

A new lepidosaur clade: the Tritosauria

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ABSTRACT—Several lizard-like taxa do not nest well within the Squamata or the Rhynchocephalia. Their anatomical differences separate them from established clades. In similar fashion, macrocnemids and cosesaurids share few traits with putative sisters among the prolacertiformes. Pterosaurs are not at all like traditional archosauriforms. Frustrated with this situation, workers have claimed that pterosaurs appeared without obvious antecedent in the fossil record. All these morphological ‘misfits’ have befuddled researchers seeking to shoehorn them into established clades using traditional restricted datasets. Here a large phylogenetic analysis of 413 taxa and 228 characters resolves these issues by opening up the possibilities, providing more opportunities for enigma taxa to nest more parsimoniously with similar sisters. Remarkably, all these ‘misfits’ nest together in a newly recovered and previously unrecognized clade of lepidosaurs, the Tritosauria or ‘third lizards,’ between the Rhynchocephalia and the Squamata. Tritosaurs range from small lizard-like forms to giant marine predators and volant monsters. Some tritosaurs were bipeds. Others had chameleon-like appendages. With origins in the Late Permian, the Tritosauria became extinct at the K–T boundary. Overall, the new tree topology sheds light on this clade and several other ‘dark corners’ in the family tree of the Amniota. Now pterosaurs have more than a dozen antecedents in the fossil record documenting a gradual accumulation of pterosaurian traits.

INTRODUCTION

The Lepidosauria was erected by Romer (1956) to include diapsids lacking archosaur characters. Later, with the advent of computer-assisted phylogenetic analyses,

many of Romer's 'lepidosaurs' (Protorosauria/Prolacertiformes, Trilophosauria, and Rhynchosauria) were transferred to the Archosauromorpha (Benton, 1985; Gauthier, 1986). With these transfers Gauthier et al. (1988) restricted the definition of the Lepidosauria to the last common ancestor of Squamata and Rhynchocephalia, and all descendants of that ancestor.

An enclosing clade, the Lepidosauriformes, was defined (Gauthier et al., 1988) as the Lepidosauria plus the Kuehneosauridae, their last common ancestor and all of its descendants.

A larger enclosing clade, the Lepidosauromorpha, was erected for Lepidosauria and all taxa sharing a more recent common ancestor with it than with Archosauria (Gauthier, 1986). According to Evans and Jones (2010), the earliest recognized lepidosauromorphs, *Lanthanolania* (Modesto and Reisz, 2002) and *Saurosternon* (Carroll, 1975), are Late Permian in age.

In the nineteenth century, the Rhynchocephalia was erected (Günther, 1867) for *Sphenodon* and its closest fossil relatives. Estes et al., (1988) defined the Squamata as the most recent common ancestor of Iguania and Scleroglossa and all of its descendants. Evans and Jones (2010) redefined the Squamata as all lepidosaurs more closely related to snakes than to *Sphenodon*. They thought the first radiation of squamates likely occurred between the Late Triassic and Middle Jurassic, as many Jurassic to Early Cretaceous taxa are either stem-squamates or basal members of major clades in their view.

Historical interest in the possible precursors of lizards and snakes arose with the description of *Sphenodon* (then known as *Hatteria*; Günther, 1867) and later with the discovery of several dozen diapsid fossil taxa, including *Prolacerta* (Parrington, 1935;

Camp, 1945; von Huene, 1956). However, Gow (1975) demonstrated that *Prolacerta* was more closely related to archosaurs than to squamates. More recently de Braga and Rieppel (1997) recovered turtles, sauropterygians and lepidosaurs in a single clade. Wiens et al., (2012) produced a molecule study of extant taxa that rearranged prior squamate trees, nesting *Dibamus* and gekkos at the base while nesting Anguimorpha and Iguania as derived sister clades. Pyron et al., (2013) produced a very large study of 4161 extant squamates that recovered a similar tree topology, but included no extinct taxa and their basalmost squamate was again, the legless *Dibamus*.

Several prehistoric lizard-like taxa are currently considered enigmas because they don't nest well within either the Rhynchocephalia or the Squamata. Lizard-like *Lacertulus* (Carroll and Thompson, 1982) is not a squamate according to Benton (1985) and Evans (2003). *Huehuecuetzpalli* (Reynoso, 1998) nests outside the Squamata. *Scandensia* (Evans and Barbadillo, 1998; Bolet and Evans, 2011) cannot be accommodated within existing squamate clades, according to Evans (2003).

