

**Saurischia** H. G. Seeley 1888 [J. A. Gauthier, M. C. Langer, F. E. Novas, J. Bittencourt, and M. D. Ezcurra], converted clade name

**Registration Number:** 195

**Definition:** The largest clade containing *Allosaurus fragilis* Marsh 1877 (*Theropoda/Carnosauria*) and *Camarasaurus supremus* Cope 1877 (*Sauropodomorpha*), but not *Stegosaurus stenops* Marsh 1887 (*Ornithischia/Stegosauridae*). This is a maximum-clade definition. Abbreviated definition:  $\max \nabla$  (*Allosaurus fragilis* Marsh 1877 & *Camarasaurus supremus* Cope 1877 ~ *Stegosaurus stenops* Marsh 1887).

**Etymology:** Derived from the Greek: σαύρος = saurian and ισχίον = hip joint (Liddell and Scott, 1882). Seeley (1888) translated ισχίον as “pelvis”.

**Reference Phylogeny:** Because it contains the largest sample of non-avian saurischians, the tree derived from the supertree analysis of Lloyd et al. (2008: supplementary Fig. 2) is selected as the primary reference phylogeny. Note that the definition uses clade addresses (e.g., *Theropoda: Carnosauria*) from Lloyd et al. (2008) to facilitate finding specifiers (e.g., *Allosaurus fragilis*) on their densely branched supertree. Taxa more inclusive than species cannot be specifiers; we do not regard these additional taxon names as parts of the formal definition, nor do we mean to endorse their use for these clades.

**Composition:** According to most phylogenetic hypotheses, *Saurischia* is composed of two primary subclades: *Sauropodomorpha* (this volume) and *Theropoda* (including *Aves*, this volume) (e.g., Gauthier, 1984, 1986; Gauthier et al., 1989; Novas, 1989, 1992; Sereno, 1999; Rauhut, 2003; Ezcurra, 2006; Langer and Benton,

2006; Irmis et al., 2007; Lloyd et al., 2008; Nesbitt et al., 2010; Nesbitt, 2011; Apaldetti et al., 2011; Martínez et al., 2011; Novas et al., 2011; Sereno et al., 2013; Niedźwiedzki et al., 2014; Pretto et al., 2015; Cabreira et al., 2016; Langer et al., 2017). Relations of a few Triassic species, most notably *Eoraptor lunensis* and *Herrerasauridae*, remain unclear even though they are represented by reasonably complete specimens (e.g., contrast Fraser et al., 2002, vs. Martínez and Alcober, 2009, vs. Nesbitt et al., 2010). Somewhat dated lists of included taxa and relationships among them were reviewed in Weishampel et al. (2004). Based on their review of the Paleobiology Database, Starrfelt and Liow (2016) found 762 species of saurischians described from the Mesozoic; as they argued, that number likely underestimates their true diversity (e.g., their estimate was about 1,628 spp.; see *Dinosauria*, this volume). That is certainly the case for avian saurischians of the Cenozoic given their poor preservation potential (see *Aves*, this volume). Nevertheless, with the addition of the 10,672 surviving species of *Aves* (Gill and Donsker, 2017), there are at least 11,434 described species currently assigned to *Saurischia*. In the recently proposed rearrangement of relationships among major dinosaur clades (Baron et al., 2017), *Saurischia* (as redefined by those authors) would include only *Sauropodomorpha* and *Herrerasauridae*, which have no living representatives.

**Diagnostic Apomorphies:** The earliest species belonging to *Saurischia*, as a maximum clade, may not have apomorphies that arose just as it diverged from its sister clade (see de Queiroz, 2007). In practice, any one of the apomorphies

arising along that deepest branch will suffice for taxon assignment (Gauthier and de Queiroz, 2001). In that circumstance, however, support for one relationship rather than another may not be strong. Nevertheless, a clade composed of sauropodomorphs and theropods (including *Aves*) has been a constant feature in dinosaur phylogenetics for the past few decades. Apomorphies shared by saurischians have been reviewed extensively (e.g., Gauthier, 1986; Gauthier et al., 1989; Novas, 1994; Sereno, 1999; Langer, 2004; Ezcurra, 2006; Langer and Benton, 2006; Yates, 2007; Irmis et al., 2007; Nesbitt et al., 2010; Apaldetti et al., 2011; Martínez et al., 2011; Sereno et al., 2013; Pretto et al., 2015; Cabreira et al., 2016).

According to Nesbitt (2011), for example, there may be as many as 25 synapomorphies for *Saurischia*, including the following (authorship credited to first explicit identification as an apomorphy, not the current optimization of that apomorphy): (1) subnarial foramen on border between premaxilla and maxilla (Benton and Clark, 1988); (2) foramen in ventral part of splenial (Rauhut, 2003); (3) epiphyses on posterior cervical vertebrae (Gauthier, 1986); (4) hyposphene-hypantrum accessory joint in trunk vertebrae (Gauthier, 1986); (5) manus comprises more than 30% of humerus + radius length (Gauthier, 1986); (6) distal carpal V absent (Sereno, 1999); (7) 1<sup>st</sup> phalanx in digit I longest non-ungual phalanx in manus (Gauthier, 1986); (8) pointed posterior prong on distal tarsal IV (Langer and Benton, 2006); (9) distinct medial process projecting from middle of distal tarsal IV (Nesbitt, 2011); (10) markedly rimmed, elliptical fossa posterior to ascending process on astragalus (Langer and Benton, 2006).

