

Addition to “The Phylogenetics of *Teleosauroidea* (*Crocodylomorpha; Thalattosuchia*) and Implications for Their Ecology and Evolution”

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Abstract

Johnson *et al.* (2020a) provided a comprehensive overview of *Teleosauroidea*, a diverse group of Mesozoic crocodylomorphs that lived in freshwater-to-marine ecosystems across the world. Johnson *et al.* (2020a) performed numerous phylogenetic analyses on *Teleosauroidea* and used them to establish a new taxonomic framework for this long-neglected clade. However, therein the numerous new teleosaroid clades were not properly registered in accordance with the *International Code of Phylogenetic Nomenclature* (PhyloCode). Herein we correct this error. We also replace the clade name *Aeolodontinae* with *Aeolodontini*, to ensure we do not inadvertently create two different names for this clade under the PhyloCode and the *International Code of Zoological Nomenclature*.

Key words: *Aeolodontinae*, *Aeolodontini*, registration

Introduction

Teleosaroid crocodylomorphs represent a key component of coastal and freshwater Early Jurassic to Early Cretaceous ecosystems (Buffetaut 1982; Hua & Buffetaut 1997; Martin *et al.* 2016; Johnson *et al.* 2020a). Johnson *et al.* (2020a) recently evaluated the taxonomy and phylogenetics of *Teleosauroidea*, which had previously been poorly understood. This addendum is to ensure that all clade names within *Teleosauroidea* are properly registered and recognized under the *International Code of Phylogenetic Nomenclature* (PhyloCode). This addendum should be consulted alongside the original publication (Johnson *et al.* 2020a).

Clades and Their Synapomorphies

Herein we highlight clades within *Teleosauroidea* and briefly discuss their synapomorphies (see Johnson *et al.* 2020a, for more details). Most importantly, we establish all clade names under the PhyloCode, providing each with a phylogenetic definition and registration number.

Teleosauroidea Delfino & Dal Sasso 2006: 350, converted clade name

Registration Number: 801.

Definition: The largest clade within *Thalattosuchia* containing *Teleosaurus cadomensis* (Lamouroux 1820), but not *Metriorhynchus brevirostris* (Holl 1829) (*Metriorhynchoidea*).

Reference Phylogeny: Johnson *et al.* (2020a: Fig. 60B).

Composition: *Plagiophthalmosuchus*, *Teleosauridae* (composed of the Chinese teleosauroid, *Indosinosuchus*, *Mystriosaurus*, *Teleosaurinae* (comprising *Platysuchus* and *Teleosaurus*)), and *Steneosaurinae* (composed of *Steneosaurus*, *Mycterosuchus*, *Aeolodon*, *Bathysuchus*, and *Sericodon*) and *Machimosauridae* (comprising *Charitomenosuchus*, *Clovesuurdameredoeor*, *Deslongchampsina*, *Macrospondylus* and *Machimosaurinae* (composed of *Anadrianoavaay*, *Neosteneosaurus*, *Proexochokefatos* and *Machimosaurini* (comprising *Yridiosuchus*, *Lemmysuchus*, and *Machimosaurus*))).

Diagnostic Apomorphies: These include absence of a sclerotic ring, the postorbital situated medial to the jugal (postorbital bar), a straightened anterior maxilla (in palatal view), reduced occipital tuberosities, paired ridges on the ventromedial surface of the basisphenoid, a spatulate anterior dentary with the maximum width at the D3-D4 couplet, D3 occluding against the premaxillary-maxillary suture, a coracoid with proximal triangular-shaped and distal fan-shape ends, a scapular blade at most as wide as the glenoid region, and presence of caudal osteoderms.

Comments: Geoffroy Saint-Hilaire (1831: 41, 53, 55; 1833: 41, 53, 55) initially defined teleosauroids (“nouvelle famille des télosauriens” = *Teleosauridae*) as a distinct clade based on features of the skull, including: (1) vertically placed orbits; (2) a “beak-like” snout; (3) large supratemporal fenestrae; (4) two cranial “arches”; (5) nasal (cranio-respiratory) canal and temporal region development; and (6) no intervention of the parietal between the jugal and temporal.

