

Pan-Lepidosauria J. A. Gauthier and K. de Queiroz, new clade name

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Definition: The total clade of the crown clade *Lepidosauria*. This is a crown-based total-clade definition. Abbreviated definition: total ∇ of *Lepidosauria*.

Etymology: Derived from *pan* (Greek), here referring to “pan-monophylum,” another term for “total clade,” and *Lepidosauria*, the name of the corresponding crown clade; hence, “the total clade of *Lepidosauria*.”

Reference Phylogeny: Gauthier et al. (1988) Figure 13, where the clade in question is named *Lepidosauromorpha* and is hypothesized to include *Younginiformes*, which is no longer considered part of the clade (see Composition).

Composition: *Pan-Lepidosauria* is composed of *Lepidosauria* (*Pan-Sphenodon* plus *Pan-Squamata*, see entry in this volume) and all extinct species (stem lepidosaurs) that share a more recent common ancestor with the species of *Lepidosauria* than they do with any other extant amniotes (*Aves*, *Testudines*, *Crocodylia*, and *Mammalia*). The Late Permian fossils *Saurosternon bainii* and *Lanthanolania ivakhnenkoi*, as well as the Permo-Triassic fossils *Paliguana whitei* and *Palaeagama vielhaueri*, have sometimes been inferred to be stem lepidosaurs (e.g., Gauthier et al., 1988; Modesto and Reisz, 2002; Evans and Jones, 2010) but other times to be stem saurians (e.g., Modesto and Reisz, 2002; Müller, 2004). The Upper Triassic *Kuehneosauridae* and its inferred Early Triassic relative *Pamelina polonica* (but see Simões et al., 2018) have often been inferred to be stem lepidosaurs (Gauthier et al., 1988; Evans, 1988,

2009; Evans and Borsuk-Bialylicka, 2009; Evans and Jones, 2010; but see Müller, 2004; Jones et al., 2013). More recently, kuehneosaurs have been inferred to be stem archosaurs close to *Trilophosaurus buettneri* by Pritchard and Nesbitt (2017), although Simões et al. (2018) placed them as either stem saurians or stem archosaurs depending on the analysis, but in either case only distantly related to *T. buettneri*. The Early Triassic *Sophineta cracoviensis* and the Middle Jurassic *Marmoretta oxoniensis* have been more consistently regarded as stem lepidosaurs, although that inference depends upon correct association among disarticulated remains (Evans, 1991; Waldman and Evans, 1994; Evans, 2009; Evans and Borsuk-Bialylicka, 2009; Evans and Jones, 2010; Jones et al., 2013; Renesto and Bernardi, 2014). Depending on the analysis, Simões et al. (2018) inferred *S. cracoviensis* to be either a stem lepidosaurian or a stem squamatan, but they consistently inferred *M. oxoniensis* as sister to *Megachirella wachtleri* on the squamate stem. Renesto and Bernardi (2014) previously placed the Middle Triassic *Megachirella wachtleri* either inside or outside of the lepidosaurian crown. The Early or Middle Jurassic *Tamaulipasaurus morenoi* may be a stem or a crown lepidosaur, but its relationships are difficult to assess because of its high degree of modification for head-first burrowing (Clark and Hernandez, 1994). The highly modified Late Triassic drepanosaurs have sometimes been inferred to be stem archosaurs (Laurin, 1991; Simões et al., 2018) or stem lepidosaurs (Evans, 2009), but most authors have inferred drepanosaurs to be stem saurians that must accordingly have diverged much earlier than the fossil record currently indicates (i.e., by the Mid-Permian; Guadalupian) (e.g.,

Müller, 2004; Senter, 2004; Renesto et al., 2010; Pritchard and Nesbitt, 2017; Simões et al., 2018). The authors of several early phylogenetic analyses inferred that *Younginiformes* are stem lepidosaurs (e.g., Benton, 1985; Evans, 1988; Gauthier et al., 1988); however, more recent analyses have placed *Younginiformes*, either as a clade or a paraphylum, on the stem of a more inclusive crown clade composed of (in addition to lepidosaurs) archosaurs and sometimes also turtles (e.g., Laurin, 1991; Gauthier, 1994; Caldwell, 1996; deBraga and Rieppel, 1997; Müller, 2004; Evans and Borsuk-Bialylicka, 2009; Renesto and Bernardi, 2014; Bever et al., 2015; Pritchard and Nesbitt, 2017; Simões et al., 2018). See Evans and Jones (2010) for other taxa that are no longer considered stem lepidosaurs.