If theropods are sister to ornithischians, and not to sauropodomorphs (Baron et al., 2017), then these apomorphies either apply to a more inclusive clade (i.e., *Dinosauria*), or they

arose convergently in sauropodomorphs and theropods.

**Synonyms:** In trees in which *Sauropodomorpha* and *Theropoda* are sisters, there are no synonyms for the taxon name *Saurischia*. In the context of the Baron et al. (2017) tree, however, *Theropoda* as defined by Gauthier (1986) is an unambiguous synonym of *Saurischia*. As the name *Saurischia* is defined here, however, that name would not apply to any clade on the Baron et al. (2017) tree (see Comments).

**Comments:** The name *Saurischia* was coined by Seeley (1888) to contain Marsh's (1882) *Theropoda* and *Sauropoda*. It was to be contrasted with Seeley's second cardinal contribution to dinosaur nomenclature published in that same article: *Ornithischia* Seeley 1888. *Saurischia* and *Ornithischia* collectively yield nearly 26,000 records in a Google Scholar search (June 29, 2018), and Seeley (1888) was also the nineteenth most-cited "Proceedings B" article during that same month according to the Royal Society of London. Although Seeley distinguished *Ornithischia* on the basis of some characters now regarded as apomorphies, he differentiated (and named) *Saurischia* exclusively on the basis of plesiomorphies in pelvic anatomy, most notably that the pubis was still directed anteroventrally as in other reptiles. Like other taxonomists of his era, Seeley did not appreciate this distinction between character states. Nor did he explicitly state whether his taxa were to be associated more with a set of taxa or a set of characters (although we suspect the latter given taxonomic practices of the time). As Joyce et al. (2004) observed in their review of the history of turtle nomenclature, in such cases we can only be sure that Seeley coined the taxon names *Ornithischia* and *Saurischia* and not how he conceptualized these taxa.

Despite continued use of *Saurischia* as a taxonomic unit in the dinosaur literature since the late nineteenth century (e.g., Matthew and Brown, 1922; Huene, 1932; Romer, 1956, 1966; Colbert, 1964; Steel, 1970), the implied close relationship between theropods and sauropodomorphs continued to be questioned. During the mid-late twentieth century, for example, saurischians were either thought to be polyphyletic (evolved from different groups of “thecodonts”, e.g., Charig et al., 1965; Thulborn, 1975), or paraphyletic (instead of being related to meat-eating theropods, at least some herbivorous sauropodomorphs were thought related to herbivorous ornithischians, e.g., Bakker and Galton, 1974; Sereno, 1984; Cooper, 1985). Indeed, the monophyly of *Saurischia* was not proposed until nearly a century after Seeley coined that name (Gauthier, 1986; and see corroborating references in Composition and Diagnostic Apomorphies above). Bonaparte’s (1975) landmark study of *Lagosuchus* presented a tree (Fig. 2) that appears to depict *Ornithischia* as sister to *Saurischia* (= herrerasaurs, “prosauro-pods”, “coelurosaur”, and “carnosaurs” according to Bonaparte). Nevertheless, the structure of Bonaparte’s (1975) argument in the text demonstrates that he thought of “saurischians” in their traditional sense, that is, as those dinosaurs that are not ornithischians, rather than as sister to *Ornithischia*. Despite being repeatedly corroborated, *Saurischia* could fall out of use, as theropods have recently been inferred to be related to ornithischians instead of sauropodomorphs (Baron et al., 2017). If that tree is correct, then the name *Saurischia* would apply to no clade at all by our definition, viz., there would be no clade including the theropod *Allosaurus fragilis* and the sauropodomorph *Camarasaurus supremus* that excludes the ornithischian *Stegosaurus stenops*.

Gauthier (1986) proposed the first phylogenetic definition of *Saurischia*: “birds and all dinosaurs that are closer to birds than they are to *Ornithischia*” (p.15). A variety of alternative

definitions were proposed subsequently differing mainly in their choice of internal and external specifiers (e.g., Padian and May, 1993; Padian, 1997; Padian et al., 1999; Sereno, 1998, 1999; Holtz and Osmólska, 2004; Langer, 2004). Gauthier’s (1986) definition of *Saurischia* violates the *PhyloCode* in two important respects: it uses clades rather than species as specifiers (*ICPN* Art. 11.1; Cantino and de Queiroz, 2020); and it uses an internal specifier (birds) that was not traditionally included in the taxon (*ICPN* Rec. 11A; Cantino and de Queiroz, 2020). Instead of using any avians as specifiers—an approach introduced by Gauthier (1986; see also Gauthier, 1984)—we selected three extinct dinosaurs: two species of saurischians—a theropod and a sauropod sensu Marsh (1882)—as internal specifiers, plus an ornithischian species as an external specifier (Sereno, 2005a, b). At least by reference to their genus names, all of these species were mentioned and figured as examples of their respective groups by Seeley (1888). If early Late Triassic (Carnian) taxa such as *Eodromaes murphi* and *Buriolestes schultzi* represent early saurischians, then the clade is at least 228 million years old (Cabreira et al., 2016).

Although no avian species is used in our definition as an internal specifier, *Aves* is part of *Saurischia* (as defined here) according to nearly every phylogenetic analysis published since Gauthier (1986). Although the name *Saurischia* (as defined here) would not apply to any clade in Baron et al.’s tree, birds would still be part of *Dinosauria* and *Theropoda* (see entries in this volume). Instead of being saurischians, they would be ornithoscelidans sensu Baron et al. (2017).

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