Following Geoffroy Saint-Hilaire’s (1831, 1833) work (Brignon 1993), teleosauroids continued to be traditionally grouped together based on their “longirostrine” skull, dorsally directed orbits and high tooth count (Young & Andrade 2009; Ballell *et al.* 2019). However, recent studies (Young *et al.* 2014; Foffa *et al.* 2019; Sachs *et al.* 2019; Johnson *et al.* 2020a) have shown that there is considerably more variation in the teleosauroid cranium than initially thought, and that skull shape and tooth count cannot purely be relied on to diagnose this clade.

There have been previous uses of the name *Teleosauroidea* (Buchy *et al.* 2006; Delfino and Dal Sasso 2006; Buch 2007) that follow Vignaud (1995), an unpublished PhD thesis. However, Young & Andrade (2009) was the first published paper that included an in-depth, detailed explanation of uniting characters and phylogenetic assessment of the clade.

***Teleosauridae* Geoffroy Saint-Hilaire 1831: 41, 55 (as famille des *Téléosauriens*), converted clade name**

Registration Number: 800.

Definition: The largest clade within *Teleosauroidea* containing *Teleosaurus cadomensis* (Lamouroux 1820) but not *Machimosaurus hugii* (von Meyer 1837).

Reference Phylogeny: Johnson *et al.* (2020a: Fig. 60B).

Composition: The Chinese teleosauroid, *Indosinosuchus*, *Mystriosaurus*, and the subclades *Teleosaurinae* (comprising *Platysuchus* and *Teleosaurus*) and *Steneosaurinae* (comprising *Steneosaurus*, *Aeolodon*, *Bathysuchus*, *Mycterosuchus* and *Sericodon*).

Diagnostic Apomorphies: These include anteriorly- or anterodorsally-facing external nares, anterior and anterolateral premaxillary margins that extend ventrally, supratemporal fenestrae with inclined anterior margins, a postorbital that overlaps the jugal, a horizontal pterygoid flange, and the basisphenoid tapers off at the anterior quadrates.

Comments: As mentioned previously, *Teleosauridae* was originally erected and defined by Geoffroy Saint-Hilaire (1831, 1833) and encompassed all teleosauroid species. However, we follow Johnson *et al.* (2020a) and herein restrict *Teleosauridae* to the nine genera (including the “Chinese teleosauroid”) listed above.

***Teleosaurinae* Bonaparte 1838: 123 (as *Teleosaurina*), converted clade name**

Registration Number: 799.

Definition: The largest clade within *Teleosauroidea* containing *Teleosaurus cadomensis* (Lamouroux 1820) but not *Aeolodon priscus* (von Sömmering 1814).

Reference Phylogeny: Johnson *et al.* (2020a: Fig. 60B).

Composition: *Platysuchus* and *Teleosaurus*.

Diagnostic Apomorphies: Four characters unite *Platysuchus* and *Teleosaurus*: the tooth row and quadrate condyle are both below the occipital condyle and are unaligned with the tooth row, the frontal-postorbital suture is below the intertemporal bar, osteoderms with small round pits that are densely packed together, and strongly curved presacral dorsal osteoderms.

Comments: Initially, Bonaparte (1838: 123) introduced the subfamily *Teleosaurina* (*Teleosaurinae*) and later provided a diagnosis: “Retro-nares maximae, eodem plano ac fossa orbitalis sitae” (“largest choana in the same plane as the orbital fossa”) (Bonaparte 1840: 91).