Diagnostic Apomorphies: As a total clade (and therefore also a maximum clade), *Pan-Lepidosauria* is not necessarily expected to have diagnostic apomorphies (characters that arose simultaneously with the split of lepidosaur stem lineage from that of archosaurs; see de Queiroz, 2007); however, any of the apomorphies that originated along the lepidosaur stem lineage (see Diagnostic Apomorphies for *Lepidosauria*, this volume), as well as those diagnosing various side branches, would allow referral of a specimen or species to *Pan-Lepidosauria*. Uncertainty in placement of several incomplete, and often highly modified, fossils further complicates the question. If, as we suspect, the Early Triassic *Sophineta cracoviensis* is a stem lepidosaur, it shares the following apomorphies with the crown: (1) maxilla participates broadly in ventral orbital margin; (2) postfrontal wraps around fronto-parietal suture; (3) lacrimal reduced, confined largely to orbital rim; (4) marginal teeth attached superficially to lingual margin of jaw (pleurodont dentition); and (5), a weak zygosphenes-zygantrum accessory inter-vertebral articulation.

Synonyms: *Lepidosauria* Haeckel 1866 of various authors (e.g., Romer, 1933, 1945, 1956, 1966; Gardiner, 1982) and *Lepidosauromorpha* Gauthier in Benton 1983 of Benton (1983, 1985) and Evans (1984) are approximate synonyms. *Eosuchia* (e.g., of Romer, 1933, 1945, 1956, 1966), characterized as being composed of “primitive lepidosaurians” and “direct ancestors of the lizards and snakes”, and *Holapsida* Underwood 1957, composed of “*Eosuchia* and *Rhynchocephalia*”, are partial (and approximate) synonyms. *Eolacertilia* Romer 1966 (often incorrectly attributed to Robinson, 1967) sensu Carroll (1975, 1977) and Estes (1983) is a partial (and approximate) synonym in the context of phylogenies that place all of the included taxa in the lepidosaur stem group (see Composition). *Lepidosauromorpha* Gauthier in Benton 1983 of Gauthier et al. (1988) is an unambiguous synonym.

Comments: Although the name *Lepidosauromorpha* has previously been defined phylogenetically as applying to the total clade of *Lepidosauria* (Gauthier et al., 1988), we have chosen instead to apply the name *Pan-Lepidosauria* to that clade in the interest of promoting a standardized form for the names of total clades (e.g., de Queiroz and Gauthier, 1992; Gauthier and de Queiroz, 2001; de Queiroz, 2007). If the name *Lepidosauromorpha* is to be retained, it could be applied to a deep node within *Pan-Lepidosauria*, although that would require careful formulation of the (non-standard) definition, given the uncertain status of many of its potential early members (see Composition). Alternatively, the name could be applied to a clade coinciding with the origin of one of the early-evolving lepidosaur apomorphies.

In the context of phylogenies in which *Sphenodon punctatus* is more closely related to turtles, crocodylians, and birds than to *Squamata* (e.g., Hedges and Poling, 1999; Zardoya and Meyer, 2000), the names *Lepidosauria* (this

volume) and *Reptilia* (this volume) are synonyms, and *Reptilia* is to be granted precedence (see *Lepidosauria* in this volume). In the context of such phylogenies, the name *Pan-Lepidosauria* should not be applied to any clade (*ICPN* Art. 14.5; Cantino and de Queiroz, 2020).

Sophineta cracoviensis and possibly *Pamelina polonica* (see Composition) are the earliest known pan-lepidosaurs (~245Ma, late Olenekian, Early Triassic; Evans, 2009; Evans and Borsuk-Białynicka, 2009). But the initial divergence of *Pan-Lepidosauria* from *Pan-Archosauria* (this volume) is likely older (~265 Ma), based on the age of the earliest-known putative pan-archosaur, *Aenigmastropheus parringtoni* (Capitanian, mid-Late Permian; Ezcurra et al., 2014).

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