

**Diapsida** H. F. Osborn 1903 [J. A. Gauthier and K. de Queiroz], converted clade name

**Registration Number:** 120

**Definition:** The clade characterized by the apomorphy ‘upper and lower temporal fenestrae’ (see Diagnostic Apomorphies and Comments below), as inherited by *Sphenodon* (*Hatteria punctatus* (Gray 1842) (*Rhynchocephalia*)). This is an apomorphy-based definition. Abbreviated definition:  $\nabla$  apo upper and lower temporal fenestrae [*Sphenodon punctatus* (Gray 1842)].

**Etymology:** Derived from the Greek *di-*, two, and the Latin *apsis*, arch.

**Reference Phylogeny:** The primary reference phylogeny is deBraga and Rieppel (1997: Fig. 1), in which the defining apomorphy of *Diapsida* originates along branch F. See also Reisz (1981: Fig. 26), Gauthier (1984: Figs. 23–24), Gauthier et al. (1988b: Fig. 3), Müller and Reisz (2006: Fig. 2), Bever et al. (2015: Fig. 4), and Simões et al. (2018: Fig. 2).

**Composition:** See *Sauria* in this volume for composition of the crown if it does not include turtles. Diapsids outside of crown *Sauria* include the following taxa: *Araeoscelidia* Williston 1913, *Weigeltisauridae* Kuhn 1939, *Younginiformes* Romer 1947, *Claudiosaurus germaini* Carroll 1981, *Lanthanolania ivakhnenkoi* Modesto and Reisz 2003, and *Orovenator mayorum* Reisz et al. 2011 (see Comments). See Comments in *Sauria* (this volume) for discussion of the relationships of drepanosaurs, turtles, ichthyosaurs, sauropterygians, thalattosaurs, and choristoderans.

**Diagnostic Apomorphies:** Upper and lower fenestrae in the temporal region of the skull bordered by a relatively slender scaffolding of

dermocranial bones, the upper and lower temporal arches (see Comments for details concerning the ancestral morphology and further modifications).

**Synonyms:** *Diaptosauria* Osborn 1903 (partial and approximate).

**Comments:** Heaton’s (1979) landmark study of captorhinid cranial anatomy illustrates the ancestral condition in stem reptiles. The dermal bones forming the skull behind the orbit—the parietal, postorbital, squamosal, jugal, and quadratojugal—completely cover the skull roof and cheek regions. In the ancestral diapsid, however, this continuous bony surface was replaced by a temporal region with two conspicuous fenestrae, the margins of which were smooth and continuous and formed distinctive emarginations in adjacent dermal bones (e.g., Reisz, 1981; Heaton and Reisz, 1986). These fenestrae are not merely the incompletely ossified, irregular-margined gaps between bones growing together during ontogeny, as seen, for example, in the cheek region of some *Milleretta* (Gow, 1972) and *Mesosaurus* (Laurin and Piñeiro, 2017), although such gaps may represent developmental (and evolutionary) precursors of temporal fenestrae (e.g., Haridy et al., 2016). On the contrary, diapsid fenestration appears to reflect reorganization of the jaw-closing muscles, both in terms of their fibrous internal frameworks as well as by concentrating their areas of origin, to yield an open, frame-like skull optimized to ensure adequate bite forces while minimizing musculoskeletal volume, weight, and maintenance costs (Curtis et al., 2011).

The upper temporal fenestra largely separates skull-roofing bones that were originally in broad contact, leaving distinct emarginations

