The dual origin of turtles from pareiasaurs

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ABSTRACT— The origin of turtles (traditional clade: Testudines) has been a vexing problem in paleontology. New light was shed with the description of *Odontochelys*, a transitional specimen with a plastron and teeth, but no carapace. Recent studies nested *Owenetta* (Late Permian), *Eunotosaurus* (Middle Permian) and *Pappochelys* (Middle Triassic) as turtle ancestors with teeth, but without a carapace or plastron. A wider gamut phylogenetic analysis of tetrapods nests *Owenetta, Eunotosaurus* and *Pappochelys* far from turtles and far apart from each other. Here dual turtle clades arise from a clade of stem turtle pareiasaurs. *Bunostegos* (Late Permian) and *Elginia* (Late Permian) give rise to dome/hard-shell turtles with late-surviving *Niolamia* (Eocene) at that base, inheriting its Baroque horned skull from *Elginia*. In parallel, *Sclerosaurus* (Middle Triassic) and *Arganaceras* (Late Permian) give rise to flat/soft-shell turtles with *Odontochelys* (Late Triassic) at that base. In all prior phylogenetic analyses taxon exclusion obscured these relationships. The present study also exposes a long-standing error. The traditional squamosal in turtles is here identified as the supratemporal. The actual squamosal remains anterior to the quadrate in all turtles, whether fused to the quadratojugal or not.

INTRODUCTION

Turtle workers trying to find the ancestors of turtles keep moving further afield as more disparate candidates are proposed. Over sixty years ago, Gregory (1946) wrote: "The gigantic known pareiasaurs seem to present almost ideal conditions for the derivation of the primitive chelonian characters... stem chelonians may have been derived from some small pareiasaurs related to *Elginia*." Later, Reisz and Laurin (1991) proposed *Owenetta* as a turtle relative. Rieppel and deBraga (1996) and deBraga and Rieppel (1997) argued for a vague diapsid/sauropterygian ancestry. Lee (1997) renewed the argument for a pareiasaur ancestry, but unfortunately used traditional pareiasaurs (see below). Li et al. (2008) made headlines with their announcement of *Odontochelys,* a Late Triassic turtle with teeth. When they nested it basal to *Proganochelys*, they failed to report an outgroup genus and assumed that turtles had a single origin. Schoch and Sues (2015) promoted Middle Triassic *Pappochelys* as a diapsid ancestor to anapsid turtles like *Odontochelys*. A summary by Joyce (2015) supported the placement of *Eunotosaurus* as a turtle ancestor and discussed the domination of molecular data that confusingly placed turtles as sisters to a wide variety of taxa throughout the Amniota, settling recently on the Archosauria. Joyce also noted molecular studies frequently recover family tree topologies that do not match those of morphological studies, or other molecular studies. Foth and Joyce (2016) reported the turtle lineage extended back to *Odontochelys, Pappochelys* (Schoch and Sues, 2015) and *Eunotosaurus* (Seeley, 1892; Lyson et al., 2010; Bever et

al., 2015). Lyson et al., (2016) explained how stem turtles used broader ribs while burrowing, employing *Eunotosaurus* as an example.

Unfortunately, all prior studies excluded relevant taxa in the ancestry of turtles and in the turtle clade. Some workers (Reisz and Laurin, 1991; Schoch and Sues, 2015; Seeley, 1892; Lyson et al., 2010; Bever et al., 2015; Lyson et al., 2016) introduced or employed unrelated taxa that converged with turtles. Some trusted DNA analyses (e.g. Field et al., 2014) without confirming the results with morphological studies. Based on those missteps, the ancestral turtle problem continues to vex paleontologists, whether they realize it or not.

An irrefutable turtle cladogram should recover a series of ancestral turtle taxa in which a gradual accumulation of traits is readily visible in the entire skeleton (not just the ribs) of every taxon. In such a cladogram ghost lineages would be minimized and all prior ancestral candidates would be tested against a substantial number of turtle taxa with primitive traits, not just *Proganochelys*.

An online morphological study (www.ReptileEvolution.com/reptile-tree.htm; subset in Fig. 1) recovers a novel dual origin of turtles after testing all prior candidates for turtle ancestry and hundreds more (Supp. Data; Figs. 2, 3). Commonly known as the large reptile tree (= LRT), this analysis has been adding taxa for the last eight years and currently documents the near and far interrelationships of 1165 taxa ranging from stem tetrapods to mammals, birds and turtles.

