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AN ARCHOSAUR-LIKE LATEROSPHEOID IN EARLY TURTLES (REPTILIA: PANTESTUDINES)

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ABSTRACT. Turtles are placed with increasing consistency by molecular phylogenetic studies within Diapsida as sister to Archosauria, but published gross morphology-based phylogenetic analyses do not recover this position. Here, we present a previously unrecognized unique morphological character offering support for this hypothesis: the presence in stem turtles of a laterosphenoid ossification identical to that in Archosauriformes. The laterosphenoid is a tripartite chondrocranial ossification, consisting of an ossified pila antotica, pila metoptica, and taenia medialis + planum suprasedale. It forms the anterior border of the exit for the trigeminal nerve (V) and partially encloses the exits for cranial nerves III, IV, and II. This ossification is unique to turtles and Archosauriformes within Vertebrata. It has been mistakenly dismissed as anatomically dissimilar in these two groups in the past, so we provide a complete description and detailed analysis of correspondence between turtles and Archosauriformes in each of its embryologically distinct components. A preliminary phylogenetic analysis suggests other potential synapomorphies of turtles and archosaurs, including a row or rows of mid-dorsal dermal ossifications.

KEY WORDS: Archosauria; Archosauriformes; Diapsida; turtle origins; chondrocranium; *Proganochelys*; *Kayentachelys*; fossil; braincase; interorbital ossification; Testudines

Turtles (Pantestudines; Joyce et al., 2004) have traditionally been classified as “anapsid” reptiles owing to their lack of the lateral and dorsal fenestration of the skull

that is ancestral for diapsid reptiles, including tuatara, lizards, crocodiles, and birds (Gauthier et al., 1988, and references therein). Early gross morphology-based phylogenetic analyses suggested that turtles are the sister taxon to Diapsida and thus one of the two branches of the initial reptilian divergence (Gauthier et al., 1988). Most subsequent morphological analyses have either supported this position (Brochu, 2001; Laurin and Reisz, 1995; Lee, 1997) or have

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placed turtles close to the marine Euryapsida along the stem of the lizard/tuatara clade Lepidosauria (Li et al., 2008; Rieppel and Reisz, 1999), thus suggesting that they are highly modified diapsids. One analysis (Merck, 1997) similarly indicated affinities to the Euryapsida but recovered a novel result because the included characters of non-turtle euryapsids placed the entire turtle + euryapsid clade as sister to the archosaur lineage (Brochu, 2001).

In contrast, a growing body of molecular phylogenetic work strongly supports a position of turtles within Diapsida as sister to the crocodile/bird clade Archosauria (Cao et al., 2000; Iwabe et al., 2005; Kumazawa and Nishida, 1999; Organ et al., 2008). Until now, no unique gross morphological support has been reported for archosaur affinities of turtles (Rieppel, 2000), and in particular, no morphological evidence has been forthcoming that would help place turtles along the archosaur stem. However, such evidence has existed, largely overlooked, since the further preparation and monographic description by Gaffney of the best-preserved stem turtle, *Proganochelys quenstedti*, from the Late Triassic (Norian) of Germany (Gaffney, 1990).

A single specimen of *P. quenstedti* (SMNS 15759) preserves the region anterior to the braincase. In this region, which would in life have been occupied by the membranous anterior braincase, a pair of dorsoventrally tall, flat ossifications articulate with the prootic and basisphenoid on each side (Fig. 1A). The initial description of this region by Gaffney (1990) documented the form of these bones but did not treat the detailed morphology of each of their processes. It was noted that they are similar to a pair of ossifications synapomorphic for the clade Archosauriformes, the pleurospenoids (Fig. 1B), which are now usually called laterospenoids (Clark et al., 1993). Howev-

er, the general consensus at the time, including the hypothesis presented by Gaffney (1990), was that turtles were sister to all other extant reptiles. These elements were thus termed "pleurospenoids," with the quotation marks indicating probable non-homology with those of Archosauriformes. We posit, in contrast, that they are in fact homologous to the laterospenoids of Archosauriformes.

MATERIALS AND METHODS

All specimens examined are from the collections of the Museum of Comparative Zoology, Harvard University. The following specimens from the Herpetology collection were examined: *Alligator mississippiensis* MCZ 17711, 34323; *Caiman crocodilus* MCZ 5031; *Crocodylus cataphractus* MCZ 13985, 175004; *C. niloticus* MCZ 4372; *C. porosus* MCZ 72937; *Gavialis gangeticus* MCZ 33950; *Osteolaemus tetraspis* MCZ 22913; *Paleosuchus palpebrosus* MCZ 84030; *Tomistoma schlegeli* MCZ 12459. From the Ornithology collection: *Tinamus major* MCZ 342723, 342774. From the Vertebrate Paleontology collection: *Eothyris parkeyi* MCZ 1161.

