

Serpentes C. Linnaeus 1758 [J. Head, K. de Queiroz and H. Greene], converted clade name

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Definition: The crown clade originating in the most recent common ancestor of *Anomalepis mexicanus* Jan 1860 (*Scolecophidia/Anomalepididae*), *Rena dulcis* Baird and Girard 1853 (*Scolecophidia/Leptotyphlopidae*), *Typhlops linneolatus* Jan 1863 (*Scolecophidia/Typhlopidae*), *Anilius* (originally *Anguis scytale* (Linnaeus 1758) (*Alethinophidia/Anilioidea*), and *Coluber constrictor* Linnaeus 1758 (*Alethinophidia/Caenophidia*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Anomalepis mexicanus* Jan 1860 & *Rena dulcis* Baird and Girard 1853 & *Typhlops linneolatus* Jan 1863 & *Anilius scytale* (Linnaeus 1758) & *Coluber constrictor* Linnaeus 1758).

Etymology: Derived from the Latin vernacular for “snake” (*serpens*, singular; *serpentis*, plural).

Reference Phylogeny: The reference phylogeny is Figure 4 of Kluge (1991), where *Coluber constrictor* is a representative of “higher snakes.” This is the first phylogeny of snakes based on an explicitly phylogenetic analysis of a taxon \times character matrix incorporating all major extant snake clades, including those containing the specifiers used here. Phylogenies based on subsequent analyses of morphological (e.g., Cundall et al., 1993; Lee and Scanlon, 2002; Gauthier et al., 2012), molecular (e.g., Slowinski and Lawson, 2002; Wilcox et al., 2002; Wiens et al., 2012), and combined data (e.g., Lee et al., 2007; Wiens et al., 2010) result in application of the name *Serpentes* to a clade of identical composition.

Composition: *Serpentes* consists of more than 3,400 currently recognized extant (Uetz, 2012)

and more than 100 currently recognized fossil species (e.g., Rage, 1984; Holman, 2000). It consists of two primary subclades: the total clades of *Scolecophidia* and *Alethinophidia* (although the former is inferred to be paraphyletic in many molecular analyses; see Comments).

Diagnostic Apomorphies: Diagnosing *Serpentes* relative to purported sister taxa is difficult because there is no consensus on the position of *Serpentes* relative to other extant *Squamata* or to putative stem-group fossils (see Comments). Despite these problems, extant snakes possess numerous morphological characters that optimize unambiguously as apomorphies relative to other extant taxa. The following list (which is not comprehensive) is derived from anatomical reviews and recent morphological phylogenetic analyses (Bellairs and Underwood, 1951; Underwood, 1967; Tchernov et al., 2000; Lee and Scanlon, 2002; Conard, 2008; Cundall and Irish, 2008; Gauthier et al., 2012).

- 1) Subolfactory process of frontal contacts parasphenoid (also in some other fossorial squamates).
- 2) Anterolateral margin of frontal subolfactory process includes prefrontal process that extends into socket of prefrontal.
- 3) Reduction in number of posterior orbital bones (also in some other squamates).
- 4) Crista circumfenestralis formed from crista prootica, crista interfenestralis, and crista tuberalis partially encloses stapedia footplate.
- 5) Platytrabic braincase.
- 6) Palatoquadrate (pterygoquadrate) cartilage reduced, forms only the quadrate.

- This character additionally describes the absence of an epipterygoid in snakes (Bellairs and Kamal, 1981).
- 7) Processus ascendens tectum synoticum absent (also in some other squamates).
 - 8) Scleral ossicles absent.
 - 9) Mandibles connected only by soft tissues; bony symphysis absent.
 - 10) Splenial reduced so that Meckel's canal is broadly open anteriorly for ~ 50% the length of the dentary tooth row (also in some other squamates).
 - 11) Posterior terminus of splenial does not extend posteriorly beyond coronoid apex (also in some other squamates).
 - 12) Intramandibular joint in which the angular receives the splenial (absent in typhlopids, anomalepidids, and many viperids).
 - 13) Vertebrae with well-developed zygosphenes, including straight to convex anterior margins and dorsolaterally angled articular facets, and zygantra with corresponding ventromedially angled articular facets (although these accessory articulations are present in some other squamates, the straight to convex anterior margin of the zygosphenes is unique to snakes).
 - 14) Loss of pectoral girdle and forelimb (also in some other squamates).
 - 15) Loss of sternal skeleton (also in some other squamates)
 - 16) Increase in preloacal vertebral numbers beyond 100 (also in some other squamates).
 - 19) Kidneys positioned well anterior of cloaca.
 - 20) Soft secondary palate formed by the closure of each choanal groove to form a ductus nasopharyngeus (Groombridge, 1979). Absent in typhlopids and leptotyphlopids, but not anomalepidids (McDowell, 1972). A secondary palate is also present in some other squamates, although often with contributions from the maxillary and palatal bones (hard secondary palate).
 - 21) Eye covered by brille (also in some other squamates).
 - 22) Tympanum lost (also in some other squamates).