MATERIALS AND METHODS

Traditionally firsthand access has been a stringent requirement in paleontology. Many prior workers had firsthand access to fossils, but omitted relevant taxa in their analyses. Here published photographs and drawings provide most of the data used in the present analysis. As results attest, omitting relevant taxa (Graybeal, 1998) is clearly the larger problem here.

The present list of 1165 genus-based taxa minimizes bias and tradition in the process of selecting ingroup and outgroup taxa for smaller, more focused studies because all major and many minor clades are well established here. All taxa in the LRT are generic, specific or species-based. Chimaeras are not employed.

No characters used in the LRT are specific to the clades that include turtles. Traits specific to turtles would have been useless on birds and tree shrews, and possibly useless on stem turtles and their ancestors. Generalized characters were chosen or invented for their ability to lump and split clades and for their visibility in a majority of tetrapod taxa, many of which had never been tested together. Although some characters are similar to those from various prior analyses, the present list (see Supporting Data; DataDryad.org/xxxxx to be completed when the ms. is accepted) was largely built from scratch. All taxon subsets of the LRT (e.g. Fig. 1) raise the character/taxon ratio.

At present, the 231 multi-state character set has proven sufficient to lump and separate 1164 taxa (the incomplete fossil of *Maelestes* is the exception), typically with high Bootstrap scores. All derived taxa document a gradual accumulation of traits in ancestral taxa going back to stem tetrapods in the Devonian. That's a strong sign that this character list is either ideal or good enough for the task at hand. In the past, certain workers considered 231 characters too small for the number of tested taxa—when the

taxon list was a quarter of the size it is now. Others thought the characters themselves were less than optimally fashioned. Not all opinions can be accommodated given the constraints of a single lifetime. Complete resolution in the LRT and high Bootstrap scores falsify any blackwashing levied against the present character list. For all of its faults, real or imagined, the LRT continues to lump and separate every new taxon as more taxa are added every week.

The fault in all prior studies has been taxon exclusion (Graybeal, 1998). That fault has been minimized here with a wide gamut taxon list.

Taxa and characters were compiled in MacClade 4.08 (Maddison and Maddison, 1990), then imported into PAUP* 4.0b (Swofford, 2002) and analyzed using parsimony analysis with the heuristic search algorithm. All characters were treated as unordered and no character weighting was used. Bootstrap support figures were calculated for 100 replicates. The cladogram, character list and data matrix accompany this manuscript and will be available in permanent repository here: www.Treebase.org/ xxxxx and www.DataDryad.org/xxxxxx (to be completed when the ms. is accepted).

RESULTS

The LRT nests 1165 taxa in near-complete resolution (Supp. Data, see above). In the more focused and completely resolved turtles and kin subset of the LRT (Fig. 1; 46 taxa), the first split separates the (Diadectes + Bolosauridae + Procolophonidae) clade from the (*Stephanospondylus* + Pareiasauridae) clade. Next the Pareiasauridae splits into a traditional pareiasaur clade and a stem turtle clade. The stem turtle clade splits

Bunostegos from *Sclerosaurus*. The *Bunostegos* clade produces *Elginia*, *Niolamia* and other hard-shell turtles (Fig. 2). The *Sclerosaurus* clade produces *Arganceras*, *Odontochelys* and other soft-shell turtles (Fig. 3).

In order to reunite turtles as a monophyletic clade, *Sclerosaurus* and *Arganaceras* need to be removed from the inclusion set. Then the remaining soft-shell clade members nest between *Elginia mirabilis* and *Niolamia*.

Looking beyond the turtle clades in the LRT, *Pappochelys* nests at the base of the placodonts with *Palatodonta*. *Eunotosaurus* nests with *Acleistorhinus*, *Microleter* and *Delorhynchus*, also far from the two turtle clades. *Owenetta* does not nest with *Procolophon*, or with turtles, but closer to the origin of lepidosauriformes (contra Reisz and Laurin, 1991). These prior candidates for turtle ancestry essentially dismiss themselves when more attractive sisters become available in a larger taxon list.

DISCUSSION

The LRT sheds new light on the dual origin of turtles and invalidates all other candidates for turtle ancestry (*Owenetta*, *Pappochelys*, *Eunotosaurus*) that nest far from the two turtle clades. Taxa within the LRT, going back to basal tetrapods, document a gradual accumulation of traits in the turtle lineage (and every other included clade). Long ghost lineages are minimized here.