Phylogenetic analyses, as described below, used a modified version of the matrix from Dilkes (1998). Both used parsimony searches in PAUP* v4.0b10 (Swofford, 2001) with the branch-and-bound search option (1,000 replicates), specifying *Petrolacosaurus* as the outgroup as in Dilkes (1998). The constrained search used the monophyly constraint option to unite *Proganochelys* with the archosauriform clade, including *Euparkeria* and *Proterosuchus*.

DESCRIPTION OF THE LATEROSPENOID IN *PROGANOCHELYS*

Following is a more complete description of the left laterospenoid in *Proganochelys*

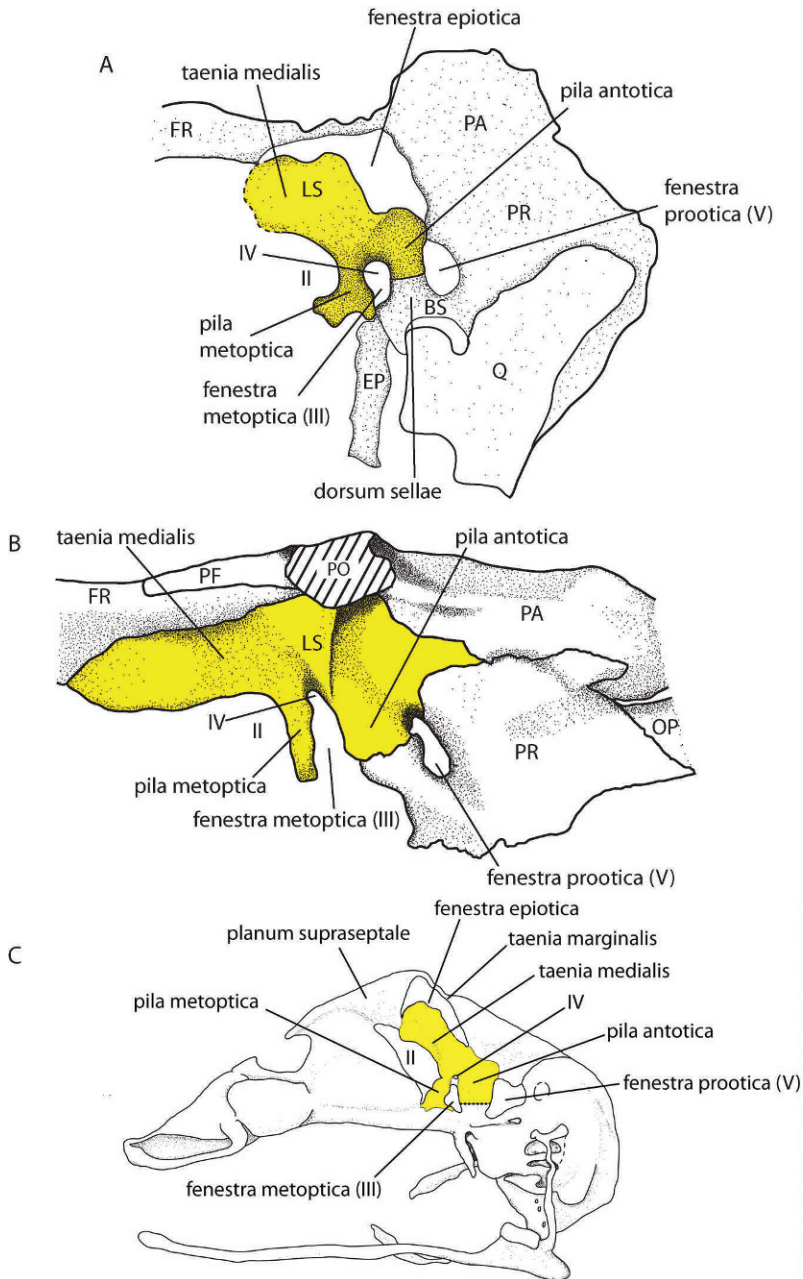


Figure 1. (A) Left laterosphenoid of *Proganochelys quenstedti* SMNS 15759 in lateral view, after Gaffney (1990). (B) Right laterosphenoid of *Proterosuchus fergusi* NMQR 1484 in lateral view, reflected, after Clark et al. (1993). (C) Chondrocranium of *Crocodylus porosus* after ref 1 with region ossified as laterosphenoid filled in. **BS**, basisphenoid; **FR**, frontal; **EP**, epipterygoid; **LS**, laterosphenoid; **OP**, opisthotic; **PA**, parietal; **PF**, postfrontal; **PO**, postorbital; **PR**, prootic; **Q**, quadrate.

than was offered in the original monograph. Our goal is to elucidate the developmental origins of the turtle laterosphenoid and thus demonstrate its exact correspondence to the archosauriform morphology.