along adjacent parietal, postorbital, and squamosal bones. On the posterior skull roof once covered by the squamosal bone, for example, only a narrow ascending process of the squamosal remains; this process, along with the supratemporal bone, forms what is here termed the post-temporal arch, which bounds the upper temporal fenestra posteriorly. The distinctive diapsid post-temporal arch was originally formed mainly by the supratemporal bone, which connected the squamosal laterally to the parietal medially (i.e., the parietal supratemporal process did not participate in the upper temporal fenestra as it does in *Sauria*; see entry in this volume and Gauthier et al., 2012). In the upper temporal arch unique to diapsids, the articulation between the postorbital and squamosal is equally diagnostic. Rather than being received in a posterodorsally sloping recess along the anterodorsal margin of the squamosal as in, for example, *Milleretta* (Gow, 1972), or in a broader and irregular-margined recess in the squamosal that is variably exposed above, rather than being entirely below, the postorbital overlap as in *Captorhinus* (Heaton, 1979; Kissel et al., 2002), the slender diapsid postorbital tapers into a narrow and smooth-margined, triangular recess that is enclosed entirely in the lateral face of the squamosal (Gauthier et al., 2012; see, e.g., *Araeoscelis* in Fig. 2 of Reisz et al., 1984, in which the postorbital is displaced to reveal this diapsid recess on the squamosal).

In amniotes ancestrally, the cheek (lower temporal) region was also completely covered by dermal bones, mainly by the squamosal, and to a lesser extent by the postorbital and jugal, with the posteroventral corner covered by the quadratojugal bone (Heaton, 1979). In contrast, diapsids possess a large lower temporal fenestra that deeply emarginates the squamosal in particular, but also the postorbital and jugal, and to a lesser extent the quadratojugal (e.g., Reisz, 1981). The squamosal, for example, still extends

the full length of the suspensorial arch (which borders the lower temporal fenestra posteriorly) to attach to the quadratojugal. But instead of contacting broadly in the posterior cheek region as in amniotes ancestrally, the quadratojugal-squamosal contact is confined to the posteroventral corner of the lower temporal fenestra in diapsids (see, e.g., *Spinoaequalis schultzei* in deBraga and Reisz, 1995: Fig. 5).

The presence of upper and lower temporal fenestrae can often be inferred from the shape of their surrounding bones, even in disarticulated remains. A triradiate postorbital bone is perhaps the single most characteristic element in this character complex, as it acquires that shape via conspicuous posterodorsal and posteroventral emarginations reflecting, respectively, formation of the upper and lower temporal fenestrae. The same holds for the triradiate jugal, with its slender maxillary, postorbital and quadratojugal processes, the latter two reflecting deep emargination of the jugal posterodorsally by the lower temporal fenestra. Finally, although the supratemporal process of the parietal is barely developed in early amniotes and diapsids (Heaton, 1979; Reisz, 1981), it is prominently developed in later diapsids (Gauthier et al., 2012), largely supplanting the supratemporal bone in the post-temporal arch (e.g., *Proterosuchus fergusi*, Ezcurra and Butler, 2015: Fig. 3; *Gambelia wislizenii*, Gauthier et al., 2012: Fig. 175).

These two fenestrae were originally bordered by slender upper and lower temporal arches, the former composed of the postorbital and squamosal and the latter by the jugal and quadratojugal (e.g., Reisz, 1981). The lower temporal arch has had a complex history. Indeed, several Permo-Triassic diapsids crownward of *Araeoscelidia* appear to lack a complete bar, at least in bone (e.g., *Claudiosaurus germani*; Carroll, 1981), while it is clearly intact in other early-diverging diapsids (e.g., *Champsosaurus* spp.; Gao and Fox, 1998). It may be noteworthy

that, even in extinct taxa in which it is known to be present, such as *Youngina capensis* (Gow, 1975), a complete bony arch cannot be observed in most specimens owing to imperfect preservation (Gauthier et al., 1988a). The lower temporal arch displays a remarkable degree of homoplasy regardless; it is, for example, currently thought to have been lost early in diapsid evolution (Müller, 2003), and then to have re-evolved in *Youngina capensis*, and several more times within *Sauria* (e.g., Dilkes, 1998; Ezcurra and Butler, 2015; Jones et al., 2013). Among extant diapsids, the upper and lower temporal arches can vary significantly in terms of which bones predominate in them (e.g., Gauthier et al., 2012). Sometimes the bony arches can be replaced by ligaments (e.g., the lower temporal arch in *Squamata*; Broom, 1925), and can even be lost entirely (e.g., the upper temporal ligament within *Serpentes*; e.g., Rieppel, 1980). Even if only a ligament remains, we follow Broom (1925) in considering that structure to represent the arch, albeit in a transformed state. A ligamentous lower temporal arch can be present even in the absence of a quadratojugal process on the jugal in squamates (Oelrich, 1956); if there is any indication of that process on the jugal, however, a robust lower temporal ligament is invariably present in squamates, enabling the jugal to re-ossify down that ligament, nearly to the quadrate in at least one instance (e.g., Mo et al., 2009).