Based on the nineteenth century discoveries of *Elginia*, *Meiolania* and *Niolamia*, the present insights into turtle origins could have been recovered anytime in the last hundred years. Unfortunately these taxa were never tested together in a phylogenetic

analysis. Gregory (1946) and Lee (1997) were correct in identifying pareiasaurs as turtle

ancestors, but they did not correctly identify meiolaniids as basalmost turtles or recover a

dual origin for turtles due to taxon exclusion. Prior workers mistakenly assumed that

Proganochelys quenstedti (Baur, 1887; Gaffney, 1990) was the basalmost turtle. Lee

(1997) included *Elginia* in a pareiasaur/turtle study, but focused on pareiasaurs and did

not include *Niolamia* and *Meiolania*. Joyce (2015) was confident in using *Proganochelys*

as the turtle outgroup taxon instead of using the stem turtles with teeth, *Elginia* and

Sclerosaurus.

Stephanospondylus and the Pareiasaur Clades

Derived from smaller millerettids, the bulky, basalmost pareiasaur,

Stephanospondylus pugnax (Early Permian; Geinitz and Deichmüller, 1882;

Stappenbeck, 1905; Romer, 1935), was omitted from all prior pareiasaur and turtle

studies because it was considered a diadectid and diadectids were considered stem

amniotes (Kissel, 2010). Provided with more taxa to be attracted to, diadectids nest with

Stephanospondylus and the pareiasaurs in the LRT (Fig. 1). Like diadectids,

Stephanospondylus lacks the large quadratojugal cheeks that characterize traditional

pareiasaurs like *Scutosaurus*. The external nares are taller than wide and oriented

anteriorly. The teeth are sharp cones with constricted bases. The palatine has short sharp

teeth. The neural spines are expanded. At least some of the anterior dorsal ribs have

expanded costal plates, as in certain *Diadectes* specimens, while other dorsal ribs extend

3x more laterally than ventrally, creating a wide, shallow, disk-like torso. Tiny ribs close

to the sacrum are narrow and straight. The pectoral girdle includes a robust clavicle,

scapula, coracoid, procoracoid and a pentagonal interclavicle. The humerus is robust with a thick waist and axial torsion. The radius and ulna are short and graviportal. The carpus is robust with ten large elements. The pelvis has a tall pareiasaur-like ilium and a ventrally separated pubis and ischium. The femur has a long, angled neck offset from the main axis, a trait retained by pareiasaurs and turtles.

At the first dichotomy following *Stephanospondylus*, pareiasaurs split between traditional pareiasaurs, like *Pareiasaurus + Scutosaurus*, and the stem turtle clade. At the base of the stem turtle clade, knob-skulled *Bunotegos* (Late Permian; Tsuji et al., 2013) splits from spike-skulled *Sclerosaurus* (late survivor in the Middle Triassic, Fig. 3; von Meyer, 1859; Sues and Reisz, 2008).

The *Bunostegos* Clade

Hard-shell turtles, like *Meiolania* and *Niolamia* (Fig. 2), are derived from the *Bunostegos* clade of pareiasaurs (Fig. 1). The skull of *Bunostegos* is ornamented with knobs anteriorly (over the nares), laterally (over the orbits and at the jaw joints) and posteriorly (at the upper skull corners). The postparietal is surrounded by the parietals and conjoined tabulars. The supratemporal descends to the quadratojugal, isolating the squamosal in the middle of the cheek. The quadratojugal descends relative to the tooth row. The small teeth have dull, slightly expanded points. The torso remains wide and disk-like. None of the dorsal ribs have large costal plates. The scapula is vertically oriented and located anterior to the dorsal ribs. The pelvis is also taller than wide with a posteriorly descending ilium, a large circular acetabulum and a widely separated, but short pubis and ischium.

Recently discovered and only partly preserved, *Elginia wuyongae* (Late Permian; Liu and Bever, 2018) and better preserved, *Elginia mirabilis* (Late Permian; Fig. 2; Newton, 1893), appear next. *E. mirabilis* is elaborately horned. The teeth are short and shaped like human incisors. The orbits are located further anteriorly. The pineal opening is large. The formerly expanded quadratojugal cheeks are reduced to three sharp lateral spikes.