Mediolaterally, the laterosphenoid is thin, especially near its periphery, and it is inclined ventromedially, reflecting the angulation of the wall of the membranous braincase within which it ossified (Fig. 1A). It has three major components. The first is a strut that extends anterodorsally from the clinoid process of the basisphenoid, but whose posterodorsal portion forms a small contact with the anterodorsal portion of the prootic. The posterior margin of the strut forms the anterior half of the border of the trigeminal (prootic) foramen transmitting cranial nerve V, which is fully encircled by virtue of its dual contacts—the ventral, broad contact with the clinoid process of the basisphenoid and the dorsal, attenuate contact with the prootic. The anterior margin of the strut forms the posterior border of a ventrally incomplete aperture that in life would have been formed around cranial nerves III and IV. Topologically and morphologically, this strut corresponds exactly to the pila antotica of the embryonic amniote chondrocranium (Fig. 1C; Bellairs and Kamal, 1981), as suggested but not fully explicated in the description by Gaffney (1990). The meeting with the prootic and thus closure of the trigeminal foramen, however, is a unique feature of laterosphenoids.

The second major component of the laterosphenoid is a broad, dorsoventrally oriented strut whose posterior margin arches over to form the anterior half of the aperture for cranial nerves III and IV (Fig. 1A). The strut becomes anteroposteriorly wider at its base and then ends, presumably where it would have sat upon the unossified fused trabeculae cranii. Its anterior margin forms the lower portion of an emargination that

would have formed around cranial nerve II (optic nerve) and its associated neurovascular structures. Thus, topologically and morphologically, this strut corresponds to the pila metoptica of the embryonic amniote chondrocranium (Fig. 1C), an observation not made in the description by Gaffney (1990).

The third major component of the laterosphenoid is an anterodorsally directed, terminally expanded lobe (Fig. 1A) connected basally to both of the other two components whose broadly curved anteroventral margin forms the majority of the emargination for cranial nerve II and whose posterodorsal margin borders an aperture that might represent the fenestra epioptica of the diapsid embryo (Bellairs and Kamal, 1981). As noted in the description by Gaffney (1990), the dorsal and anterior margins of the lobe appear unfinished. This morphology could represent breakage, but considering the general completeness of the surrounding elements, we think it more plausible that it is instead the border between the ossified and cartilaginous portions of the structure. The rough but not jagged texture of the surfaces supports this interpretation. The original description emphasizes that there are no signs on the parietal of a bony suture with the laterosphenoid. Topologically and morphologically, the lobe corresponds to the taenia medialis and perhaps a portion of the planum suprasettale of the chondrocranium (Fig. 1C)—not the planum suprasettale exclusively as suggested by Gaffney (1990).

COMPARATIVE NOTES

The laterosphenoid of *Proganochelys* is identical to the laterosphenoid present in the clade Archosauriformes (Clark et al., 1993) with the sole exception that it retains an open suture with the skull roof. The stem turtle *Kayentachelys aprix*, closer to the crown than

Proganochelys, also possesses laterosphe-
noids (again described as “pleurosphe-
noids”), though in existing specimens their
detailed morphology is not discernable
(Sterli and Joyce, 2007). This distribution
suggests their ancestral presence in the turtle
lineage. Unfortunately, specimens of the
oldest known stem turtle, *Odontochelys*
semitestacea, are dorsoventrally crushed,
obscuring the relevant region (Li et al.,
2008). In modern turtles, ventral down-
growths of the parietal articulate directly
with the prootic and have thus obliterated
any remnant of the laterosphe-
noids.

The archosauriform laterosphe-
noid shows the three components listed above in every
case where it is known, though there is some
variation in their relative prominence
(Fig. 1C). In crocodylians, for instance, and
particularly *Alligator*, the pila metoptica
component is reduced but present. The
morphology and topology of the latero-
sphe-
noid in turtles and Archosauriformes
are unique among all vertebrates. It appears
that the identity of the turtle laterosphe-
noid has simply been overlooked. The element
is not mentioned in comprehensive reviews
of the archosaur condition (Clark et al., 1993).

