Sauria J. Macartney 1802 [J. A. Gauthier and K. de Queiroz], converted clade name

Registration Number: 114

Definition: The smallest crown clade containing *Alligator* (originally *Crocdilus*) *mississippiensis* (Daudin 1802) (*Crocodylia*), *Sphenodon* (originally *Hatteria*) *punctatus* (Gray 1842), and *Lacerta agilis* Linnaeus 1758 (*Squamata*), but neither *Testudo graeca* Linnaeus 1758 (*Testudines*) nor *Homo sapiens* Linnaeus 1758 (*Mammalia*). This is a minimum-crown-clade definition with external specifiers. Abbreviated definition: min crown ∇ (*Alligator mississippiensis* (Daudin 1802) & *Sphenodon punctatus* (Gray 1842) & *Lacerta agilis* Linnaeus 1758 ~ *Testudo graeca* Linnaeus 1758 v *Homo sapiens* Linnaeus 1758).

Etymology: Derived from the Greek *sauros* (“lizard”).

Reference Phylogeny: The primary reference phylogeny is Figure 3 in Gauthier et al. (1988b), in which *Alligator mississippiensis* is part of *Pseudosuchia* (and *Archosauria*), *Lacerta agilis* and *Sphenodon punctatus* are in *Lepidosauromorpha* (= *Pan-Lepidosauria*), *Testudo graeca* is part of *Testudines*, and *Homo sapiens* is in *Mammalia*. See also Ezcurra et al. (2014: Fig. 1), Pritchard and Nesbitt (2017: Fig. 9), and Simões et al. (2018: Fig. 2).

Composition: *Pan-Archosauria* and *Pan-Lepidosauria*, which include the extant crocodilians, birds, tuatara, and lizards (including snakes) (see entries for *Pan-Archosauria*, *Archosauria*, *Pan-Lepidosauria*, and *Lepidosauria* in this volume for details concerning included taxa). *Sauria* is represented in the extant biota by more than 20,000 currently recognized species.

Diagnostic Apomorphies: Gauthier et al. (1988b) listed more than 35 apomorphies for *Sauria* relative to other crown amniotes. Comparison to stem taxa shortens that list considerably (e.g., Gauthier, 1994; Dilkes, 1998; Gottmann-Quesada and Sander, 2009; Ezcurra et al., 2014; Pritchard and Nesbitt, 2017; Simões et al., 2018; Li et al., 2018), partly from scant knowledge of soft anatomy in fossils, but also because of incomplete knowledge of hard anatomy in stem saurians that are closer to the crown than is *Petrolacosaurus kansensis* (*Araeoscelidia*) (e.g., Reisz, 1981). However, the primary challenge to diagnosing *Sauria* is that it remains unclear exactly which Permo-Triassic diapsids, most especially the highly modified aquatic forms (e.g., *Ichthyopterygia*), lie inside or outside of the crown (see Comments).

Relative to *Petrolacosaurus kansensis*, (crown) saurians can be diagnosed by possessing the following “hard” apomorphies that can be ascertained in fossils (see references above): (1) reduced anterior extent of lacrimal bone, accompanied by an enlarged maxilla facial process contacting the nasal bone, excluding lacrimal from naris; (2) loss of caniniform maxillary teeth; (3) origin of temporal adductor muscles spreads onto dorsal surface of lateral edge of parietal table; (4) reduction of supratemporal bone in post-temporal arch and concomitant increase in size of parietal supratemporal process to closely approach the squamosal; (5) loss of tabular bone in skull; (6) quadrate exposed behind squamosal in lateral view; (7) quadrate head hemispherical and received in fossa beneath squamosal; (8) an impedance-matching ear, including a tympanum, a quadrate shaft bowed anteriorly and jaw-opening muscles displaced posteriorly onto a prominent mandibular retroarticular process, to facilitate passage of middle ear cavity traversed by a slender stapes that enables transmission of high frequency, low-intensity airborne sounds from tympanum to inner ear; (9) loss of posterior coracoid bone in endochondral shoulder girdle (= scapulocoracoid cartilage); (10) loss of cleithrum in dermal shoulder girdle; (11) larger pelvic muscles indicated by an enlarged, subtriangular iliac blade with a horizontally oriented dorsal margin; (12) hindlimbs much longer than forelimbs (femur > 40% longer than humerus); (13) distal femoral condyles in approximately the same plane; (14) short and broad-based 5th metatarsal.