In summary, membership within the Lepidosauria has shifted over time. Interrelationships have likewise found little consensus. Molecule studies do not match morphological studies.

Here a phylogenetic analysis large enough to provide hundreds of possible nesting opportunities for extant and extinct amniote taxa is presented. Rather than trying to shoehorn misfit taxa into existing clades, the present study opens to the possibility of recovering new clades.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; BES SC, Museo Civico di Storia Naturale di Milano, Italy; BSPHM,

Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; **BPI**, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, South Africa; **FMNH (UC)**, Field Museum of Natural History (University of Chicago), Chicago, U.S.A.; **GMV**, Geological Museum of China, Beijing, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **KUVP**, University of Kansas Museum of Natural History, Lawrence, U.S.A.; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.; **MFSN**, Museo Friulano di Storia Naturale of Udine, Italy; **MNG**, Museum der Natur in Gotha, Germany; **MPUM**, Museo Paleontologia Università degli Studi di Milano, Italy; **NMS G**, National Museums Scotland, Edinburgh Scotland; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland; **PIN**, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; **PVL**: Paleontologia de Vertebrados Lillo, Universidad Nacional de Tucuman, Tucuman, Argentina; **PVSJ**, Museo do Ciencias Naturales, Universidad Nacional de San Juan, Argentina; **QR/C**, National Museum, Bloemfontein, South Africa; **RC**, Rubidge Collection, Wellwood, Graaff Reinet, South Africa; **SAM**, South African Museum, Cape Town, South Africa; **SMF**: Senckenberg Museum, Frankfurt, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **UC**, University of Chicago, Chicago, U.S.A.; **T**, Universität Zürich Paläontologisches Institut und Museum, Zurich, Switzerland; **TA**, Adpression code for Museum für Naturkunde Chemnitz, Germany; **TM**, Ditsong: National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa.

MATERIALS AND METHODS

The present phylogenetic analysis (Supp. Data) employs 413 specimen- to genus-based extinct and extant taxa along with 228 characters. The great size of the present study minimizes the effects of tradition and/or subjective decision-making while creating a taxon inclusion set. The large list also provides a greater number of possible nesting sites for all included taxa.

Although some characters used here are similar to those from various prior analyses, the present list of character traits (Supp. Data) was largely built from scratch. Characters were chosen or invented for their ability to lump and split large clades and for the trait's visibility in a majority of taxa. Small and hard-to-see foramina were not included.

Due to the size of the inclusion set, data were collected from firsthand observation, digital photographs, and the literature. 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 for 100 replicates were calculated for overlapping subsets; then combined and documented in the tree (Fig. 1, Supp. Data).

RESULTS

The present phylogenetic analysis of 413 taxa and 228 characters recovered three

optimal trees (Supp. Data), each with a length of 6465 steps, a Consistency Index (CI) of .091, a Retention Index (RI) of .748, a Rescaled Consistency Index (RC) of .068 and a Homoplasy Index (HI) of .909. The homoplasy score was high due to the great propensity of tested taxa to converge on traits and to the high number of taxa within the inclusion set. Loss of resolution occurred only at the node in which the skull of *Gualosuchus* nested with the skull-less *Lagerpeton* (Supp. Data). Otherwise smaller subsets (Fig. 1) recovered single optimal trees with the same topology. Virtually all branches had high Bootstrap scores. Lower scores associate with incomplete taxa.

A subset of that large tree is presented here (Fig. 1). The taxon list was reduced to the 65 taxa that surround and include the 26 members of a new clade of lepidosaurs nesting between the Rhynchocephalia and the Squamata. This single tree had a length of 1103 steps, a Consistency Index (CI) of .316, a Retention Index (RI) of .677, a Rescaled Consistency Index (RC) of .214 and a Homoplasy Index (HI) of .684. In the subset 30 characters are constant and 11 variable characters are parsimony uninformative. The character: taxon ratio is 2.87:1 based on the 187 informative characters.

The present phylogenetic analysis (Fig. 1, Supp. Data) produced a clear record of the interrelationships between the various tested specimens leading to and within the Amniota. Sister taxa all appear similar (share a large number of traits) with no great morphological gaps separating them.