Post-crania is unknown in *E. mirablis*, so whether it had a carapace and plastron, like its phylogenetic successors, *Niolamia* and *Meiolania* or not, like its proximal ancestors, *Bunostegos* and *E. wuyongae*, remains unknown. However, in *E. wuyongae*, small osteoderms, apparently the genesis of the carapace, line the dorsal vertebrae. Phylogenetic bracketing indicates the carapace and plastron first appeared in hard shell turtles near the *E. mirabilis* grade in the Late Permian. The *Meiolania* plastron has a large central fenestra, so it is a not the result of expanding gastralia (contra Schoch and Sues, 2015, who considered *Pappochelys* a stem turtle). Gastralia are absent in pareiasaurs.

Basalmost hard-shell turtles

Here (Fig. 1) the larger horned turtles, *Niolamia* (late-surviving in the Eocene; Ameghino, 1899; Sterli and de la Fuente, 2011) and *Meiolania* (late-surviving in the Oligocene; Owen, 1882, 1886; Gaffney, 1983, 1985, 1996), are recovered for the first time as basalmost hard-shell turtles close to their only other 'match' in the entire LRT, the small pareiasaur, *Elginia* (Fig. 2). In all prior studies meiolaniids were considered aberrant late arrivals. With its larger headdress, *Niolamia* is the more primitive of the two tested meiolaniids. In *Niolamia* small parts of a *Meiolania*-like carapace and a spiked tail

ring were present among the few post-cranial scraps known for this taxon (Sterli and de la Fuente, 2011).

The skull of *Niolamia* (Fig. 2) is similar to *Elginia* in every view with the following slightly derivations: The premaxillae lack an ascending process, making the nares confluent and invisible in lateral view. The orbit is located further anteriorly. The notch at the posterior maxilla located below the posterior orbit in *Elginia* moves forward, below the anterior orbit in *Niolamia*. Teeth are absent, but tiny empty alveoli remain. The many small anterior cranial spikes of *Elginia* are absent in *Niolamia*, but the posterior tabular spikes are greatly expanded to form a dorsal shield. On the supratemporal the posterior two spikes of *Elginia* are enlarged in *Niolamia*. The base of the lower spike descends toward the quadratojugal perhaps without touching it. The quadratojugal is no longer laterally expanded or spiked. The postorbital is overlapped by the postfrontal from above and by the jugal from below. The squamosal descends to overlap the quadratojugal, contacting the jawline. The pineal opening is reduced to absent in *Niolamia* on a parietal that is now no longer than the frontal.

In a smaller, likely juvenile specimen related to *Niolamia*, *Crossochelys* (Simpson, 1938), the postparietals are dorsally exposed and bordered by fenestrae. In *Niolamia* the tabulars expand to fill those fenestrae and extend medially to cover the postparietals creating a solid shield.

In the more derived *Meiolania* (Fig. 2) cranial spikes are reduced. Spikes are absent in all descendant taxa. The descending ramus of the supratemporal creates a suture with the quadratojugal leaving a lateral temporal fenestra (the incisura columellae auris) posterior to the squamosal. Distinct from known pareiasaurs, the tail in *Meiolania* is long,

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robust, armored and provided with a club tip, traits inherited only by later proganochelids. Confirming their primitive status, meiolaniids are the only known hard-shell turtles in which the forelimbs can still extend laterally, as in most tetrapods. In all derived hard-shell turtles, the humerus extends more or less anteriorly from the opening formed between the carapace and plastron.

The *Sclerosaurus* Clade

A separate, but parallel clade of turtles with 'soft' shells arose from the small horned pareiasaur, *Sclerosaurus* (a late survivor in the Middle Triassic, Fig. 3; von Meyer, 1859; Sues and Reisz, 2008) and *Arganaceras vacanti* (Late Permian; Jalil and Janvier, 2005). *Arganaceras* is the larger of the two, but is more derived in having smaller horns and other skull traits lacking in ancestral pareiasaurs (see below). Phylogenetically *Arganaceras* pushes the origin of the more primitive, but late surviving *Sclerosaurus* to the early Late Permian. Workers with firsthand access to the specimen (Sues and Reisz, 2008), but without the current taxon list, considered *Sclerosaurus* a procolophonid.