Exactly which, if any, of these apomorphies is diagnostic of the crown relative to all known (or suspected) diapsids that are closer to the crown than is *Petrolacosaurus kansensis* remains unclear.

Synonyms: *Diapsida* Osborn 1903 (approximate, partial); *Diaptosauria* Osborn 1903 (approximate, partial), *Eosuchia* Broom 1914 (approximate, partial); *Neodiapsida* Benton 1985 (approximate).

Comments: *Sauria* has been a conspicuous component of terrestrial ecosystems since the dawn of the Mesozoic. It has long been a globally distributed clade, the members of which crawl, run, climb, and slither through disparate habitats on land (and burrow in it), swim in freshwaters and on the high seas, and twice took to the skies in powered flight. It has suffered mass extinctions but re-radiated in their wake, and is still represented by at least 20,000 living species (nearly all of which are either birds or lizards, including snakes). Its members span several orders of magnitude in size—from tiny bee hummingbirds (i.e., *Mellisuga hellenae*) to enormous sauropods (e.g., *Argentinosaurus huinculensis*)—and are just as spectacularly disparate ecologically and morphologically—from head-first burrowing threadsnakes (e.g., *Rena humilis*), to amphibious crocodilians (e.g., *Gavialis gangeticus*), to arboreal chameleons (e.g., *Trioceros jacksonii*), to birds that fly in the air (e.g., *Upupa epops*) or underwater (e.g., *Aptenodytes patagonicus*), or are bipedal cursors unable to fly at all (e.g., *Struthio camelus*), as well as more "lizard-like" forms, including the unusually cold-adapted, nocturnal tuatara (*Sphenodon punctatus*).

Several early naturalists recognized a group composed of four-legged, long-tailed, non-shelled, and (mostly) oviparous vertebrates, including "lizards" (non-serpentiform squamates) and crocodilians (e.g., Linnaeus, 1758; Laurenti, 1768; Blumenbach, 1779), although the scale-less salamanders were soon removed from the group (e.g., Brongniart, 1800; Cuvier, 1800). It was for such a group that Cuvier's (1800) "Les Sauriens" was Latinized to *Sauria* by Macartney (1802). *Crocodylia* was subsequently removed (e.g., Blainville, 1816, 1822; Merrem, 1820), and "*Sauria*" became associated with "lizards" alone (as indicated by standard English translations of the Ancient Greek term "saurian"). A close relationship between *Serpentes* and "lizards" was proposed by some of the same authors (e.g., Oppel, 1811; Blainville, 1816, 1822; Merrem, 1820), although the nesting of snakes deep within "lizards" was not recognized until relatively recently (e.g., Estes et al., 1988; see *Squamata*, this volume).

Osborn's (1903) *Diapsida*, which refers to the presence of two temporal arches (and fenestrae; see entry in this volume), largely supplanted *Sauria* as the favored name for a taxon that included only *Sphenodon, Squamata* and *Crocodylia* among extant "reptiles". Although Osborn (1903) acknowledged an evolutionary relationship between birds and his "diapsid reptiles", *Aves* was not explicitly included in *Diapsida* until much later (e.g., Gauthier, 1986), in the context of a revised concept of monophyly (Hennig, 1966). *Youngina capensis* from the Late Permian of South Africa lent key early support to Osborn's concept of "*Diapsida*". Broom (1914) relied on this very early and relatively unmodified two-arched species as the basis of his "*Eosuchia*", a taxon that he conceptualized as the ancestral group from which all other "diapsid reptiles" would later emerge (see also Romer, 1966).

