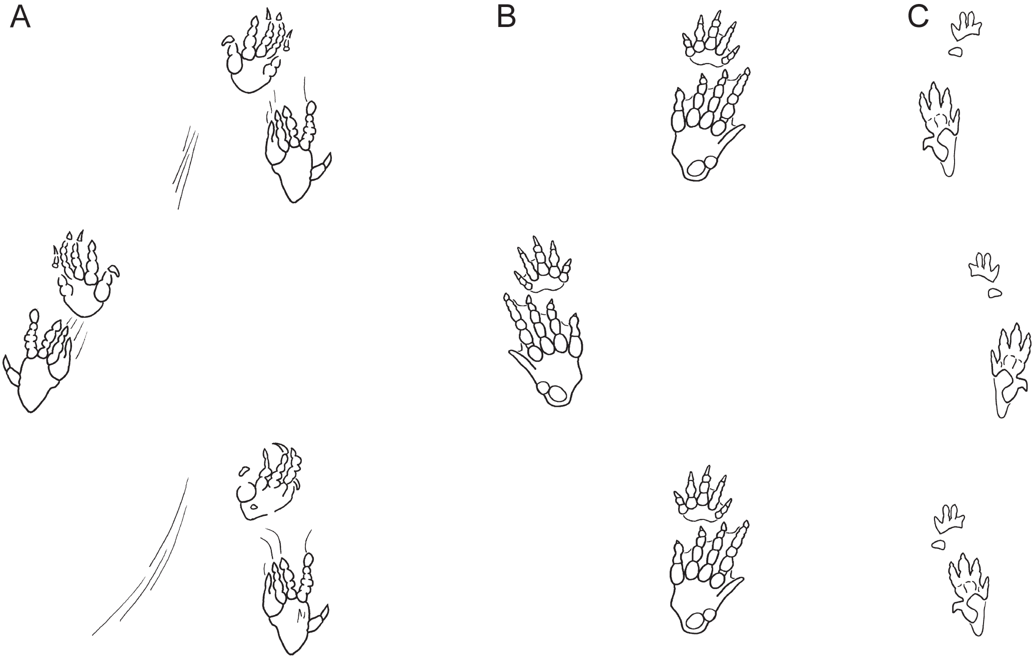

Figure 5. Comparison of trackways among tetrapod vertebrates with "sprawling" (A), "upright" (B, C) and "narrow-track" (C) limb postures. All trackways are scaled to the same stride length. **A,** Tracks of the extant varanid lizard *Varanus komodoensis*, redrawn from Padian and Olson (1984). **B,** Tracks from the Triassic trackway called *Apatopus lineatus*, redrawn from Baird (1957). **C,** Tracks from the Triassic trackway called *Chirotherium storetonense*, based on specimen OUM G.55.

Crocodylus johnstoni Zug 1974; Webb and Gans 1982). And although large alligatorids are not particularly nimble, forest-dwelling *Paleosuchus* spp.—so committed to a terrestrial existence as to have lost the webbing on their feet—are said to be remarkably agile and fleet-footed, even if their ability to gallop has yet to be determined (P. Brazaitis to J. A. Gauthier, pers. comm. 2010). Given the overall similarity in postcranial anatomy among most living crocodilians, it is tempting to consider that the ability to produce a gallop at speed could be regarded as a potential behavior for the ancestor of crown Crocodylia.

In any case, this gait was simply not available to the diapsid ancestor, which still retained an unmodified amniote femur with an internal trochanter, an intertrochanteric fossa, a ventral ridge system, asymmetrical feet and an obligately sprawling limb posture (Romer 1956). In contrast, basal archosaurs display characteristically "crocodyloid" femora, with prominent fourth trochanters, in which the original ventral features are gone, enabling the femur to swing closer to the body in a more parasagittal plane (Romer 1956). Given their small size relative to extant crocodilians, their long and powerful diapsid hindlimbs and their presumed terrestrial habits, the basalmost archosaurs could well have been able to achieve a gallop while sprinting in an upright posture. Likewise, provided it was not too heavy, that ancestor could even have been able to achieve a bipedal gait at speed (Ewer 1965); that seems especially likely for Triassic stem avians such as *Lagosuchus talampayensis,* whose very long hindlimbs relative to presacral column length are distinctly bird-like in this respect (Bonaparte 1975; Sereno 1991).