In his unpublished PhD thesis, Vignaud (1995) conceptualized the subfamily *Teleosaurinae* as including *Platysuchus* and all *Teleosaurus* species, based on characteristics “moindre adaptation au milieu marin” (“less adapted to a marine environment”), specifically the tightly interlocked and ornamented dorsal osteoderms, sudden “widening” immediately anterior to the orbits (either referring to the upturned orbital margin or dorsoventral compression due to preservation), and reduced supratemporal fenestrae. The genus *Teleosaurus* is currently limited to one species, the type species *Teleosaurus cadomensis* (Jouve 2009; Johnson *et al.* 2020a, for more details); otherwise, our definition of *Teleosaurinae* follows the concept of Vignaud (1995).

Aeolodontini, new clade name

Registration Number: 758.

Definition: The largest clade within *Teleosauroidea* containing *Aeolodon priscus* (von Sömmering 1814) but not *Steneosaurus megistorhynchus* (Eudes-Deslongchamps 1866) and *Teleosaurus cadomensis* (Lamouroux 1820).

Reference Phylogeny: Johnson *et al.* (2020a: Fig. 60B), where *Steneosaurus megistorhynchus* is called *Seldsienean megistorhynchus*.

Composition: *Mycterosuchus*, *Aeolodon*, *Bathysuchus*, and *Sericodon*.

Diagnostic Apomorphies: These include “8”-shaped premaxilla in anterior view (Foffa *et al.* 2019), reduced basioccipital tuberosities, laterally oriented first (P1) and second (P2) premaxillary alveoli, P1 and P2 do not form a couplet and are positioned on the anterior margin of the premaxilla, P1 and P2 are on the same transverse plane, and the anterior margin between P2-P3 is sub-rectangular (with P3 clearly lateral to P2).

Comments: The clade here named *Aeolodontini* is consistently recovered as monophyletic, regardless of taxon sampling, characters, or phylogenetic software (parsimony or Bayesian criteria). It is interesting to note that, while similar in many aspects of the skull (particularly the premaxillae), the postcranial material of *Mycterosuchus* is vastly different from other members of the group (see Johnson *et al.* 2020a, for details).

Herein, we replaced *Aeolodontinae* of Johnson *et al.* (2020a) with *Aeolodontini*. This is due to the position of *Steneosaurus megistorhynchus* (=*Seldsienean megistorhynchus*). Young *et al.* (in review) have applied to the International Commission on Zoological to designate this taxon as the new type species of *Steneosaurus*, given that the original type species, *S. rostromajor*, is undiagnostic (Johnson *et al.* 2020b). In addition, new phylogenetic analyses (Young *et al.* in review) disagrees with Johnson *et al.* (2020a) on the position of *Steneosaurus megistorhynchus*, finding it to be the sister taxon to *Aeolodontini* within *Teleosauridae* rather than within *Machimosauridae*. However, all other teleosauroid clades remain the same (Fig. 1). We await the decision of the ICZN before proposing the name “*Steneosaurinae*”, as we do not wish to inadvertently create two parallel taxonomies for *Teleosauroidea* under the Zoological Code (ICZN 1999) and the PhyloCode (Cantino and de Queiroz 2020).

Machimosauridae Johnson *et al.* 2020a: 117, converted clade name

Registration Number: 757.

Definition: The largest clade within *Teleosauroidea* containing *Machimosaurus hugii* (von Meyer 1837) but not *Teleosaurus cadomensis* (Lamouroux 1820).

Reference Phylogeny: Johnson *et al.* (2020a: Fig. 60B).

Composition: *Charitomenosuchus*, *Clovesuurdameredeor*, *Deslongchampsina*, *Macropondylus* and *Machimosaurinae* (comprising *Andrianavoay*, *Neosteneosaurus*, *Proexochokefalos* and *Machimosaurini* (comprising *Lemmysuchus*, *Machimosaurus* and *Yridiosuchus*)).

