

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

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

Etymology: Derived from the Greek *pan* (all, every), here referring to “pan-monophylum,” another term for “total clade,” and *Squamata*, the name of the corresponding crown (for etymology, see *Squamata* in this volume); hence, “the total clade of *Squamata*.”

Reference Phylogeny: Figure 1 of Gauthier et al. (2012) is the primary reference phylogeny (see also Evans, 1984: Fig. 3; Gauthier, 1984: Fig. 32; Benton, 1985: Fig. 10; Evans, 1988: Fig. 6.2; Gauthier et al., 1988: Fig. 13; Reynoso, 1998: Fig. 10; Evans and Barbadillo, 1998: Fig. 10; Lee, 1998: Fig. 1; Evans and Barbadillo, 1999: Fig. 6; Evans et al., 2005: Fig. 18B; Conrad, 2008: Fig. 56; Evans and Wang, 2010: Fig. 11; Bolet and Evans, 2010: Fig. 6; Simões et al., 2018: Fig. 2). On the primary reference phylogeny, *Squamata* includes *Anolis carolinensis* and all taxa below it in the figure, while *Pan-Squamata* includes those taxa plus *Huehuecuetzpalli mixtecus*.

Composition: *Squamata* and its stem group—that is, *Squamata* and all extinct species that are more closely related to that crown clade than they are to *Sphenodon punctatus*. Although several extinct taxa have, at one time or another, been considered stem squamates, the best candidate for a stem squamate is the Early Cretaceous *Huehuecuetzpalli mixtecus* (Reynoso, 1998; Gauthier et al., 2012). See Comments for further discussion of *H. mixtecus* and other potential stem squamates.

Diagnostic Apomorphies: Possession of any of the putative synapomorphies of *Squamata* (this volume), or those diagnosing its subclades, permit referral of fossils to *Pan-Squamata*. Some of the most obvious characters that are likely to be preserved in fossils are included in the Diagnostic Apomorphies for *Squamata* (this volume). According to Gauthier et al. (2012), these include the following apomorphies that the stem squamate *Huehuecuetzpalli mixtecus* shares with *Squamata*: (1) frontoparietal suture roughly transverse; (2) jugal closely approaches prefrontal below orbit; (3) jugal entirely exposed above orbital margin of maxilla; (4) jugal quadratojugal process absent; (5) quadrate head pivots on slender tapering tip of squamosal; (6) quadratojugal absent; (7) pterygoid only narrowly overlaps quadrate; (8) epipterygoid columelliform; (9) processus ascendens of synotic tectum present; (10) angular does not reach level of mandibular condyle; (11) coronoid eminence formed entirely by coronoid; (12) coronoid arches over dorsal margin of mandible to reach lateral face of surangular; (13) coronoid posteromedial process present; (14) scapulocoracoid emargination present; (15) anterior coracoid emargination present; (16) pubis symphyseal process tapered distally; (17) penultimate phalanges in hand longer than antepenultimate phalanges; (18) fibula-astragalar joint involves most of distal end of fibula; (19) tibia and fibula only narrowly separated on ankle.

Synonyms: All of the names listed as approximate synonyms of *Squamata* (this volume) can also be interpreted as approximate synonyms of *Pan-Squamata* because the authors of those names did not explicitly distinguish between crown and total clades. In addition, *Lacertilia* of de Queiroz and Gauthier (1992) is an unambiguous synonym.

Comments: See *Squamata* (this volume) for historical information concerning the recognition of a group corresponding to one or more of the clades in the squamatan total-crown series. The authors of early phylogenetic analyses corroborating the existence of this clade either did not distinguish nomenclaturally between crown and total clades (e.g., Rage, 1982; Evans, 1984, 1988) or applied the name *Squamata* to the crown (Gauthier, 1984; Gauthier et al., 1988; Estes et al., 1988). Because no known taxa were inferred to be stem squamatans, there was not then a pressing need to name the total clade and, in any case, it was not named. De Queiroz and Gauthier (1992) proposed using the name *Lacertilia* for the squamatan total clade; however, that proposal was ignored when both previously known and newly discovered taxa were referred to the squamatan stem (e.g., Reynoso, 1998; Evans and Barbadillo, 1998, 1999; Simões et al., 2018). The name *Lacertilia* is a less appropriate choice for a clade containing *Squamata* because it has commonly been applied to a (paraphyletic) subgroup of *Squamata* (e.g., Williston, 1925; Romer, 1956, 1966; Carroll, 1988). Among the names that have been applied ambiguously to this clade (see Synonyms for *Squamata*, this volume), the best-known names (e.g., *Sauria*) have disadvantages similar to those of *Lacertilia* or are more appropriately applied to different clades (e.g., *Reptilia*, *Lepidosauria*, *Pholidota*), while the remaining names (e.g., *Saurophidia*, *Streptostylica*, *Lyognathi*) have been used so infrequently that there would be little advantage to selecting one of them as the name of the total clade. Consequently, use of a pan-clade name in this case seems uncontroversial, and because of the advantages of basing the name of a total clade on that of its corresponding crown (de Queiroz, 2007), we have chosen to name the total clade *Pan-Squamata*.