The New Lepidosauromorpha

At the first dichotomy (Supp. Data) the Amniota splits the new Lepidosauromorpha (taxa closer to Lepidosauria; Gauthier, 1986) from the new

Archosauromorpha (taxa closer to Archosauria). *Gephyrostegus bohemicus* (Jaekel, 1902) is their last common ancestor.

Basal taxa in the new Lepidosauromorpha include in ascending order: *Bruktererpeton*, *Thuringothyris*, a clade that includes the Captorhinomorpha, *Saurorictus*, *Milleretta*, a clade that includes the Caseasauria, Diadectomorpha and Procolophonia (sans Owenettidae), a clade that includes the Pareiasauria and Chelonia, a clade that includes *Macroleter* and *Lanthanosuchus*, *Nyctiphruretus* and the Owenettidae.

The Lepidosauriformes include Lepidosauria, Kuehneosauridae, and their last common ancestor (Gauthier et al., 1988). Here (Fig. 1, Supp. Data) those last common ancestors are *Sophineta* (Evans and Borsuk-Bialynicka, 2009) and *Santaisaurus* (Koh, 1940). It is interesting to note that only one other Early Triassic precursor taxon, *Paliguana* (Broom, 1903), also has an upper temporal fenestra and is the most basal taxon in this lineage with this trait. Broom (1903) considered it a ‘true lizard,’ and until *Sophineta* and *Santaisaurus* were included in the present tree, *Paliguana* was that last common ancestor of Lepidosauria and Kuehneosauridae.

Derived from Late Permian owenettids, the base of the Lepidosauriformes includes *Paliguana*, *Sophineta*, and *Santaisaurus* (all Early Triassic). The next dichotomy splits the Kuehneosauridae plus their non-gliding ancestors (Late Permian to Early Cretaceous) from the Lepidosauria (Late Permian to the present). Note that the two former lepidosauromorphs mentioned earlier, *Lanthanolania* and *Saurosternon*, now nest within the Lepidosauriformes as ‘rib’-glider precursors.

The first dichotomy within the Lepidosauria splits the Rhynchocephalia (Middle Triassic to the present day) from the remaining lepidosaurs. Basal rhynchocephalians

include *Gephyrosaurus*, *Marmoretta*, *Megachirella* and the Sphenodontia. Derived members include *Azendohsaurus*, *Trilophosaurus*, *Mesosuchus*, *Priosphenodon*, and the Rhynchosauria (Early Triassic to early Late Cretaceous).

Scandensia (Early Cretaceous) nests as a transitional taxon between the base of the Rhynchocephalia and the remaining Lepidosauria. A sister taxon, the MFSN 19235 specimen (originally and erroneously attributed to *Langobardisaurus*, Bizzarini and Muscio, 1995; Bizzarini et al., 1995; Renesto and Dalla Vecchia, 2007; Late Triassic) nests as the last common ancestor of squamates and the new clade of lepidosaurs.

The base of the new lepidosaur clade includes *Homoeosaurus*, the IVPP V 14386 specimen, and *Dalinghosaurus*. Other basal taxa include *Hoyalacerta*, *Carusia*, *Meyasaurus*, the Daohugou lizard (IVPP V 13747), *Bavarisaurus*, *Lacertulus*, *Tijubina*, and *Huehuecuetzpalli*. The next dichotomy divides *Jesairosaurus*, *Hypuronector*, and the Drepanosauridae from several *Macrocnemus* specimens plus *Dinocephalosaurus*. The next dichotomy divides *Langobardisaurus* plus *Tanytrachelos* and *Tanystropheus* from the Fenestrasauria (Peters, 2000), which includes *Cosesaurus*, *Kyrgyzsaurus*, *Sharovipteryx*, *Longisquama* and the Pterosauria.

In the Squamata the first dichotomy recovered the Iguania and the Scleroglossa, matching Estes, et al. (1988). Contra de Braga and Rieppel (1997), turtles and sauropterygians do not nest with lepidosaurs in the present study (Supp. Data). Contra Benton (1985) and Gauthier et al., (1988) *Trilophosaurus* and the Rhynchosauria do not nest with the Archosauriformes, but with derived rhynchocephalians. Contra Gauthier et al. (1988) and Nesbitt (2011) pterosaurs do not nest with archosaurs or archosauriforms,

but in the new clade of lepidosaurs. Several other novel taxon nestings are also recovered here.