Diagnostic Apomorphies: These include dorsally-directed external nares, the anterior and anterolateral margins of the premaxilla do not extend ventrally and are not sub-vertical, a sub-rectangular and somewhat interdigitating (noticeably near the midline) premaxilla-maxilla suture, no anterolateral expansion of the supratemporal fenestrae, the orbit posteroventral margin does not include the postorbital, a generally horizontal pterygoid with a distinct posterolateral angle, and an exposed cultriform process that divides the pterygoids.

***Machimosaurinae* Johnson et al. 2020a: 118, converted clade name**

Registration Number: 759.

Definition: The largest clade within *Teleosauroidea* containing *Machimosaurus hugii* (von Meyer 1837) but not *Macropondylus bollensis* (Jaeger 1828), *Deslongchampsina larteti* (Eudes-Deslongchamps 1866), and *Charitomenosuchus leedsi* (Andrews 1909).

Reference Phylogeny: Johnson et al. (2020a: Fig. 60B).

Composition: *Andrianavoay*, *Proexochokefalos*, *Neosteneosaurus*, and *Machimosaurini* (comprising *Lemmysuchus*, *Machimosaurus* and *Yridiosuchus*).

Diagnostic Apomorphies: These include the supratemporal fenestra length is two times the width, a shallow Meckelian groove, a sharply dorsally curved angular, and non-procumbent dentition.

***Machimosaurini* Jouve et al. 2016: 6, converted clade name**

Registration Number: 798.

Definition: The largest clade within *Teleosauroidea* containing *Machimosaurus hugii* (von Meyer 1837) but not *Neosteneosaurus edwardsi* (Eudes-Deslongchamps 1868).

Reference Phylogeny: Johnson et al. (2020a: Fig. 60B).

Composition: *Yridiosuchus*, *Lemmysuchus*, *Machimosaurus* and possibly *Andrianavoay*.

Diagnostic Apomorphies: There are multiple features uniting *Machimosaurini*, including parallelogram-shaped supratemporal fenestrae, all apices are blunt with a strongly developed anastomosed pattern, no curvature in the middle and posterior dentition, false ziphodont serrations are restricted to posterior tooth crowns, incipient ziphodont carinae and true denticles, microziphodonty, three sacral vertebrae, sub-square and reduced ischial plate, ventrally angled tibial tuberosity, and keeled osteoderms with variable, elongated and “starburst-patterned” pits.

Comments: Jouve et al. (2016) initially diagnosed the tribe *Machimosaurini* based on the following characteristic features: (1) shortened rostra; (2) enlarged supratemporal fenestrae; (3) reduced tooth counts; and (4) blunt, ornamented dentition.

Specific characteristics of machimosaurins, particularly their teeth, have been documented for several years; *Mac. hugii* was first described by von Meyer in 1837, in which he comments on the “...stumpfkönischen und dicht gestreiften Zähnen besonders charakteristisch herauszustellen...” (“...particularly (conspicuous in) conical and densely striped teeth...”) (von Meyer, 1837: 560). More recently, multiple papers have highlighted and discussed machimosaurine features in great detail, including: the dentition (Young & Steel 2014; Young et al. 2015a; Jouve et al. 2016); cranial features (Hua 1996; Young et al. 2014; Fanti et al. 2016; Johnson et al. 2017; Johnson et al. 2019); pelvic bones (Johnson et al. 2017); and the unique sacral anatomy (Martin & Vincent 2013; Young et al. 2014; Johnson et al., 2017).

Note that Fig 59A in Johnson et al., 2020, *Neosteneosaurus edwardsi* is mislabeled as *Leptocranius edwardsi*. The genus *Leptocranius* is a non-valid genus and is a synonym of *Steneosaurus* (Johnson et al. 2020b).