The assignment of fossils to the squamatan stem is disputed. *Pan-Squamata*, which encompasses that stem, must extend deep into the Triassic (if not the Permian; Simões et al., 2018), as its sister clade (represented by *Sphenodon punctatus* in the extant biota) was already diverse, disparate and widespread by the Late Triassic (e.g., Fraser and Benton, 1989). There is also a substantial set of apomorphies diagnosing the squamatan crown relative to rhynchocephalians, suggesting a stem lineage of substantial duration. Thus, it is surprising that so few potential stem squamatans have been identified, although this situation results in part from disagreements concerning relationships within *Squamata* inferred from morphological versus molecular data (see Comments for *Squamata*, this volume).

Caldwell et al. (2015) referred the Upper Jurassic/Lower Cretaceous *Parviraptor estesi*, originally described by Evans (1994b) as related to varanoid anguimorphs, to *Serpentes*. However, while tooth form and implantation are indeed snake-like, the rest of the associated elements—including notochordal vertebrae, an anteriorly bowed fronto-parietal suture, and paired parietals—suggest that this species could instead represent a stem squamatan with a snake-like dentition.

Reynoso (1998) inferred that the Early Cretaceous Mexican fossil *Huehuecuetzpalli mixtecus* was a stem squamatan, although he noted that it possessed a few iguanian apomorphies. In Conrad's (2008) analysis, *H. mixtecus* was part of a trichotomy at the squamatan crown node in a strict consensus tree (Fig. 54), but part of the iguanian stem group in an Adams consensus (Fig. 60; see also Evans and Wang, 2010). Gauthier et al. (2012) inferred *H. mixtecus* to be a stem squamatan in both parsimony and Bayesian analyses. In an analysis combining morphological and molecular characters (Wiens et al., 2010), *H. mixtecus* again appears on the

iguanian stem, although that tree has *Iguania* deeply nested within *Squamata*, far from its position inferred from morphological characters as one of the two primary squamatan subclades (e.g., Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012). In a more recent combined analysis in which *Iguania* was similarly nested within *Squamata*, however, *H. mixtecus* was consistently inferred to be a stem squamatan (Simões et al., 2018).

Evans and Barbadillo (1998, 1999) presented results suggesting that the extinct taxa *Ardeosaurus brevipes*, *Eichstaettisaurus schroederi*, *Scandensia ciervensis*, *Hoyalacerta sanzi*, and *Bavarisaurus macrodactylus* are representatives of the squamatan stem group—that is, members of *Pan-Squamata* but not *Squamata*. *A. brevipes*, *E. schroederi*, and *B. macrodactylus* had previously been interpreted as related to gekkotans and thus nested within *Squamata* (e.g., Hoffstetter, 1962, 1964, 1967; Estes, 1983; Evans, 1994a). By contrast, when added to Lee's (1998) dataset, these species were placed inside the squamatan crown (Evans et al., 2005). Similarly, Conrad's (2008) analysis placed all of these fossils, the putative stem gekkotans as well as *H. sanzi* and *S. ciervensis*, within the crown, a result confirmed by others adding new Mesozoic fossil taxa, as well as new material of *S. ciervensis*, to Conrad's dataset (e.g., Evans and Wang, 2010; Bolet and Evans, 2010, 2011). Gauthier et al. (2012) found strong support for placement of *E. schroederi* within the crown as part of the gekkotan stem, and Simões et al. (2017) placed both *E. schroederi* and *Ardeosaurus digitaellus* as stem gekkotans.