Soft-tissue apomorphies of extant snakes (but unknown in fossils) relative to other extant squamates include:

- 17) Gall bladder separated from liver (posteriorly) by a distinct gap.
- 18) Left lung reduced or absent (also in some other elongate squamates).

The osteological apomorphies described above (characters 1–16) are diagnostic for *Serpentes* if *Dinilysia patagonica*, *Pachyophiidae* and *Madtsoiidae* are nested within the snake crown (Tchernov et al., 2000; Rieppel et al., 2002; Apesteguía and Zaher, 2006; Conrad, 2008; Wilson et al., 2010). If some or all of these taxa are outside of the crown (Lee and Caldwell, 1998; Lee, 1998; Scanlon and Lee, 2000; Scanlon, 2006; Longrich et al., 2012; Zaher and Scanferla, 2012; Palci et al., 2013), then some of the listed characters may diagnose slightly larger clades.

Synonyms: Approximate (and sometimes partial—see Comments) synonyms include *Serpentia* (e.g., Linnaeus, 1735, 1740, 1748, 1759; Laurenti, 1768; Scopoli, 1777), *Serpens* (e.g., Aldrovandi, 1640; Klein, 1755; Lacépède, 1788, 1790; Sonnini and Latreille, 1801—see Harper, 1940 for publication date information); *Ophidia* (Macartney, 1802—see Gill, 1900); *Ophidii* (e.g., Latreille, 1804, 1825; Oppel, 1811; Gray, 1825); *Epalpebrata* (Haworth, 1825); *Ophes* (Wagler, 1828); *Idiophides* (Latreille, 1825; Bonaparte, 1831); and *Ophides* (Swainson, 1838–1839).

Comments: Recognition of a group called *Serpentes*, *Ophidia*, or a variant of one of those names can be found in some of the earliest writings on natural history (e.g., Aristotle's *Historia Animalium*; Aldrovandi, 1640; Ray, 1693); however, early concepts seem to have been based primarily on the elongate, limb-reduced body form and therefore included several taxa now thought to have independently evolved this body form that are no longer considered snakes, such as *Anguis*, *Amphisbaena*, and *Caecilia* (e.g., Linnaeus, 1758; Laurenti, 1768; Scopoli, 1777; Gmelin, 1788; Daudin, 1801–3; Rafinesque, 1815). During the early nineteenth century, *Caecilia* was removed and placed among the amphibians (e.g., Oppel, 1811; Blainville, 1816; Merrem, 1820); *Anguis* (and *Ophisaurus*) was removed and placed among the “lizards” or in a separate group for limbless squamates other than snakes (e.g., Oppel, 1811; Gray, 1825; Bonaparte, 1831); and *Amphisbaena* was removed and placed among the “lizards”, in a separate group for limbless squamates other than snakes, or in a separate amphisbaenian group (e.g., Gray, 1825; Bonaparte, 1831; Wiegmann, 1834). By the middle of the nineteenth century, the composition of the snake taxon had become congruent with contemporary concepts (e.g., Wagler, 1830; Duméril and Bibron, 1834–1854; Fitzinger, 1843; Bonaparte, 1850; Duméril and Duméril, 1851; Stannius, 1856; Jan, 1857; Cope, 1864). Monophyly of the taxon is supported by numerous morphological characters (see Diagnostic Apomorphies) and has been inferred by most authors in the evolutionary era, often with strong support (e.g., Cope, 1900; Estes et al., 1988; Lee, 1998; Vidal and Hedges, 2009; Gauthier et al., 2012; Wiens et al., 2012; but see McDowell and Bogert, 1954).

Cope (1900) presented one of the first phylogenetic hypotheses regarding relationships within snakes. He recognized an ancestral taxon