DISCUSSION

The present results shed new light on lepidosaur origins and interrelationships. Taxa once removed from the Lepidosauria, including *Trilophosaurus* and the Rhynchosauria (Benton 1985, Gauthier et al., 1988), are returned here. Taxa once thought related to *Prolacerta*, such as *Macrocnemus* and *Tanystropheus* (Benton, 1985; Gauthier et al., 1988; Peters, 2000), are nested more parsimoniously within the new lepidosaur clade. The Pterosauria, once considered to have appeared in the fossil record without obvious antecedent (Hone and Benton, 2007), now nests in a lepidosaur lineage that clearly demonstrates a gradual accumulation of pterosaurian traits over a dozen taxa (Peters 2000, 2001, see below). Here (Fig. 1; Supp. Data) several other former enigmas and problematic taxa now nest with similar sister taxa.

The present phylogenetic analysis shows that the last common ancestor of lepidosaurs and archosaurs is the basalmost amniote, *Gephyrostegus bohemicus* in the Westphalian (310 Ma). More derived, yet more ancient amniotes, including *Westlothiana* and *Casineria*, appear thirty million years earlier, in the Viséan (340 Ma). The present topology expands the traditional taxon list for both the Archosauromorpha and the Lepidosauromorpha. The topology also indicates that the diapsid skull morphology evolved separately in archosaurs and lepidosaurs.

The traditional taxon list for the Lepidosauriformes (Lepidosauria + Kuehneosauridae) does not change in the present tree topology. The traditional taxon list for the Lepidosauria is supplemented with the addition of a new clade.

The Tritosauria

The proposed name for the new lepidosaur clade is the Tritosauria, or ‘third lizards,’ because this clade nests between the two traditional lepidosaur clades, the Rhynchocephalia and the Squamata. The Tritosauria also nests outside of the two major lizard clades, the Iguania and the Scleroglossa. The Tritosauria is defined as *Pteranodon*, *Dalinghosaurus*, their last common ancestor and all of its descendants. No unique individual traits identify this clade. Tritosaurs do have an unfused proximal tarsus, distinct from most other lepidosaurs, but that trait is convergent with rhynchosaur, a clade that rejoins the lepidosaurs here. Tritosaurs have a unique suite of traits (see below) that could only have been recovered in phylogenetic analysis. The removal of twenty derived tritosaurs from the present analysis does not affect tree topology. Rather it indicates that the remaining six basal tritosaurs were themselves a distinct clade.

Representatives of the Tritosauria first appeared in the Late Permian with *Lacertulus*. The Tritosauria reached the acme of their diversity in the Triassic, and then became extinct at the K-T boundary with the disappearance of *Quetzalcoatlus*. Most clade members were small terrestrial, lizard-like forms. Some, the drepanosaurs, were small and arboreal (Pinna, 1980). Others, including *Dinocephalosaurus* (Li et al., 2004), were large and aquatic. The Tritosauria also includes the first flying reptiles, the pterosaurs.

Ironically, several basal taxa, like *Huehuecuetzpalli* and *Scandensia*, are only known from Early Cretaceous sediments. Several derived taxa, like *Macrocnemus* and *Tanystropheus*, are only known from Triassic sediments. These and other anachronisms testify to a largely undocumented radiation of tritosaurs in the Middle to Late Permian along with the ability of basal taxa to conserve traits and survive as a species for over 100 million years.

Tritosaur Character Trait Evolution

The following tested characters appear within basal members of the Tritosauria to the exclusion of a penultimate outgroup taxon, the MFSN 19235 specimen. Reversals can and do occur in derived taxa. Traits restricted to tritosaur offshoot clades are not listed, so in essence this list documents the gradual accumulation of traits leading to the most derived tritosaur taxon listed here, the MPUM 6009 specimen, a basal pterosaur.

Tritosaur proximal outgroup taxa include two basal members of the Squamata, *Iguana* and *Liushusaurus*. Several character traits listed below for basal tritosaurs are noted with an asterisk because these traits are shared with these basal squamates.

Basal Tritosauria Clade One (*Homoeosaurus*, *Dalinghosaurus*, IVPP V 14386) and Descendant Taxa—(1) pineal foramen smaller than 20 percent of parietal length*; (2) frontal nasal suture anteriorly oriented (posteriorly pointed)*; (3) jugal does not contact squamosal; (4) posterior ectopterygoid aligns with posterior pterygoid transverse process without a sharp lateral pterygoid angle; (5) retroarticular process straight; (6) cervical centra longer than tall; (7) scapula and coracoid subequal; (8) scapulocoracoid fenestrated*; (9) manual unguals not trenchant and without penultimate

phalanges longer than others; (10) astragalus and calcaneum not fused; (11) metatarsus compact; (12) metatarsal one less than half the length of metatarsal three.