Overall smaller and distinct from *Bunostegos*, the incomplete skull of *Sclerosaurus* elongates the supratemporal horns without producing a descending ramus to the quadratojugals. That leaves the small squamosal exposed posteriorly, anterior to the quadrate. The orbit is taller than wide, relatively larger and exposed in dorsal view due to narrower dorsal skull elements. These traits are retained by soft shell turtles and readily distinguish them from the hard shell lineage. The temple, measured at the squamosal, is anteroposteriorly much shorter. The laterally expanded quadratojugal has two short,

robust spikes. The teeth are shorter and more robust. The torso and limbs are shaped similar to those of *Bunostegos*, but are more gracile due to the smaller size. The scapula is relatively smaller, no larger than the paired coracoids. In lateral view the pelvis is symmetrical with tiny fused pubes and ischia. A small hypoischium is present. A narrow quilt of tiny osteoderms protects the dorsal vertebrae. No gastralia are present, so the plastron found in soft-shell turtles, like *Odontochelys,* is also a novel ossification (contra Schoch and Sues, 2015).

In *Arganaceras* (Late Permian; Jalil and Janvier, 2005) the supratemporal and quadratojugal spikes of *Sclerosaurus* are much reduced, but a nasal bump remains. Distinct from hard-shell turtles, the naris is elongate and lateral in position. The quadratojugal is much reduced with a single posterior spike. The dorsal process of the published quadratojugal (in Jalil and Janvier, 2005) is actually the ventral squamosal in long contact with the jugal as in *Bunostegos* and *Sclerosaurus*. *Arganaceras* has smaller teeth than in *Sclerosaurus*.

The loose bones of the disarticulated skull can be arranged to create a long gap between the medial crania and the lateral supratemporal. A comparable cranial gap in *Odontochelys* and *Trionyx* is a skull depression, the posttemporal fenestra, extending from the occiput to the jugal and postorbital.

Arganaceras (Fig. 3) lacks post-cranial data. If it had a plastron, like *Odontochelys*, it might be considered a turtle. These are transitional taxa.

Odontochelys (Late Triassic; Li et al., 2008; Fig. 3) was preserved more completely and is known from several specimens. In dorsal view the skull is lower and wider with large openings for the nares and orbits. Posttemporal depressions (fenestrae)

extend anteriorly to the jugal. Originally (Lie et al., 2008) the skull was mistakenly illustrated without posttemporal fenestrae, following the morphology of the turtle previously considered the basalmost representative of the clade, *Proganochelys*. In *Odontochelys* the premaxillary ascending processes continues to separate the nares and contact the nasals. The pineal opening is absent. In ventral view the palate is essentially solid with robust elements surrounding the tiny medial nares on either side of a robust set of wide, fused and toothy vomers. In lateral view the jugal and squamosal are reduced in height. The quadratojugal is a vestige below the jugal. With that loss, the quadrate is now laterally exposed and located posterior to the squamosal. The supratemporal continues to sit on top of the quadrate and remains pointed posteriorly, as shown in *Trionyx* (where the supratemporal is also traditionally mislabeled the squamosal). The marginal teeth are small, simple cones in *Odontochelys*.

The five cervicals of *Odontochelys* are elongate with tiny ribs, a trait retained by soft-shell turtles, distinct from meiolaniids. The ten dorsals are also long with laterally extended paddle-like ribs. Three sacrals converge laterally on the small ilium. The slender and tapering tail is subequal to the cervicals + dorsals in length. The ventral view is dominated by a radiating plastron composed of seven laterally paired elements between the interclavicle and pubis, all without a central fenestra, distinct from meiolaniids. The pectoral girdle is relatively smaller with a narrower scapula. The coracoid has a stem-like process and the clavicle is much shorter. The humerus is relatively slender, more gracile than the short, robust antebrachium and broad symmetrical manus. Due to the great breadth of the plastron the humerus is restricted in motion to an anterior-to-lateral quadrant. The ilium is tiny compared to the robust pubis and ischium. The hypoischium is

larger than in *Sclerosaurus*. The hind limb is comparatively gracile with a narrower asymmetric pes.