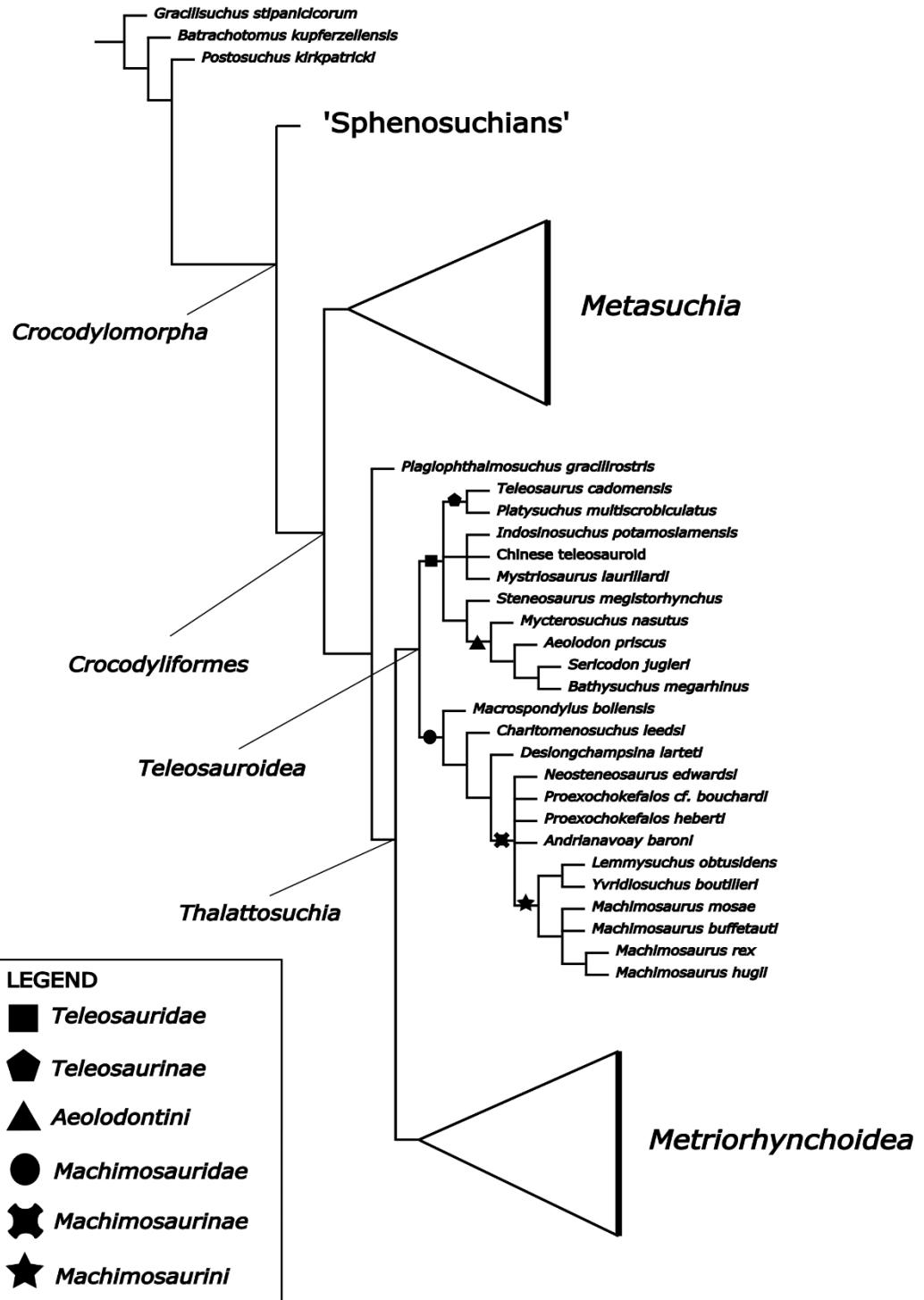


FIGURE 1. Strict consensus topology of Teleosauroidea (modified from Young *et al.* in review). Shapes on branches represent the following clades: square: Teleosauridae; pentagon: Teleosaurinae; triangle: Steneosaurinae; circle: Machimosauridae; wheel: Machimosaurinae; and star: Machimosaurini.

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