As noted in the original description of
Proganochelys and in subsequent works,
stem reptiles had a more anterior spheneth-
moid ossification, Y-shaped or V-shaped in
transverse section. This ossification is lost in
diapsids (de Braga and Rieppel, 1997). There
is limited overlap between the region of
ossification of the stem reptile spheneth-
moid and the turtle/archosauriform laterosphe-
noid. The posteriormost interorbital region,
notably the base of the pila antotica, is only
ossified in Archosauriformes and turtles (de
Braga and Rieppel, 1997; Gaffney, 1990).

The stem reptile spheneth-
moid and turtle
laterosphe-
noid were con-
founded and
claimed to be
homologous in
some recent
work, suggest-
ing pareiasaur
affinities for

turtles (Lee, 1993, 1995, 1997). Interestingly,
a rebuttal of many of the conclusions of that
work (de Braga and Rieppel, 1997) asserted
that both stem turtles and pareiasaurs have
spheneth-
moids. However, the anatomical
criteria they set out for a spheneth-
moid (e.g., complete enclosure of the optic
nerve
foramen) do not describe the structure in
Proganochelys, although it does fit the
structure in pareiasaurs. Simultaneously,
their criteria for a true laterosphe-
noid (“pleurosphe-
noid”) precisely describe the
structure in *Proganochelys*. The only plausi-
ble explanation for this oversight is that the
authors of that paper accepted the homology
assessments of the study they were rebutting
(Lee, 1995) without referring to the descrip-
tion of *Proganochelys* by Gaffney (1990).

CHARACTER DISTRIBUTION ON THE ARCHOSAUR STEM WITH TURTLES INCLUDED

Not all stem archosaurs have a latero-
sphe-
noid—as described earlier, the bone is a
synapomorphy of Archosauriformes (Clarke
et al., 1993), which excludes protorosaurs,
rhynchosaurs, and *Trilophosaurus* (Dilkes,
1998; Modesto and Sues, 2004; Sues, 2003).
The presence of a laterosphe-
noid in turtles
suggests a close relationship to Archosauri-
formes to the exclusion of non-archosauri-
form archosauromorphs. Additionally, the
presence of a tight suture of the latero-
sphe-
noid to the parietal might unite Arch-
osauriformes to the exclusion of turtles,
suggesting, on the basis of this character, a
sister-group relationship between the two.
Unfortunately, the highly derived nature of
the remainder of the turtle skull and post-
cranium results in widely inconsistent results
when turtles are included in morphological
character matrices taken from other studies
of reptilian relationships that did not initially
include turtles. Typically, these analyses have

not included a large number of characters within Archosauromorpha that would allow the precise placement of turtles within that clade (e.g., Müller and Reisz, 2006, and references therein). A full analysis of relationships will require considerable additional work.

As a preliminary exercise, we scored *P. quenstedti* using the 144-character matrix by Dilkes (1998), the most comprehensive archosauromorph matrix in the literature. The characters listed by Dilkes (1998) as candidates for ordering were ordered. To his matrix, we added three characters:

145. Laterosphenoid (0) not sutured to parietal or (1) sutured to parietal.
146. Skull (0) broadly wedge-shaped or (1) tall and mediolaterally narrow.
147. Mid-dorsal region dermal ossifications (0) absent or (1) present.

We briefly discuss each of these in turn. See the Appendix for individual character scores.

The skull of *Euparkeria* and archosaurs is tall and mediolaterally compressed compared with that of non-Archosauriformes and to an extent *Proterosuchus*. *Proganochelys* shows what appears to be the primitive condition. Scoring of this character does not affect the current analysis, but it is a codification of this basic observation on skull proportions and will be useful as more taxa within Archosauria are added to the analyses. A row of ossifications close to the midline of the back is another overlooked potential synapomorphy of turtles and Archosauriformes. It is especially interesting because *Odontochelys* has only the mid-dorsal ossifications, the rest of the carapace remaining unossified (Li et al, 2008). If this is the primitive condition in the turtle lineage, it would be even more similar to the state in Archosauriformes, which have a pair of rows of osteoderms running down the center of the back (Gauthier et al., 1988). It is true that

turtles appear to have a single row of discrete ossifications, whereas Archosauriformes have two, but despite this difference, they share the presence of a longitudinal series of dermal bone elements in the mid-dorsal region.