In post-*Odontochelys* tested taxa, like *Trionyx*, all teeth and the premaxillae are absent. In *Trionyx* the supraoccipital develops a long posterior process with a dorsal crest. The parietals have a complex shape, flat dorsally, concave laterally with lateral wings forming the base of the posttemporal fenestra. Completing the floor of the posttemporal fenestra, the postparietal and tabular are lower than the laterally framing supratemporal. The squamosal, still between the jugal and quadrate, is the smallest lateral element. The laterally hollow quadrate is larger, dipping down to meet the descending posterior mandible. The cervicals and caudals are shorter. The dorsal ribs extend slightly beyond a complete set of interlocking osteoderms forming a low, flat carapace. The humerus extends anteriorly, convergent with derived hard-shell turtles. Distinct from *Odontochelys,* the limbs are gracile with elongate metapodials and phalanges.

Other Turtle Ancestor Candidates

In the LRT, *Pappochelys* (Middle Triassic) nests with basal placodonts close to *Palatodonta* (Middle Triassic). The basal pachypleurosaur/sauropterygian, *Diandongosaurus* (Early Triassic; Shang et al., 2011), is a proximal out-group taxon. Placodonts have dorsal and lateral temporal fenestrae inherited from Pennsylvanian basal diapsids like *Petrolacosaurus*. Such temporal openings are not found in any turtle or pareiasaur. Several other placodonts, not closely related to *Pappochelys*, but derived from *Placodus*, develop a carapace universally considered convergent with that of turtles.

Also converging with turtles, *Eunotosaurus* had fewer and broader ribs than its closest relatives in the LRT that preserve post-crania, like *Eocasea*. Unfortunately, the closest tested relatives of *Eunotosaurus*: *Acleistorhinus*, *Microleter* and *Delorhynchus*, are known chiefly from skulls. All have a lateral temporal fenestra that opens ventrally and other traits not found in basal turtles or pareiasaurs.

Bever et al. (2015) reported an upper temporal fenestra in a juvenile *Eunotosaurus* and so concluded it was a diapsid with implications for turtle ancestry. In the LRT no diapsid and no turtle nests near *Eunotosaurus*. The supratemporal that should have covered that opening was taphonomically dislocated closer to the midline of the skull, but was not reported by Bever et al. The left supratemporal remained in place, but with a small hole punched in the center, either incompletely ossified or taphonomically damaged. As Bever et al. acknowledged: adult *Eunotosaurus* specimens do not have an upper temporal fenestra. A supratemporal covers it.

Triassic Turtle Tracks

Lichtig et al. (2017) described *Chelonipus* ichnites from the early Middle Triassic and the late Early Triassic. The authors matched those tracks to the pes of hard-shell taxa like *Proganochelys*, distinct from *Odontochelys*. They concluded, "the resemblance of these tracks to pareiasaur tracks (*Pachypes*) supports arguments of the origin of turtles from pareiasaurs."

Nomenclature Issues

Joyce et al. (2004) reported on the changing and confusing history of naming turtle clades. Unfortunately their publication preceded the later discoveries of *Odontochelys*, *Bunostegos* and *Arganaceras*. Joyce et al. (2004) also omitted *Elginia* and *Sclerosaurus*. Based on the absence of these key taxa, Joyce et al. nested *Meiolania* and *Trionyx* in the clade Cryptodira, even though neither has the ability to pull the head back under the carapace.

The dual origin of turtles from pareiasaurs was not anticipated in prior nomenclature. Turtle clade nomenclature needs to be updated to reflect the evolutionary events and clades recovered here.

The traditional clade, Pantestudines, is defined only by extant taxa and the precise composition remained unclear even to Joyce et al. (2004). Pantestudines has neither utility, nor monophyly in the LRT.

The traditional clade, Testudines (Batsch, 1788; Chelonia + *Chelus* and descendants, Joyce et al., 2004), remains monophyletic in the LRT, but no longer includes several basal hard-shell turtles or any soft-shell turtles.

The traditional clade, Testudinata (Klein, 1760; first member of Pantestudines with a complete turtle shell that is homologous with the shell present in *Chelonia,* Joyce et al., 2004), continues to include *Meiolania, Niolamia* their last common ancestor and its descendants. However, soft-shell turtles are now excluded from this clade.

The traditional clade Trionychia (Hummel, 1929; *Trionyx* and kin, Joyce et al. 2004) remains monophyletic in the LRT.

A new clade, Protestudinata ("before *Testudo* and kin"), is proposed for *Bunostegos*, *Elginia*, their last common ancestor and all of its descendants, the hard-shell turtles.

A new clade Protrionychia ("before *Trionyx* and kin") is proposed for *Sclerosaurus*, *Arganaceras*, their last common ancestor and all of its descendants, the soft-shell turtles.