Basal Tritosauria Clade Two: (*Hoyalacerta* and Descendant Taxa)—(1) in lateral view, rostral shape straight (not convex); (2) naris displaced or posteriorly elongate; (3) orbit half again longer than tall; (4) lateral temporal arch absent*; (5) posterior maxillary tooth at mid orbit*; (6) scapula and coracoid subequal*.

Tritosauria Clade Three: (*Meyasaurus*, *Carusia* and Descendant Taxa)—(1) skull table convex; (2) major axis of naris horizontal to 30°; (3) mandible tip straight (does not rise); (4) second caudal transverse process not wider than centrum; (5) metacarpal three is the longest; (6) manual 4.4 not longer than manual 4.3 (digit 4, phalanx 3);

Tritosauria Clade Four: (IVPP V 13747 and Descendant Taxa)—(1) naris opening lateral; (2) postorbital-parietal contact tentative; (3) caudal transverse processes absent beyond eighth caudal; (4) proximal metatarsals subequal in width; (5) metatarsal 5 straight.

Tritosauria Clade Five: (*Lacertulus*, *Bavarisaurus* and Descendant Taxa)—(1) premaxilla invades nasals; (2) more than four premaxillary teeth; (3) ventral mandible straight; (4) tibia not less than twice ilium length.

Tritosauria Clade Six: (*Tijubina* and Descendant Taxa)—(1) premaxilla orientation horizontal (not transverse); (2) orbit length shorter than rostrum; (3) quadrate anterior lean; (4) premaxillary teeth not tiny; (5) cervical number seven or more; (6) metatarsal one longer than half of metatarsal three.

Tritosauria Clade Seven: (*Huehuecuetzpalli* and Descendant Taxa)—(1) premaxilla ascending process extends beyond naris; (2) postfrontal does not contact upper temporal fenestra; (3) squamosal descending process extends to mid orbit; (4) coronoid process low; (5) cervicals number eight or more; (6) mid caudal vertebrae not three times longer than tall; (7) metacarpal three equals metatarsal four in length; (8) ilium with small anterior process; (9) fibula diameter not greater than half tibia diameter; (10) longest metatarsal(s) three and four; (11) metatarsal five is the widest; (12) metatarsal five torsioned.

Tritosauria Clade Eight: (*Jesairosaurus*, *Drepanosauridae* and Descendant Taxa)—(1) preorbital skull longer than postorbital skull; (2) antorbital fenestra without a fossa; (3) quadratojugal appears on jugal ramus; (4) procumbent premaxillary teeth; (5) gastralia present (reversed in drepanosaurs); (6) scapula larger (taller) than coracoid; (7) pubis ventrally oriented; (8) tibia not shorter than femur; (9) fibula appressed to tibia.

Tritosauria Clade Nine, Tapinoplatia: (Peters, 2000; *Macrocnemus*, *Dinocephalosaurus* and Descendant Taxa)—(1) skull shorter than cervicals; (2) nasals longer than frontals; (3) squamosal ledge present; (4) lower temporal arch present; (5) quadrate vertical; (6) supratemporal fused to squamosal; (7) retroarticular ascends; (8) cervical ribs with free anterior process; (9) cervical ribs slender, parallel to centra; (10) chevrons parallel to centra; (11) caudals shorter than precaudals; (12) scapula/coracoid not fenestrated; (13) olecranon process not present; (14) femur not shorter than half the glenoid-acetabulum length.

Tritosauria Clade Ten, Characiopoda: (Peters, 2000; *Langobardisaurus*, *Tanytrachelos*, *Tanytropheus* and Descendant Taxa)—(1) narial opening dorsolateral;

(2) naris not larger than antorbital fenestra (antorbital fenestra lost in *Tanystropheus*); (3) prefrontal does not contact maxilla; (4) jugal posterior process straight; (5) dorsal vertebrae with transverse processes; (6) 25 or fewer presacrals (reduced from 26 or more); (7) second caudal transverse process wider than centrum width; (8) advanced metatarsal type of tarsus.