Growing knowledge of the Late Pennsylvanian *Petrolacosaurus kansensis* (Lane, 1945, 1946; Peabody, 1952; Reisz, 1977, 1981), most particularly that it possessed a two-arched skull, led palaeontologists to apply the name *Diapsida* to a more inclusive clade originating in the Carboniferous (see *Diapsida*, this volume). That left the crown (which emerged much later in the Permian) without a name, so Gauthier et al. (1988a) proposed using *Sauria* for that clade. *Neodiapsida* (Benton, 1985) is sometimes considered a synonym of *Sauria* (e.g., Evans, 1988). However, Benton did not define the name explicitly in terms of ancestry. Thus, when *Younginiformes*, one of the extinct groups he included in *Neodiapsida*, was later inferred to be outside of the crown (e.g., Laurin, 1991), *Neodiapsida* became associated with clade(s) more inclusive than the crown (e.g., Senter, 2004; Reisz et al., 2011). Like Benton (1985), Gauthier et al. (1988a) also regarded younginiforms to be part of *Sauria,* as they were thought to represent the deepest divergence on the lepidosaur stem at the time (see also Benton, 1982, 1983; Gauthier, 1984; Evans, 1988). But because Gauthier et al. (1988a) explicitly defined *Sauria* as applying to the crown, when younginiforms were inferred to be outside of that clade, they were accordingly excluded from it by subsequent workers (e.g., Laurin, 1991; Clark et al., 1993; Gauthier, 1994; deBraga and Rieppel, 1997; Müller, 2004; Senter, 2004; Ezcurra et al., 2014; Nesbitt et al., 2015; Pritchard and Nesbitt, 2017; Pritchard et al., 2018). Although younginiforms are now widely thought to be near-crown stem saurians, it is not entirely clear that they are all related to one another (see, e.g., Müller [2004] and Bickelmann et al. [2009] vs. Gauthier et al. [1988a] and Pritchard and Nesbitt [2017]).

The highly modified drepanosaurs, a radiation of chameleon-like arboreal diapsids with sharp-snouted skulls, have had a more checkered taxonomic history (summarized in Pritchard and Nesbitt, 2017). They were often thought to be early diverging stem archosaurs (e.g., Evans, 1988; Gauthier, 1994; Renesto, 1994; Merck, 1997; Dilkes, 1998; Renesto et al., 2010; and see *Pan-Archosauria,* this volume). But sometimes they were inferred to be outside of crown *Sauria* (e.g., Senter, 2004; Müller, 2004), albeit in variable positions on its stem. Pritchard and Nesbitt's (2017) comprehensive study firmly placed Late Triassic drepanosaurs deep on the saurian stem, with only the Early Permian *Orovenator mayorum* and the Late Pennsylvanian *Araeoscelidia* being more basally branching among diapsids. This requires a long ghost lineage in keeping with their many morphological modifications. According to Pritchard and Nesbitt (2017), drepanosaurs show no trace of the apomorphies associated with the saurian ear, nor do they possess the peg-in-socket quadrate-squamosal articulation of the crown (Gauthier et al., 2012).

The situation is murkier for diapsids that are highly modified for life underwater: the marine *Sauropterygia*, *Ichthyopterygia*, and *Thalattosauria*, and the freshwater *Choristodera*. They must have diverged in the Palaeozoic based on their positions on most trees of early saurians (e.g., Gauthier, 1994; Simões et al., 2018). But even the earliest examples of the marine clades, which first appear in the Early Triassic, already display significant adaptations to marine environments (e.g., Nakajima et al., 2014). Choristoderans are not known with certainty before the Middle Jurassic (Gao et al., 2013). They have variously been allied to either lepidosaurs or archosaurs, and thus inside the crown (e.g., Gauthier et al., 1988b; Rieppel, 1993; Gauthier, 1994; Merck, 1997). The most recent analysis to consider their relationships among diapsids is that of Simões et al. (2018). Their preferred relaxed-clock Bayesian tree based on combined morphological and molecular data inferred strong support for Merck's (1997) marine clade *Euryapsida* Colbert 1945 (= thalattosaurs, sauropterygians, and ichthyosaurs). Euryapsids and choristoderans formed a polytomy just below a weakly supported crown node, so it is not yet clear if they are crown saurians.

Turtles (*Pan-Testudines*, see entry this volume) present yet another challenge. Crown turtles (*Testudines*, see entry this volume) possess an impedance-matching auditory system reminiscent of that in saurians (and some parareptiles; Lyson et al., 2010). But they appear to have acquired many of the associated apomorphies convergently, as most of them are absent in stem turtles (Bever et al., 2015). Nevertheless, even stem turtles have a saurian-like ear in some respects, such as, for example, in having a slenderer stapes that is more horizontally disposed, rather than being thicker, shorter, and more ventrolaterally oriented as in reptiles ancestrally (Gaffney, 1990). Absence of the full suite of saurian ear apomorphies is consistent with other evidence, such as retention of the cleithrum in the shoulder girdle (Lyson et al., 2013b), indicating that turtles lie outside of *Sauria*, all of whose members lack this bone (e.g., Lyson et al., 2010; Lyson et al., 2013a). Likewise, saurians have conspicuously long hindlimbs compared to those of even the earliest stem turtles, which retain the more even limb proportions of the earliest diapsid, *Petrolacosaurus kansensis* (Gauthier et al., 2011).