In addition to the synapomorphies included in the matrix, *P. quenstedti* has what appears to be a typical diapsid infraorbital foramen, despite the lack of a separate ectopterygoid. This infraorbital foramen becomes progressively smaller along the lineage to extant turtles and is given the name "foramen palatinum posterius" (Joyce, 2007). This terminology implies homology to a very small vascular foramen present in stem reptiles (Gaffney, 1990), despite the greater resemblance of the large foramen of plesiomorphic stem turtles to the diapsid infraorbital foramen. Only more crown-ward turtles have a very small foramen.

The first, unconstrained parsimony analysis yielded a single most parsimonious tree of 397 steps and recovered *P. quenstedti* as sister to Archosauromorpha (Fig. 2), suggesting archosaurian affinities for turtles, but a dual origin of the laterosphenoid. Synapomorphies supporting this placement are: 36(1), quadrate exposed laterally; 47(1), crista prootica present; 107(1), entepicondylar foramen absent; 122(1), fifth metatarsal hooked without deflection. Unambiguous synapomorphies along the lineage leading to Archosauriformes, but lacking in *Proganochelys* (requiring reversal if *Proganochelys* is allied to Archosauriformes), are: 2(1), snout greater than or equal to 50% of skull length; 5(1), antorbital fenestra present; 8(1), maxillary ramus of premaxilla extends as posterodorsal process to form caudal border of naris; 18(1), ratio of lengths of nasal and frontal greater than 1.0; 29(0), postparietal present; 37(1), quadrate emargination present with conch; 43(1), orientation of basipterygoid processes lateral; 45(1), internal

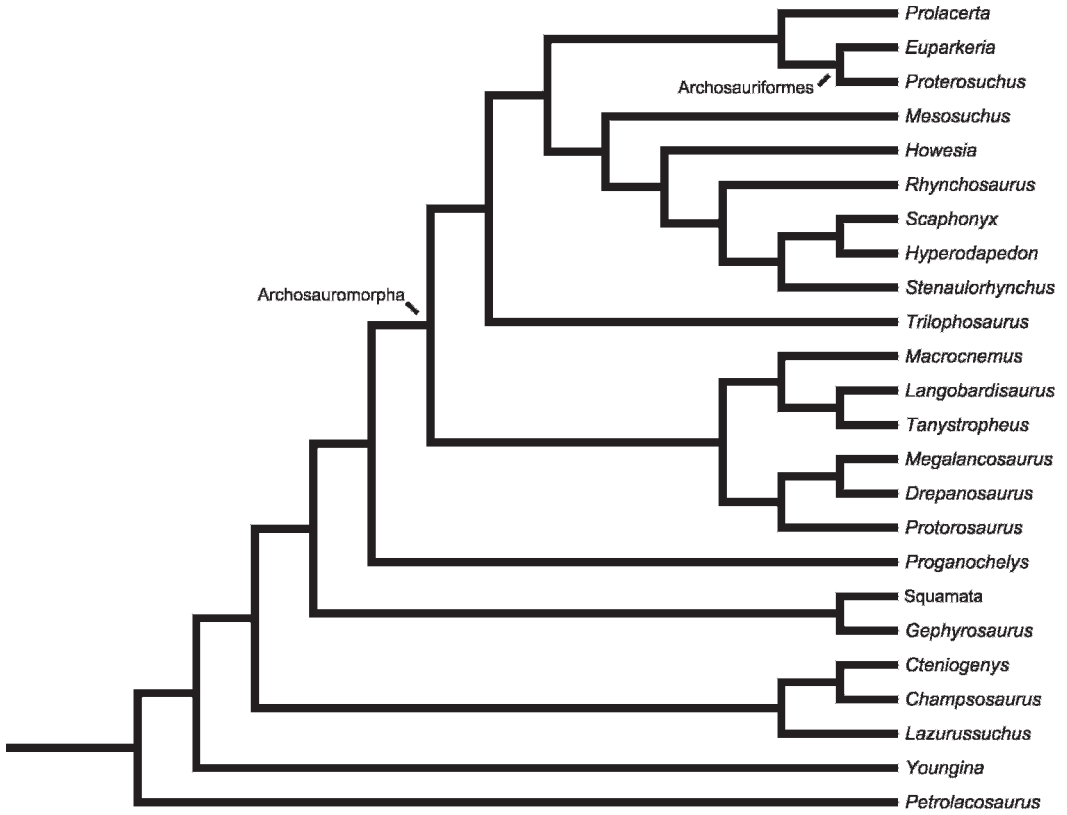


Figure 2. Single most parsimonious tree resulting from unconstrained phylogenetic analysis with the use of modified matrix from Dilkes (1998).

carotid foramina on ventral surface of parasphenoid; 53(1), post-temporal fenestra small; 75(1), upturned retroarticular process; 76(1), lateral mandibular fenestra; 79(0), postaxial cervical intercentra present; 87(2), second sacral rib bifurcate with caudal process truncated sharply; 88(2), proximal caudal neural spines very tall; 96(0), interclavicle broad diamond; 97(1), notch in interclavicle between clavicles; 104(1), anterior apron of pubis present; 109(1), medial centrale of carpus absent; 116(1), lateral tuber of calcaneum; 126(1), pterygoids remain separate cranially.