Testing the Null Hypothesis: Striding Bipedality in Poposaurus gracilis

Given its phylogenetic position, it seems safe to infer that *Poposaurus gracilis* could at least perform the "high walk" at low speed, which is to say that it had an "upright" posture as that term is defined here (see Figure 4). Instead of the usual "semi-erect" and "fully erect" distinction, we prefer to think of the stages in archosaur locomotor evolution as first being "upright" followed by the fixation of "bipedal" habits along the avian stem. The upright posture is facilitated mainly by the hindlimbs, as anatomical correlation indicates that the forelimbs were held in a more flexed pose in the archosaur ancestor (e.g., Santa Luca 1980), as they are in crocodilians (and avians) today. "Fully erect" postures, in which the forelimbs are also held in a vertical pose close to the body, apply in archosaurs mainly to some giant dinosaurs in which the demands of bearing weight are paramount.

Ultimately, the fossil itself must condition further inferences about the full range of the locomotor capabilities of *Poposaurus gracilis.* That is to say, inferences about the ancestral archosaur based on observations of its living descendants hardly guarantees that every descendant can, for example, "high walk" (hummingbirds cannot walk). Although there may be substantial limits to inferences that are based on anatomical correlation—not the least of which is that specialized functions can be performed by non-specialized forms (Greene 1982)—some morphological modifications are nonetheless tightly coupled with particular activities (such as a prominent anterior process on the ilium and the capacity to extend the ankle anterior to the knee in sprawling lizards) and others are mechanically limiting (for example, avian hip, knee and ankle anatomy prohibits sprawling limb postures).

The pelvic and femoral morphology of *Poposaurus gracilis* makes it clear that it was upright. We submit further that it also walked with footfalls very close to the mid-line, more like an avian than a crocodilian (see Figure 5). We base this inference primarily on hallmark modifications to the pelvic girdle—most notably an overhanging, finger-like extension of a prominent supra-acetabular buttress that entraps the femoral head dorsolaterally—that prevent the hindlimb from assuming a sprawling pose without disarticulating at the hip joint (see Figures 1 and 2). This constraint would also fix the height of the acetabulum relative to footfall while running, yielding the more graceful gait with less vertical displacement of the center of mass as in cursorial mammals and birds and very unlike the more lumbering gait of living crocodilians (Reilly et al. 2006).

That the hindlimbs were typically held in a more vertical pose is also supported by additional tightly coupled functional modifications to the acetabulum: the hip socket is deep, ventrally oriented and partly open medially owing to an incomplete ventral margin of the ilium and reduced contributions of the pubis and ischium to the acetabulum. These modifications indicate that the weight of *Poposaurus gracilis*, as in other suchians (Bonaparte 1981), was primarily transmitted vertically down the hindlimbs, rather than laterally through the acetabular wall and out the femur as in sprawling tetrapods. The caudal aspect of each femoral shaft also shows enlarged attachment sites for the adductor muscles, which would have kept the limbs aligned along the parasagittal plane during locomotion (Schachner 2010). This was possibly a myological adaptation associated with the "pillar-erect" suchian hip joint, although this hypothesis has yet to be tested.

Two additional apomorphies in the pelvis suggest that the hindlimb was habitually held close to the body in a parasagittal pose: a long and transversely narrow pubis and ischium indicating a deep but compressed body form (consistent with the carcass being preserved on its side with both limbs on the same side of the body) and a calcaneal tuber that is directed posteriorly at a right angle to the rotary ankle joint. Neither condition is seen in reptiles with habitually sprawling limb postures.