Tritosauria Clade Eleven, Fenestrasauria: (Peters, 2000; *Cosesaurus* and Descendant Taxa)—(1) skull width less than 1.2x height; (2) orbit not half again longer than tall; (3) maxilla palatal process present; (4) premaxilla excluded from choana; (5) internal nares deflected medially with narrow vomers; (6) vomer teeth absent; (7) pterygoid narrow, transverse process absent; (8) palatal teeth absent; (9) premaxillary teeth not procumbent; (10) four sacral vertebrae; (11) caudals not shorter than presacrals; (12) interclavicle fused to sternum (creating a sternal complex); (13) expanded fenestration erodes coracoid to stem shape; (14) ilium anterior process longer than acetabulum length; (15) ilium posterior process not longer than anterior process; (16) ventral pelvis fused; (17) prepubis present; (18) tibia less than twice ilium length.

Tritosauria Clade Twelve: (*Kyrgyzsaurus* and Descendant Taxa)—(1) lacrimal deeper than maxilla; (2) pineal foramen absent; (3) quadrate not posteriorly concave; (4) postorbital extends to posterior parietal; (5) vomer maxilla contact; (6) posterior mandible not deeper anteriorly; (7) retroarticular straight.

Tritosauria Clade Thirteen: (*Sharovipteryx* and Descendant Taxa)—(1) squamosal descending process acute; (2) quadrate posterior lean; (3) internal nares not close to premaxillary teeth; (4) multicuspid teeth; (5) five or more sacral vertebrae; (6) midcaudal vertebrae three times longer than tall; (7) olecranon process present; (8) fore

limb/hind limb ratio less than 0.55; (9) radiale and ulnare enlarged to blocks; (10) manus and pes subequal; (11) metatarsus not compact; (12) longest metatarsal four; (13) pedal 3.1 not longer than pedal 2.1.

Tritosauria Clade Fourteen: (*Longisquama* and MPUM 6009, Pterosaur)—(1) orbit does not enter anterior half of skull; (2) jugal posterior process descends; (3) squamosal descending process extends only to the dorsal cheek; (4) retroarticular process descends; (5) cervical centra not longer than tall; (6) cervicals decrease anteriorly; (7) clavicles fused medially; (8) manual unguals trenchant with penultimate phalanges longer than others.

Tritosauria Clade Fifteen: (MPUM 6009, Pterosaur)—(1) snout-occiput length not less than half the presacral length; (2) premaxillary teeth procumbent; (3) lacrimal not deeper than maxilla; (4) dentary contributes to coronoid process; (5) humerus longer than femur; (6) fore limb/hind limb ratio more than 1.0; (7) manus larger than pes; (8) manual 4.4 longer than manual 4.3; (9) pedal digit five has three phalanges (including the ungual).

In Addition to the Above—Tooth implantation becomes thecodont perhaps at clade eight, certainly at clade nine. The radius and ulna are parallel and appressed at clade eight. The epipterygoid is lost at clade nine. Cervicals, often elongate, descend from the back of the skull in a sine curve at clade nine. Pedal 5.1 becomes metapodial at clade ten. The scapula is strap-like and the interclavicle develops an anterior process at clade eleven. Uroptagia and other extradermal membranes appear at clade eleven. Facultative bipedal locomotion appears at clade eleven and obligate bipedalism appears at clade thirteen. The humerus develops a large deltopectoral crest at clade thirteen. The

clavicles wrap posteriorly around the sternal complex rim at clade fourteen.

Hyperelongation of manual digit 4 and axial rotation of metacarpal 4 to facilitate wing folding (Peters, 2001) appears at clade fifteen. Multicusped posterior teeth appear at clade fifteen or perhaps thirteen with convergence in *Langobardisaurus* at clade ten.

CONCLUDING REMARKS

The present phylogenetic analysis of 413 taxa recovers a new tree topology in which a third clade of lepidosaurs, the Tritosauria, is recovered between the two traditional clades, the Rhynchocephalia and the Squamata. Tritosaurs include a wide variety of morphologies. All but drepanosaurs had unfused proximal tarsals, distinct from those of most other lepidosaurs. Some tritosaurs evolved thecodont teeth and an antorbital fenestra. Some tritosaurs became bipeds. Some became volant, others aquatic. The new tree topology sheds light on lepidosaur origins and radiations.