The highly-modified burrowing form *Tamaulipasaurus morenoi* has been interpreted as a possible stem squamatan, although the data are ambiguous (Clark and Hernandez, 1994): shortest trees placed it on either the lepidosaurian or the squamatan stem. In either case, its paired premaxillae, primitive quadrate suspension,

complete lower temporal bar (including a quadratojugal), and the large size of its jugular foramen—indicating passage of the jugular vein and an undivided metotic fissure—suggest that it is outside the squamatan crown. Derived states that *T. morenoi* shares with crown squamatans, such as procoelous vertebrae lacking intercentra, are absent in other potential stem squamatans (e.g., *Huehuecuetzpalli mixtecus*) that share other derived states with crown squamatans (most notably a mobile peg-and-socket squamosal-quadrate articulation, for which *T. morenoi* retains the plesiomorphic condition (for *Diapsida*) in which the quadrate head sits in a fossa below the squamosal), suggesting that the resemblances of *T. morenoi* to squamatans may be homoplastic.

Megachirella wachtleri, from the Middle Triassic of Italy, was originally inferred to be a stem squamatan in some analyses but a stem lepidosaur in others (Renesto and Bernardi, 2014). Renesto and Bernardi (2014) considered its placement within the total clade of *Lepidosauria* well supported but noted that more data were needed to assess its relationships to *Squamata*. Simões et al. (2018) have recently inferred this species to be a stem squamatan closely related to the Middle Jurassic *Marmoretta oxoniensis*, a taxon previously regarded as a stem lepidosaur (e.g., Evans, 1991), in several analyses using either morphology only or morphology in combination with DNA-sequence data. Relationships of *M. oxoniensis* appear somewhat unstable, however, as the relaxed-clock Bayesian analysis of Simões et al. (2018) placed it with *Huehuecuetzpalli mixtecus*; all three species were nevertheless inferred to be stem squamatans in all their analyses.

Gephyrosaurus bridensis, from the Early Jurassic of Wales, was placed by Evans (1984: Fig. 3) as a stem squamatan. However, she noted that other characters suggested a closer relationship to *Sphenodon*, and most subsequent analyses

have placed this taxon as the earliest-diverging member of *Rhynchocephalia*, and thus part of the stem group of *Sphenodon* (e.g., Evans, 1988, 2003; Gauthier et al., 1988, 2012; Fraser, 1988; Fraser and Benton, 1989; Bever and Norell, 2017).

Kuroyuriella mikikoi, from the Early Cretaceous of Japan, was placed on the squamatan stem in some analyses but on the stem of *Scincidae* (i.e., within crown *Squamata*) in others (Evans and Matsumoto, 2015). Evans and Matsumoto (2015) considered placement on the squamatan stem “problematic and probably artifactual” and treated the relationships of *K. mikikoi* as *incertae sedis*, presumably within the total clade of *Squamata*.

Thus, there are currently no undisputed representatives of the squamatan stem group. In our view, *Huehuecuetzpalli mixtecus* is the best candidate for a stem squamatan. It retains a number of ancestral features that are inferred to have been modified prior to the crown node, including paired premaxillae, parietals that fuse late in post-hatching ontogeny, a long supratemporal and short parietal supratemporal process, a plesiomorphic postorbital-squamosal relationship, as well as unicuspid teeth, amphicoelous vertebrae, persistent trunk intercentra, and a second distal tarsal in the foot (Reynoso, 1998; Gauthier et al., 2012). However, the deep nesting of this fossil within crown *Squamata* (as a stem iguanian) as inferred from some analyses of combined morphological and molecular data (Wiens et al., 2010) suggests that its status as a stem versus crown squamatan must await resolution of the current incongruence between trees inferred from morphological versus molecular data (see Losos et al., 2012; McMahan et al., 2015; Reeder et al., 2015). On the other hand, recent combined analyses (Simões et al., 2018) inferred a similarly nested position

for *Iguania*, but still had *H. mixtecus* as a stem squamatan.

Based on their relaxed-clock Bayesian estimate, Simões et al. (2018) inferred that the squamatan stem originated in the latest Permian (~255 Ma). But with the possible exception of *Megachirella wachtleri*, no other pan-squamatan stem members are known from anywhere in the world from throughout the Permian, Triassic or Early Jurassic (Evans, 2003); they must have been present in the early Mesozoic, however, as rhynchocephalians are diverse, disparate and distributed world-wide by at least ~220 Ma (late Carnian; early Late Triassic; e.g., Hsiou et al., 2015), and are known from the Middle Triassic of Germany (~240 Ma; Anisian; Jones et al., 2013). Microvertebrate-producing localities usually yield pan-squamatan remains from the latter part of the Jurassic to the present, and the disparity in relative abundance between the two primary subclades of *Lepidosauria* is currently attributed to the early ecological dominance of rhynchocephalians (see *Pan-Lepidosauria*, this volume).

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