Peropoda (boas, pythons, dwarf boas) from which were derived two groups, one composed of *Scolecophidia* (typhlopids and leptotyphlopids) and *Tortricina* (*Anilius*, *Cylindrophis*, uropeltids) and the other composed of *Aglyphodonta* (*Xenopeltis*, caenophidians without grooved teeth), *Opisthoglypha* (caenophidians with posterior grooved teeth on the maxilla), *Proteroglypha* (caenophidians with an anterior tubular tooth on the maxilla), and *Solenoglypha* (caenophidians with only an anterior tubular tooth on the maxilla*). Nopcsa (1923) presented a phylogeny of snakes in which an ancestral snake taxon *Cholophidia* (fossil forms) gave rise to two groups: *Angiostomata* (typhlopids and leptotyphlopids) and *Alethinophidia* (“true snakes”). Hoffstetter (1939) proposed a taxonomy that recognized four major mutually exclusive taxa of snakes: *Cholophidia*, *Scolecophidia*, *Henophidia* (“relatively ancient” snakes), and *Caenophidia* (“new or modern” snakes), the last two corresponding to Nopcsa's *Alethinophidia*. Subsequent phylogenetic analyses have demonstrated the paraphyly of *Cholophidia* and *Henophidia* but supported the monophyly of both *Scolecophidia* and *Alethinophidia*, including those of Rieppel (1988), Kluge (1991), Tchernov et al. (2000), Scanlon and Lee (2000), Lee and Scanlon (2002), Apesteguía and Zaher (2006), Scanlon (2006), Gauthier et al. (2012), and Longrich et al. (2012) based on morphology, and Slowinski and Lawson (2002), Wilcox et al. (2002), Vidal and Hedges (2002, 2004), and Vidal and David (2004) based on molecular sequence data. Heise et al. (1995), Conrad (2008), Wiens et al. (2012), and Pyron et al. (2013) inferred a monophyletic *Serpentes*, but not a monophyletic *Scolecophidia*.

* Duméril and Bibron (1834–1854), who proposed the taxon *Solenoglyphes*, characterized its members as having a single fang in each maxilla. In reality, there are two tooth positions in each maxilla, although for most of the tooth replacement cycle only one position or the other bears a tooth that is firmly attached to the jaw (Klauber, 1972; Gauthier et al., 2012; Nagy et al., 2013).

The first explicit phylogenetic definition of the name *Serpentes* is that of Estes et al. (1988), who, contrary to their convention of using widely known names for crown clades (Gauthier et al., 1988: 62), defined the name *Serpentes* as referring to a total clade. However, most subsequent authors have used *Serpentes* for the crown, either implicitly (e.g., Rieppel, 1988; Lee, 1998; Palci and Caldwell, 2007) or explicitly (Lee, 1997; Greene and Cundall, 2000; Conrad, 2008; Gauthier et al., 2012). We have used the name *Serpentes* for the snake crown clade because (1) when defined explicitly, that is the clade to which the name is most commonly applied, (2) it is by far the most widely used of existing names that have been at least loosely associated with that clade (roughly five times more commonly used than *Ophidia*, the most widely used of the approximate synonyms), (3) there are advantages to using the most widely known name for the crown clade (de Queiroz and Gauthier, 1992), and (4) the name refers etymologically only to a vague character (< Latin *serpere*, to creep, crawl) rather than a specific apomorphy (see de Queiroz, 2007). Based on the commonly inferred basal split between the stems of *Scolecophidia* and *Alethinophidia*, as well as the fact that *Scolecophidia* is not always inferred to be monophyletic, we selected distantly related species within each of those clades as internal specifiers.

Despite possessing a highly modified body form and unique feeding morphologies relative to other squamates, determination of unambiguous synapomorphies for the snake crown clade is complicated by the disparate phylogenetic hypotheses concerning the relationships of *Serpentes* both to other extant *Squamata* and to fossil taxa. Phylogenies derived from molecular sequence data place *Serpentes* closest to *Anguimorpha* and/or *Iguania* (Townsend et al., 2004; Fry et al., 2006; Wiens et al., 2006; Vidal and Hedges, 2009; Lee, 2009; Wiens et al.,

2012), those derived from morphology place the clade closest to *Amphisbaenia* or *Amphisbaenia* + *Dibamidae* (Evans and Barbadillo, 1998; Kearney, 2003a, b; Evans and Wang, 2005; Evans et al., 2005; Conrad, 2008; Gauthier et al., 2012), and combined analyses place *Serpentes* closest to either *Anguimorpha* (Wiens et al., 2010; Müller et al., 2011) or *Anguimorpha* + *Iguania* (Wiens et al., 2010; Wiens et al., 2012). The fossil clades *Pachyophiidae* and *Madtsoiidae* have been inferred to be either stem snakes (Lee and Caldwell, 1998; Lee, 1998; Scanlon and Lee, 2000; Lee and Scanlon, 2002; Scanlon, 2006; Palci et al., 2013) or crown snakes nested within or on the stem of *Alethinophidia* (Tchernov et al., 2000; Rieppel et al., 2002; Rieppel and Head, 2004; Apesteguía and Zaher, 2006; Wilson et al., 2010; Zaher and Scanferla, 2012; Gauthier et al., 2012; Longrich et al., 2012, for *Pachyophiidae*) or on the alethinophidian stem (Longrich et al., 2012; for *Madtsoiidae*). Similarly, the fossil taxon *Dinilysia patagonica* has been considered either a stem snake (Zaher and Scanferla, 2012; Gauthier et al., 2012) or a stem alethinophidian (Wilson et al., 2010; Longrich et al., 2012). As a result, the diagnosis of both the snake crown and its total clade are considerably more difficult than expected given the distinctiveness of snakes.

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