These inferences find compelling support in trackways attributed to "rauisuchians." The trackway called *Chirotherium storetonense* (see Figure 5), for example, represents a less modified foot than that of *P. gracilis,* because it still has five fully functional toes, including a prominent and divergent fifth toe that in *P. gracilis* is reduced to a mere splint appressed to the fourth metatarsal. The emphasis on the robust middle three toes for support, and especially a slender first toe less than half the length of the second, are striking apomorphic resemblances shared by the track maker and *P. gracilis.* The impressions of both the hands and feet, like those attributed to suchians generally (King et al. 2005), support the thesis that the ancestral suchian normally walked with a narrow-tracked parasagittal gait in an upright quadrupedal pose (Brusatte et al. 2008; but see Carpenter 2009).

Additional modifications in the postcranial skeleton of *Poposaurus gracilis* also suggest that this animal was a fleet-footed cursor. This species

TABLE 2. Measurements of the new specimen of *Poposaurus gracilis* (YPM VP 057100). All measurements were taken in millimeters and rounded to the next half centimeter.

Spinal column	
Estimated length of vertebral column	405.0 cm
Estimated number of vertebrae (assumes 7 cervicals present)	87
Estimated presacral column length (measured from acetabulum and including functional sacrals)	120.0 cm
Forelimb	
Scapula	20.5 cm
Humerus	17.5 cm
Ulna	19.5 cm
Preserved gap of carpals	2.5 cm
Metacarpal III	4.0 cm
Digit III of manus	4.0 cm
Total length of forelimb	47.5 cm
Total length of the third digit of the manus	10.5 cm
Hindlimb	
Pubis	39.0 cm
Ischium	27.0 cm
Femur	37.0 cm
Tibia	30.5 cm
Astragalus	3.0 cm
Metatarsal III	15.0 cm
Digit III of pes	15.5 cm
Total length of hindlimb	101.0 cm
Total length of the third digit of the pes	30.5 cm
Forelimb-to-hindlimb ratio	47%
Manus-to-pes ratio	34%
Hindlimb-to-presacral column ratio	84%

is, for example, conspicuous for having a calcaneal tuber—a lever-like heel that shifts the insertion tendon for the gastrocnemius muscle (which rotates the foot about the ankle) distally away from the ankle joint—that ranks among the largest known in any archosaur. Perhaps most significantly, exceptionally long hindlimbs (84% of presacral column length) with long, appressed metatarsals (Table 2), coupled with a narrow foot that functionally is nearly tridactyl, are tied closely to cursorial habits among living amniotes (Snyder 1962; Sereno 1991).

It is not clear whether *Poposaurus gracilis* walked on the balls of its feet only (digitigrade) or whether it first placed the sole of its foot on the ground and then rolled up onto the ball while walking (plantigrade), like archosaurs ancestrally (see Figure 5). Note that even some otherwise plantigrade lizards with relatively long appressed metatarsals like those of *P. gracilis* can produce short bouts of digitigrady while sprinting (such as *Callisaurus draconoides,* albeit in a "sprawling" bipedal gait in which the body rotates the hindlimbs medially so that they assume a slightly more erect pose; Irschick and Jayne 1999; Rocha-Barbosa et al. 2008). There was no medial or lateral rotation of the pes in *P. gracilis* because of the tight articulation of the proximal surface of the astragalus and the distal articular surfaces of the tibia and fibula, as well as the morphology of the calcaneal rotary joint. Wear facets on the flexor surfaces of the metatarsals and calcaneum, in conjunction with the overall morphology of the pes, suggest that *P. gracilis* could have shifted back and fourth between both foot postures—plantigrady when walking and digitigrady while running—during locomotion. This hypothesis has, however, yet to be tested.

Body mass is an obvious limiting factor in cursorial tetrapods. The optimal weight in cursorial mammals is around 119 kg (van Damme and Vanhooydonck 2001). In this measure *Poposaurus gracilis* is well positioned: according to midshaft femoral circumference our subadult specimen would weigh in at roughly 60 to 75 kg, with the larger type specimen at 90 to 100 kg (Anderson et al. 1985).