In addition to modifications in the continuity and composition of the bounding arches, the temporal fenestrae have been modified further in other ways. Thus, the upper temporal fenestra has in some cases been covered over secondarily (e.g., Gauthier et al., 2012; Bever et al., 2015). The lower temporal fenestra has also been closed secondarily several times, as seen in some araeoscelidians (e.g., Reisz et al., 1984), choristoderans (e.g., Gao and Fox, 2005), early archosauromorphs (e.g., Gregory, 1945), and

squamates (e.g., Savage, 1963). Early in the history of amniote phylogenetics, the presence of this fenestra in synapsids and diapsids, and its absence in fully shelled turtles from the Late Triassic to the Recent, was part of the argument for turtles being sister to all other amniotes (e.g., Gaffney, 1980). However, a lower temporal fenestra (presumably bordered ventrally by a ligamentous arch) is now known to have been present in Permian stem turtles (e.g., Lyson et al., 2010; Bever et al., 2015). Thus, *Testudines* appears to present yet another example of secondary closure among diapsids (see *Sauria*, this volume).

To complicate matters, a lower temporal fenestra—or at least an incompletely ossified cheek region—is also common among parareptiles, albeit in varying degrees of differentiation and situated between somewhat different bones (e.g., Haridy et al., 2016). Moreover, *Synapsida* also has a lower temporal fenestra, and it resembles that of *Diapsida* in being bordered by post-orbital, squamosal, and jugal bones. But the lower temporal fenestra of *Diapsida* differs from that ancestral for synapsids in that it was also bordered by the quadratojugal. (There are only four bones in the cheek region, and their borders near the center of the cheek only ossify fully during post-hatching ontogeny; see, e.g., *Araeoscelis* in Reisz et al., 1984, and *Delorhynchus cifellii* in Haridy et al., 2016.) The matter is further complicated by mesosaurs, highly modified aquatic amniotes from the Early Permian of Gondwana. They are widely thought to have diverged near the base of the reptilian tree (e.g., Gauthier et al., 1988c), although their precise relationships to other reptiles and, indeed, whether they have a lower temporal fenestra, have long been debated (e.g., MacDougall et al., 2018). So it is possible that a lower temporal fenestra was ancestral for *Amniota* (e.g., Piñeiro et al., 2012). Nevertheless, the inferred nearest extinct relatives of *Diapsida* lack both lower and upper

temporal fenestrae (e.g., Gauthier, 1994; Müller and Reisz, 2006; Bickelmann et al., 2009; Reisz et al., 2011; MacDougall et al., 2018).

The Late Pennsylvanian araeoscelidians *Petrolacosaurus kansensis* (Reisz, 1977) and *Spinoaequalis schultzei* (deBraga and Reisz, 1995), both of which are known from fairly complete skeletons, are universally considered to be the earliest-diverging diapsids. There has also been general agreement that the Early Permian *Orovenator mayorum* (Reisz et al., 2011) from Oklahoma represents the next earliest divergence from the saurian stem (e.g., Pritchard and Nesbitt, 2017). As for Late Permian diapsids, *Lanthanolania ivakhnenkoi* (Modesto and Reisz, 2003) from the early Late Permian of Russia is both the earliest and least complete, although it has some of the same saurian apomorphies seen in *Orovenator mayorum*; because of poor preservation, neither species otherwise adds much to our knowledge of Permian *Diapsida*. Apart from some of the end-Permian diapsids from South Africa, the late-surviving araeoscelidian *Araeoscelis casei* from the Early Permian of Texas is by far the best-known Permian diapsid (Reisz et al., 1984).