Nevertheless, there is growing evidence that turtles are diapsids (*contra* e.g., Gaffney, 1980; Gauthier, 1984; Gauthier et al., 1988a,b,c; Gauthier et al., 1989; Reisz and Laurin, 1991; Gauthier, 1994; Lee, 1996), at least in the sense of having descended from an ancestor with upper and lower temporal fenestrae (see *Diapsida*, this volume). For example, in addition to a lower temporal fenestra, there appears to be an upper temporal fenestra, albeit covered over secondarily by an enlarged supratemporal, in the earliest and least-modified stem turtle currently known, *Eunotosaurus africanus* (Bever et al., 2015). This fenestra is unique to diapsids among amniotes. That, coupled with weak morphological support linking them with lepidosaurs (e.g., deBraga and Rieppel, 1997; Bever et al., 2015), and strong molecular support allying them to archosaurs (e.g., Field et al., 2014; Crawford et al., 2015), suggests that turtles might well be crown diapsids (see also Rest et al. [2003], Hugall et al. [2007], and Crawford et al. [2012]; but see Frost et al. [2006], and especially Lu et al. [2013], for an alternative view). However, at least one of these inferences must be mistaken, as turtles cannot simultaneously be sister to archosaurs and sister to lepidosaurs. To further complicate matters, Simões et al. (2018) inferred moderate support from a combined morphological and molecular dataset for turtles being outside of, if near to, *Sauria* (see also Li et al., 2018).

Provided that turtles are not included, the name *Sauria* is the most appropriate name for the clade in question, which is convenient given that it is the root word from which the names of its primary subclades, *Archosauria* and *Lepidosauria,* are formed. It has been defined explicitly as applying to this clade (Gauthier et al., 1988a), and that practice has generally been followed in subsequent phylogenetic studies (e.g., Laurin, 1991; Clark et al., 1993; Gauthier, 1994; deBraga and Rieppel, 1997; Müller, 2004; Senter, 2004; Ezcurra et al., 2014; Nesbitt et al., 2015; Pritchard and Nesbitt, 2017; Pritchard et al., 2018). By contrast, the approximate synonyms *Diapsida* and *Neodiapsida* are commonly applied to more inclusive clades (e.g., Reisz et al., 2011). The name *Eosuchia* has also been defined as applying to a more inclusive clade (Laurin, 1991), and it has traditionally been applied to a group long understood to be a wastebasket of miscellaneous early diapsids without clear connections to either archosaurs or lepidosaurs (e.g., Broom, 1926; Kuhn, 1952; Romer, 1956, 1966; Tatarinov, 1964; Cruickshank, 1972; Gow, 1972, 1975; Carroll, 1976, 1978, 1981; Sigogneau-Russell and Russell, 1978; Olsen, 1978; Evans, 1980).

We here update the definition of *Sauria* proposed by Gauthier et al. (1988a) by using species as specifiers that are consistent with the composition of the taxon as originally circumscribed by Macartney (1802). Although not originally included in *Reptilia* (and thus not listed among our internal specifiers), birds (and snakes) are unambiguously part of this clade (see e.g., *Archosauria*, *Dinosauria* and *Aves* in this volume). We have included a turtle species as an external specifier in our definition so that the name *Sauria* will not apply to any clade in the context of phylogenies in which turtles are descended from the most recent common ancestor of lepidosaurs and archosaurs. In that case, *Reptilia* would be the name of the crown composed of all three clades. These clades appear to have diversified rapidly around 260 million years ago in the early Late Permian, based on the stem turtle *Eunotosaurus africanus* (Capitanian; Lyson et al., 2010) and the stem archosaur *Aenigmastropheus parringtoni* (Guadalupian; Ezcurra et al., 2014). However, Simões et al. (2018) estimated that the primary saurian divergence occurred much earlier, in the Carboniferous.

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Date Accepted: 22 October 2018

Primary Editor: Philip Cantino