Finally, we propose that *Poposaurus gracilis* was also an obligate biped not only while running, but also while walking, or even standing still, balanced on its hindlimbs alone just like a stem avian. The sacrum could support an increased load because of its five sacral vertebrae, rather than the two present ancestrally in archosaurs, and the counterbalancing tail is remarkably long. The forelimbs are much too short and gracile to play a role in bearing weight or in locomotion (the forelimb-to-hindlimb ratio is 47%) and the hindlimbs are easily long enough (the hindlimb-presacral-column ratio is 84%), and the feet large enough (30% of total hindlimb length), to support the entire body weight. These values are well within the range observed in undisputed striding bipedal theropod dinosaurs of the early Mesozoic (Jones et al. 2000; see Table 2). The *Chirotherium storetonense* trackways indicate that poposauroids, or at least the most recent common ancestor of *Effigia okeeffeae* and *P. gracilis*, derived their bipedal habits from an erect-postured ancestor that already walked with a very narrow-tracked gait, even if in a quadrupedal stance (see Figure 5).

Discussion

Archosaur Locomotion as Innovation

Skulls of stem archosaurs from the late Permian display several conspicuous modifications—including dentary fangs and serrated teeth—suiting them to subduing and ingesting larger prey (macrocarnivory; see Clark et al. 1993). Subsequent postcranial modifications during the early Triassic suggest that they foraged widely for prey (Gauthier 1994). At the same time, sprawlers such as stem lepidosaurs remained small enough to dash beneath cover or climb out of reach, stem turtles effectively became armored tanks, and the small and more erect-postured cynodont stem mammals might have already embarked on the mammalian "crown habit" of emerging at night.

The new *Poposaurus gracilis* specimen provides fresh insight into an early sideline of crocodilian evolution, classically termed the "rauisuchians." This sideline potentially rivaled stem avians for dominance in the top-carnivore guild during the Triassic (see Brusatte et al. 2008) when the crocodylian line was considerably more diverse than the bird line (conservatively approximately 70 species compared with about 40 species, respectively; pers. obs. S. J. Nesbitt), in conspicuous contrast to the reversed diversity of today's archosaurs (23 species compared with about 10,000 species). The two bipedal clades—poposaurids and pan-avians—display remarkable convergences, although the sequence of character acquisition differs somewhat in each case. Approximately one-third of all homoplasy between *P. gracilis* and stem avians is associated with posture and gait, although this character class comprises only one-fourth of all characters in Nesbitt's (in press) phylogenetic analysis. Moreover, nearly all characters displayed in the contemporary theropod dinosaur *Coelophysis bauri* that pertain to striding bipedality are expressed in *P. gracilis* as well. These include an extreme reduction of the forelimb and manus, powerful cursorial hindlimbs, integration of five vertebrae into the sacrum, loss of dermal armor and an obligately upright bipedal posture.

Innovations, or evolutionary novelties that add new dimensions to evolutionary history (Wagner and Stadler 2003), are often identified by significant correlations between organismal characters and species diversification rates (Moore 2007). Innovations lead to the reproductive success of organisms that have them, and thus to the geographic expansion of the species these organisms belong to, thereby exposing them to more opportunities for subdivision into new evolutionary lineages (species sensu de Queiroz 1998). Implicit in this is that innovative characters must persist over time—becoming more deeply burdened by subsequent evolutionary change (Riedl 1978)—and spread through space across Earth's surface even as the clades bearing them differentiate through ecospace. Evolutionary stasis in organismal characters, as well as the character-bearing clade's geographic distribution, could thus provide additional means by which to identify innovation, quite apart from the plethora of phenomena that might influence diversification rates (e.g., *Trends in Ecology and Evolution* 2001; the K/T boundary asteroid impact). Thus clades with comparatively few species, such as the 313 extant species of crown turtles (*Testudines*) with unexceptional diversification rates for vertebrates (Alfaro et al. 2009), might still have evolutionary innovations. Crown-clade turtles arose at least 150 mya (Joyce and Gauthier 2004), have an unmistakable "body plan" and are distributed worldwide (even if driven toward the equator during Neogene "Ice House" climatic regimes). Likewise, a single species, such as *Homo sapiens*, could even qualify: the descendants of "Eve," with their enormous brains and elaborate cultures based on hunting and gathering, emerged