For the second analysis, we constrained *P. quenstedti* to be sister to Archosauriformes to

determine potential synapomorphies in the case of a single origin of the laterosphenoid. A single most parsimonious tree of 413 steps was recovered (Fig. 3). In this tree, the *Proganochelys*/Archosauriformes clade was sister to the remaining archosauromorphs. Synapomorphies supporting a sister-group relationship between *P. quenstedti* and Archosauriformes are: 14(1), septomaxilla absent; 50(1), laterosphenoid present; 74(2), retroarticular process present, large, and formed by articular; 77(1), slender and tapering cervical ribs at low angle to vertebrae present; 83(1), notochordal canal absent in adult; 89(1), ratio of lengths of caudal transverse processes and centra greater than 1.0; 102(1),

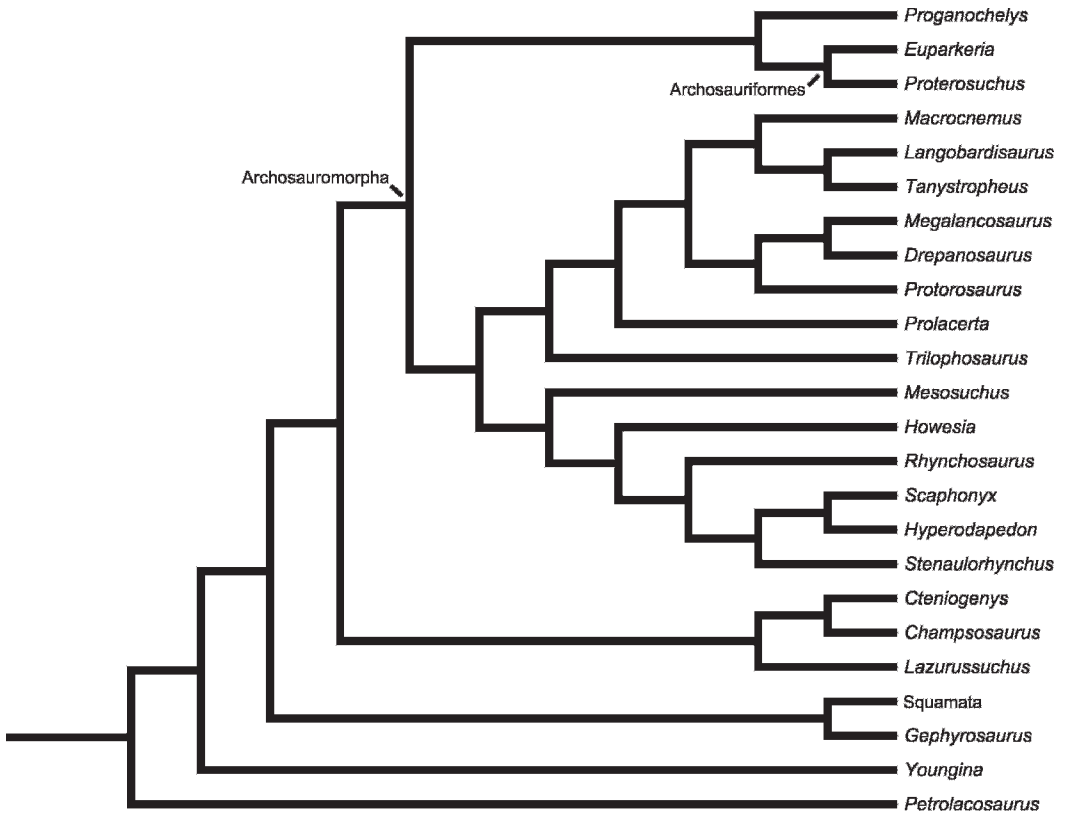


Figure 3. Single most parsimonious tree resulting from phylogenetic analysis with *Proganochelys quenstedti* constrained as sister to Archosauriformes with the use of modified matrix from Dilkes (1998).

dorsal margin of ilium with large posterior process and smaller anterior process; 143(1), distal ends of cervical neural spines expanded in form of flat table; 147(1), mid-dorsal region dermal ossifications present.