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FIGURE CAPTIONS

FIGURE 1. A subset of the 1253-taxon tree (Supp. Data), reduced to the 65 taxa that surround and include the 26 members of the Tritosauria, a new lepidosaur clade nesting between the Rhynchocephalia and the Squamata. Bootstrap scores are shown. Gray type refers to chronological age: **LP**, Late Permian; **ETr**, Early Triassic; **MTr**, Middle Triassic; **LTr**, Late Triassic, **EJu**, Early Jurassic; **MJu**, Middle Jurassic; **LJu**, Late Jurassic; **EK**, Early Cretaceous. [one column]

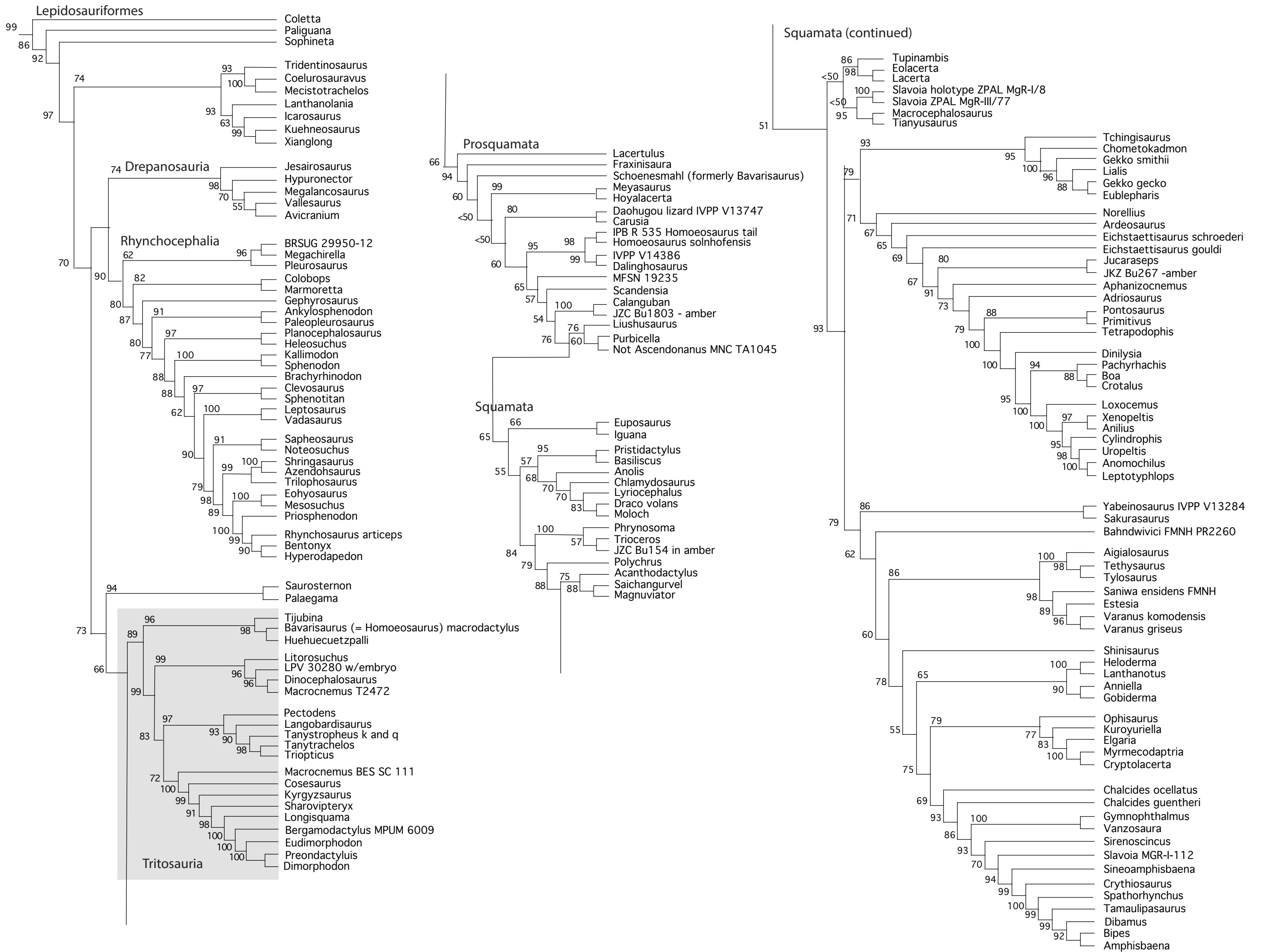


Figure 1.