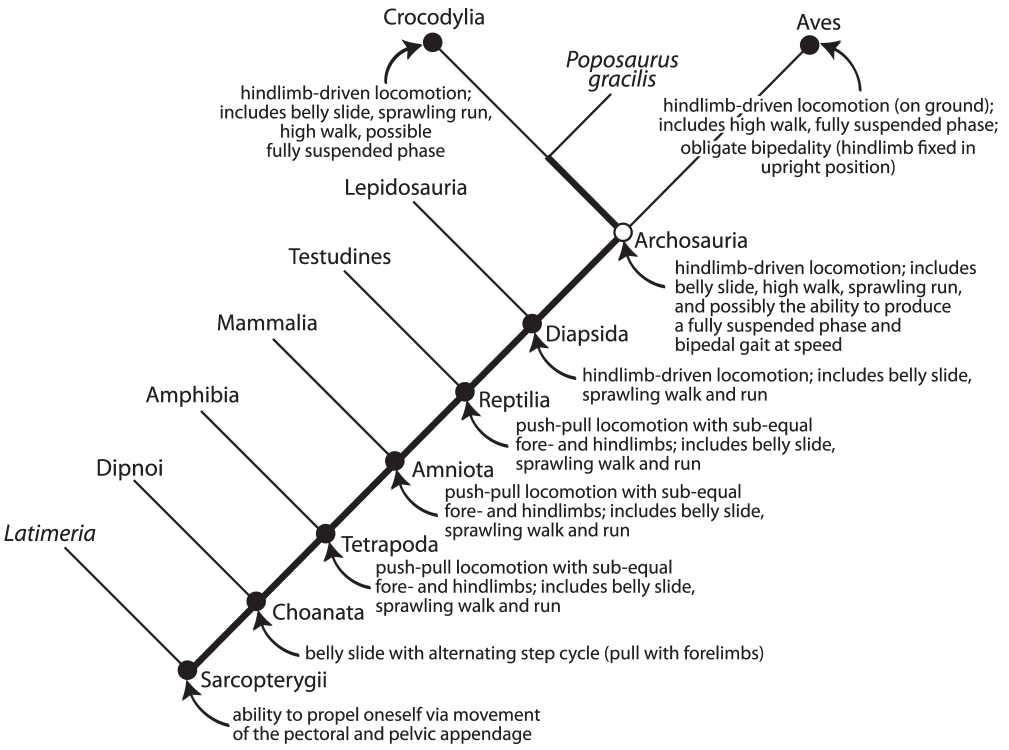

Figure 6. Inferred ancestral locomotor repertoires for the major crown clades in the direct lineage uniting the ancestral sarcopterygian and *Poposaurus gracilis* (thick line). The ancestral archosaurian repertoire represents the predicted repertoire for the avian and crocodilian stems and thus provides a null hypothesis for studying the functional anatomy of *P. gracilis*. The inferred repertoires may reflect either derived or ancestral behaviors.

in sub-Saharan Africa to spread around the globe, reaching Monte Verde, Colombia, in a mere 125,000 years (based on the time interval between "Eve" at about 140,000 years BP [Campbell and Tishkoff 2008] to the first appearance in South America around 14,500 years BP [Dillehay et al. 2008]).

The evolutionary sequence of locomotor behaviors in sarcopterygians—shifting, so to speak, from front-wheel, to all-wheel, to rear-wheel drive—up the branch leading to the diapsid crown, certainly has those qualities (Figure 6). We accordingly propose that the ability to bring the hindlimbs beneath the body—coupled with the capacity to breathe while running and thereby increase stamina during vigorous exercise, persisting for more than 245 Ma in the novel behaviors and facilitating morphologies underlying archosaur locomotion, in diverse ecological settings and with a global distribution—should qualify as an evolutionary innovation (sensu Wagner and Schwenk 2000).

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