A new clade Keratospiti ("horned house") is proposed for *Bunostegos*, *Sclerosaurus*, their last common ancestor and all of its descendants, which includes all stem turtles and turtles. Not all clade members have a "horned house."

A new clade Propareiasauria ("before pareiasaurs") is proposed for *Stephanospondylus*, *Pareiasaurus*, their last common ancestor and all of its descendants, which includes all pareiasaurs, stem turtles and turtles.

CONCLUSIONS

All current candidates for turtle ancestry are tested here. The addition of relevant taxa nests turtles with stem-turtle pareiasaurs and nests other candidates elsewhere, confirming the pre-cladistic observations and assessment of Wm. King Gregory (1946), who linked *Elginia* to turtles. Two clades of pareiasaurs arise from a sister to *Stephanospondylus*. One clade produced large traditional pareiasaurs. The other clade produced the stem turtles, *Bunostegos, Elginia* and *Sclerosaurus*. Spiky *Elginia* was basal to a clade of hard-shell turtles starting with the spiky grade Meiolaniidae. *Sclerosaurus* descendants lose their spikes more quickly, giving rise to *Arganaceras*, *Odontochelys* and

other soft-shell turtles, like *Trionyx*. The pareiasaur ancestry of turtles sheds light on the identity of traditionally misidentified turtle cranial bones. The upper corner cranial bone is no longer the squamosal, but the supratemporal. The real squamosal continues to form the posterior rim of the skull, anterior to the quadrate, even if the quadrate is not visible laterally.

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Figure captions

FIGURE 1. Subset of the large reptile tree (www.ReptileEvolution.com/reptile-tree.htm) focusing on the dual turtle clades and their proximal outgroups. Intended for 1 column.

FIGURE 2. The skulls of *Elginia*, *Niolamia*, *Meiolania* and *Proganochelys* in three views. Squamosal and supratemporal are reidentified here based on *Elginia*. Intended for page width.

FIGURE 3. Select views of the skulls of *Sclerosaurus*, *Arganceras*, *Odontochelys* and *Trionyx*. Squamosal and supratemporal are reidentified here based on *Elginia*. Intended for page width.

Diadectes & kin

98 — *Diadectes* CM25471
71 ┤ *Silvadectes absitus* MNG 8853
92 — *Phonodus*
96 — *Bolosaurus*
Bolosauridae — *Belebey*
98 — *Oradectes sanmiguelensis*
58 — *Diadectes* UC706
— *Diadectes sideropelicus*
52 — *Procolophon*
69 — *Scolaparia* NSM 99 GF82.1
98 — *Leptopleuron*
99 — *Pentaedrusaurus*
Procolophonidae — *Hypsognathus*

67

77

99

Pareiasauria

68 — *Stephanospondylus*
87 — *Provelosaurus*
81 — *Deltavjatia* KPM232
64 — *Scutosaurus*
91 — *Bradysaurus* NHMW
64 — *Anthodon*
— *Pareiasuchus*
— *Pumiliopareia*

73 — *Sclerosaurus*
87 — *Arganaceras*

Soft shell turtles
80 — *Odontochelys*
83 — *Trionyx*
— *Ocepechelon*

81

71 — *Bunostegos*
69 — *Elginia wuyongae*
— *Elginia mirabilis*

57
98
Hard shell turtles
77 — *Niolamia*
— *Meiolania*
88 — *Proterochersis*
53 — *Proganochelys*
89 — *Kayentachelys*
93 — *Mongolochelys*
— *Chubutemys*
99 — *Chelonia*
91 — *Santanachelys*
100 — *Dermochelys*
92 — *Macrochelys temminckii*
90 — *Terrapene carolina*
67 — *Foxemys*
87 — *Carettochelys*
95 — *Pelomedusa*
69 — *Araripemys*
100 — *Chelus*

■ Phylogenetic miniaturization

25

Tabular
Supratemporal
Tabular
Supratemporal
Squamosal
Proganochelys

Supratemporal
Tabular
Supratemporal
Squamosal
Tabular
Meiolania

Tabular
Supratemporal
Squamosal
Tabular
Supratemporal
Niolamia

10cm

Supratemporal
Tabular
Tabular
Supratemporal
Squamosal
Tabular
Supratemporal
Squamosal
Elginia

Trionyx

Odontocheys

Arganaceras

Sclerosaurus