DISCUSSION

The tree recovered by our first (unconstrained) analysis agrees in its general topology with the preferred tree discussed by Dilkes (1998). This topology suggests a dual origin of the laterosphenoid; note, however, the caveats below about the overall topology of the tree. Nevertheless, *Proganochelys* does

emerge on the basis of this dataset both as a diapsid and as part of the archosaur stem lineage. Constraining *Proganochelys* as sister to Archosauriformes (and therefore forcing a single origin of the laterosphenoid) pulls that clade into a sister-taxon relationship with the remaining archosauromorphs. That *Proganochelys* would exert a pull toward the archosauromorph base is unsurprising given that the apparently primitive reptilian characters of turtles generally place them as the sister taxon to the remaining reptiles in morphological phylogenetic analyses (Gauthier et al., 1988). Additionally, the positions of *Trilophosaurus* and *Prolacerta* are labile,

with *Prolacerta* jumping from an affinity with Archosauriformes in the unconstrained tree to a more traditional position allied with other “primitive” archosauromorphs in the constrained tree. *Trilophosaurus* is highly autapomorphic and jumps from a sister-taxon relationship to a “higher” archosauromorph clade, including Archosauriformes, in the unconstrained analysis to a position sister to the “primitive” archosauromorph clade in the constrained analysis. Note that the new characters we added did not affect the broad-scale topology of the tree exclusive of *Proganochelys*.

Because of the lability of the trees recovered using the matrix from Dilkes (1998) and the incongruence among various hypotheses of diapsid relationships, we consider that a good deal of additional work is required to create a truly comprehensive character list allowing a robust placement of turtles among fossil and extant taxa. The exercise described above is directed only at examining, in a preliminary way, the distribution of potentially interesting characters within Archosauromorpha if turtles have archosaur affinities. The continued lack of consensus about relationships within archosauromorphs is why we are careful to distinguish between physical identity between the laterosphenoids of turtles and archosauriforms, which we have shown, and homology between the structures. We subscribe to the “historical” homology concept, elegantly stated by Van Valen (1982) as “continuity of information” from ancestor to descendant. Thus, a conclusive homology statement depends on a robust phylogenetic tree.

The laterosphenoids in turtles and archosauriforms fulfill the requirements for a hypothesis of homology as set forth by Patterson (1982), including topology and ontogeny. Ontogeny, however, has since been discredited as a separate, special criterion for homology or character polarity

determination (de Queiroz, 1985). Rather, characters from different times in an organism’s existence simply represent additional points of identity between putatively homologous structures. The total existence of every organism in time consists of a series of “frames” or semaphoronts (*sensu* Hennig, 1966), and points of identity that might be homology relations can be sought between any semaphoronts, no matter their relative sequence. Interestingly, Owen (1848) already understood, as stated explicitly in the introduction to the cited work, that different modes of development (early semaphoronts) do not preclude homology of later structures.

Although the debate on turtle origins and the evolution of their unique anatomy remains unresolved, molecular studies overwhelmingly indicate archosaurian affinities for turtles. The preliminary analyses we ran identified a number of interesting characters that might represent synapomorphies of turtles and various archosauromorph clades. Yet, the laterosphenoid alone is a character shared between turtles and a monophyletic group within archosauromorphs that does not appear elsewhere among vertebrates. It represents potential morphological support for the hypothesis that turtles are part of a major stem archosaur radiation and another example of the immense variety of the archosaur lineage.

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APPENDIX 1:
ADDITIONS TO DILKES (1998) CHARACTER MATRIX

For new characters, order is: Pe, Y, G, Sq, Pr, Ma, Ta, Tr, Ho, Me, R, Sc, St, Hy, Ph, E, Ch, Ct, L, Po, Mg, Ln, D. See Dilkes (1998) for key to abbreviations.

Character 145: ??????????????11???????

Character 146: 00000000000000001000000?

Character 147: 000000000000000?10000000

Proganochelys quenstedtii: 10??000010

1111200000 000?0?1011 0000?121??