The globally distributed, gliding *Weigeltisauridae* poses another challenge, less from non-preservation than from a high degree of morphological modification, which renders some anatomical details difficult to interpret. Nevertheless, they have been inferred to be outside of crown *Sauria* since Evans and Haubold (1987; see also Evans, 1988; Laurin, 1991). The same is true of the long-necked aquatic species *Claudiosaurus germaini* of Madagascar (e.g., Carroll, 1981; Evans, 1988; Gauthier, 1994). There seems little agreement, however, regarding the relative positions of weigeltisaurids and *Claudiosaurus* on the saurian stem (e.g., Pritchard and Nesbitt [2017] vs. Simões et al. [2018]).

All of these Permian taxa are like *Younginiiformes* (whether as a clade or a

paraphylum) in having at least some saurian apomorphies, including upper and lower temporal fenestrae (whether the lower arch is entirely ossified or the lower fenestra nearly closed). Nevertheless, most lack the osteological correlates of an impedance-matching auditory system characteristic of crown *Sauria* (e.g., Laurin, 1991; Gauthier, 1994; deBraga and Rieppel, 1997; Dilkes, 1998; Müller, 2004; Senter, 2004; Ezcurra et al., 2014; Nesbitt et al., 2015; Pritchard and Nesbitt, 2017; Li et al., 2018).

As noted by Reisz et al. (2010), diapsids are relatively common in the fossil record from the early Mesozoic onward. Diapsid stem saurians are, however, relatively rare during the Palaeozoic, when other amniotes, particularly captorhinids but also parareptiles and diverse clades among the earliest stem mammals (e.g., *Varanops brevirostris*), predominated in terrestrial ecosystems. The reptile-mammal split marking the origin of *Amniota* is not particularly well constrained temporally (Müller and Reisz, 2005). It is estimated to have taken place roughly 312 million years ago (Benton and Donoghue, 2007), and the earliest known diapsids, such as *Petrolacosaurus kansensis* (Reisz, 1981) and *Spinoaequalis schultzei* (deBraga and Reisz, 1995), are estimated to have lived around 302 million years ago (Falcon-Lang et al., 2007). Taken at face value, these data suggest that the initial diversification of *Amniota* and the origin of *Diapsida* took place in the latter part of the Carboniferous. Simões et al. (2018) used a relaxed-clock Bayesian analysis to infer that *Diapsida* originated much earlier, in the Devonian, approximately 70 million years before any amniotes, let alone diapsids, are known in the fossil record.

Since Osborn (1903) coined the name *Diapsida*, palaeontologists have always associated that name with the clade bearing two temporal fenestrae/arches. Indeed, as soon as

this apomorphy was confirmed in a fossil, they promptly shifted it from a less inclusive clade (e.g., the *Youngina* node) to a more inclusive clade (e.g., the *Petrolacosaurus* node) (e.g., Reisz, 1977, 1981; Gaffney 1979, 1980; Thulborn, 1980; Evans, 1980, 1982, 1984, 1988; Benton, 1982, 1983, 1984, 1985; Gauthier, 1984; Heaton and Reisz, 1986; Gauthier et al., 1988a,b,c, 1989). We have accordingly chosen to continue a tradition that has persisted from Osborn (1903) to the present day (e.g., Pritchard et al., 2018), by proposing an apomorphy-based definition for this taxon name. Consequently, our definition ties the name *Diapsida* to a potentially more inclusive clade than do previous explicitly stated (minimum-clade) phylogenetic definitions that tied the name to the clade originating in the most recent common ancestor of araeoscelidians, lepidosaurs and archosaurs (e.g., Laurin, 1991). Selection of the name *Diapsida* over its approximate synonym *Diaptosauria* is straightforward, as the former has been used much more frequently (particularly in the recent literature) and the match in composition to that of the named clade has always been much closer (*Diaptosauria* was originally conceptualized as the ancestral group from which other diapsids were derived).

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