??01011101 2100????? ????0002?0

0012001011 011??0110 1??010021

0100111101 00?010???? 1112000000

0000?000? 0?10001

LITERATURE CITED

- BELLAIRS, A. D'A., AND A. M. KAMAL. 1981. The chondrocranium and the development of the skull in Recent reptiles, pp. 1–262. *In* C. GANS and T. S. PARSONS (eds.), *Biology of the Reptilia*, Volume 11: Morphology F. London, Academic Press.
- BROCHU, C. A. 2001. Progress and future directions in archosaur phylogenetics. *Journal of Paleontology*, **75**: 1185–1201.
- CLARK, J. M., J. A. WELMAN, J. GAUTHIER, AND M. PARRISH. 1993. The laterosphenoid bone of early archosauriforms. *Journal of Vertebrate Paleontology*, **13**: 48–57.
- CAO, Y., M. D. SORENSEN, Y. KUMAZAWA, D. P. MINDELL, AND M. HASEGAWA. 2000. Phylogenetic position of turtles among amniotes: evidence from mitochondrial and nuclear genes. *Gene*, **259**: 139–148.
- DE QUEIROZ, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Systematic Zoology*, **34**: 280–299.
- DEBRAGA, M., AND O. RIEPPEL. 1997. Reptile phylogeny and the interrelationships of turtles. *Zoological Journal of the Linnean Society*, **120**: 281–354.
- DILKES, D. W. 1998. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauriform reptiles. *Philosophical Transactions of the Royal Society of London B*, **353**: 501–541.
- GAFFNEY, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, **194**: 1–263.
- GAUTHIER, J., A. G. KLUGE, AND T. ROWE. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, **4**: 105–209.
- HENNIG, W. 1966. *Phylogenetic Systematics*. Urbana, University of Illinois Press.
- IWABE, N., Y. HARA, Y. KUMAZAWA, K. SHIBAMOTO, Y. SAITO, T. MIYATA, AND K. KATOH. 2005. Sister group relationship of turtles to the bird–crocodilian clade revealed by nuclear DNA-coded proteins. *Molecular Biology and Evolution*, **22**: 810–813.
- JOYCE, W. G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*, **48**: 3–102.
- , J. F. PARHAM, AND J. A. GAUTHIER. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology*, **78**: 989–1013.
- KUMAZAWA, Y., AND M. NISHIDA. 1999. Complete mitochondrial DNA sequences of the green turtle and blue-tailed mole skink: statistical evidence for archosaurian affinities of turtles. *Molecular Biology and Evolution*, **16**: 784–792.
- LAURIN, M., AND R. R. REISZ. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, **113**: 165–223.
- LEE, M. S. Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science*, **261**: 1716–1720.
- . 1995. Historical burden in systematics and the interrelationships of “parareptiles.” *Proceedings of the Royal Society B*, **263**: 111–117.
- . 1997. Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnean Society*, **120**: 197–280.
- LI, C., X. WU, O. RIEPPEL, L. WANG, AND L. ZHAO. 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature*, **456**: 497–501.
- MERCK, J. W. 1997. A phylogenetic analysis of the Euryapsid reptiles. Ph.D. Dissertation. The University of Texas at Austin. 785 pp.
- MODESTO, S. P., AND H.-D. SUES. 2004. The skull of the Early Triassic archosauriform reptile *Prolacerta broomi* and its phylogenetic significance. *Zoological Journal of the Linnean Society*, **140**: 335–351.
- MÜLLER, J., AND R. R. REISZ. 2006. The phylogeny of early eureptiles: comparing parsimony and Bayesian approaches in the investigation of a basal fossil clade. *Systematic Biology*, **55**: 503–511.

- ORGAN, C. L., R. G. MORENO, AND S. V. EDWARDS. 2008. Three tiers of genome evolution in reptiles. *Integrative and Comparative Biology*, **48**: 494–504.
- OWEN, R. 1848. On the Archetype and Homologies of the Vertebrate Skeleton. London, John van Voorst.
- PATTERSON, C. 1982. Morphological characters and homology, pp. 21–74. *In* K. A. JOYSEY and A. E. FRIDAY (eds.), *Problems of Phylogenetic Reconstruction*. London and New York, Academic Press.
- RIEPEL, O. 2000. Turtles as diapsid reptiles. *Zoologica Scripta*, **29**: 199–212.
- , AND R. R. REISZ. 1999. The origin and early evolution of turtles. *Annual Review of Ecology and Systematics*, **30**: 1–22.
- STERLI, J., AND W. G. JOYCE. 2007. The cranial anatomy of the Early Jurassic turtle *Kayentachelys aprix*. *Acta Palaeontologica Polonica*, **52**: 675–694.
- SUES, H.-D. 2003. An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. *Canadian Journal of Earth Sciences*, **40**: 635–649.
- SWOFFORD, D. L. 2001. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sunderland, Massachusetts, Sinauer Associates.
- VAN VALEN, L. 1982. Homology and causes. *Journal of Morphology*, **173**: 305–312.