

## ***Pan-Serpentes*** J. Head, K. de Queiroz and H. Greene, new clade name

**Registration Number:** 121

**Definition:** The total clade of the crown clade *Serpentes*. This is a crown-based total-clade definition. Abbreviated definition: total  $\nabla$  of *Serpentes*.

**Etymology:** *Pan* (prefix indicating that the name refers to a total clade; derived from the Greek *Pantos*, all, the whole) + *Serpentes* (see etymology for *Serpentes* in this volume).

**Reference Phylogeny:** The reference phylogeny is Figure 1 of Gauthier et al. (2012), where *Pan-Serpentes* includes *Najash rionegrina*† and all taxa below it (p. 12). This is the result of the first morphological phylogenetic analysis that: (1) tests monophyly of *Serpentes* and constituent subclades via extensive taxon sampling; (2) infers at least some fossil taxa as stem snakes; and (3) places the snake total clade within a comprehensive phylogenetic hypothesis of *Squamata*. Previous analyses have satisfied some, but not all, of these criteria (e.g., Lee, 1997, 1998; Tchernov et al., 2000; Rieppel and Zaher, 2000; Scanlon and Lee, 2000; Lee and Scanlon, 2002; Apesteguía and Zaher, 2006; Scanlon, 2006; Conrad, 2008; Wilson et al., 2010; Müller et al., 2011; Zaher and Scanferla, 2012).

**Composition:** *Serpentes* and all taxa sharing a more recent ancestry with that crown clade than with the most closely related crown group. See Comments for a discussion of taxa that have been hypothesized to be members of the snake stem group.

**Diagnostic Apomorphies:** As a total clade, *Pan-Serpentes* may not have any apomorphies

(de Queiroz, 2007); however, possession of any of the apomorphies of *Serpentes* (this volume) constitutes evidence for inclusion of a species or specimen within *Pan-Serpentes*. In addition, Apesteguía and Zaher (2006) and Longrich et al. (2012) inferred characters to be synapomorphies of *Serpentes* and the putative stem snakes *Najash rionegrina* and *Coniophis precedens*. Well-delineated characters shared by these fossils and crown snakes include interdental ridges forming partial alveoli in marginal tooth-bearing elements (present in some other squamates); parietal descending process contacts dorsal and anterior margins of prootic and dorsal margin of parasphenoid rostrum, laterally enclosing braincase; loss of upper temporal arch and squamosal (also in some other squamates); subcentral paralympathic fossae present on posterior precloacal vertebrae; lymphapophyses present on cloacal vertebrae (also in some other long-bodied limb-reduced squamates); haemapophyses and pleuropophyses present on caudal vertebrae; and pleurocentral hypapophyses on (at least) anterior precloacal vertebrae (also in some other squamates).

**Synonyms:** Approximate (some of which are also partial) synonyms are the same as those listed for *Serpentes* (this volume). *Serpentes* of Estes et al. (1988) is an unambiguous synonym.

**Comments:** Although the concept of the snake total clade is straightforward, there is considerable disagreement concerning both the closest extant relatives of snakes and the members of the snake stem group. Various fossil taxa have been proposed to be stem snakes, including *Dinilysia patagonica* (Scanlon and Lee, 2000; Lee and Scanlon, 2002, Zaher and Scanferla,

2012), *Najash rionegrina* (Apesteguía and Zaher, 2006), *Coniophis precedens* (Longrich et al., 2012) the pachyophiids *Pachyrhachis problematicus* (Lee, 1998; Lee and Caldwell, 2000; Lee and Scanlon, 2002), *Pachyophis woodwardi* (Lee et al., 1999; Lee and Caldwell, 2000), *Haasiophis terrasanctus* (Lee and Scanlon, 2002; Scanlon, 2006; Lee, 2009), and *Eupodophis descouensii* (Rage and Escuille, 2000; Palci et al., 2013), and madtsoiids such as *Wonambi naracoortensis* and *Yurlunggur spp.* (Scanlon and Lee, 2000; Lee and Scanlon, 2002; Scanlon, 2006). All of the above taxa have highly elongated bodies and highly reduced limbs, based on specimens preserving articulated or directly associated cranial and postcranial elements, except for *Coniophis*, whose postcranial body form is inferred from the hypothesized association of isolated, disarticulated elements, and all have been alternatively considered to be crown snakes (Hecht, 1959; Rieppel and Zaher, 2000; Tchernov et al., 2000; Rieppel et al., 2002; Apesteguía and Zaher, 2006; Conrad, 2008; Wilson et al., 2010; Gauthier et al., 2012; Longrich et al., 2012; Vasile et al., 2013). Other taxa exhibiting minimal to moderate body elongation and fully formed (if sometimes modified) limbs have also sometimes been inferred to be members of the snake stem group, specifically “aigialosaurs”, mosasaurids (highly aquatic forms), dolichosaurids, *Aphanizocnemus*, and *Adriosaurus* (Lee, 1997, 1998, 2009; Lee and Caldwell, 2000). However, more recent and more comprehensive morphological phylogenetic analyses of *Squamata* (Conrad, 2008; Gauthier et al., 2012) and analyses using combined morphological and molecular data (Wiens et al., 2010; Müller et al., 2011) do not support dolichosaurids, *Adriosaurus*, “aigialosaurs”, or mosasaurids as stem snakes.

Estes et al. (1988) applied the name *Serpentes* to the total clade of snakes using an explicit phylogenetic definition. However, that proposal

contradicted their own stated adoption of the conventions proposed by Gauthier et al. (1988), which include using the best-known names for crown clades. We have adopted that convention and thus apply the name *Serpentes* (in this volume) to the snake crown clade. Conrad (2008) mentioned the possibility of using the name *Ophidia* for the snake total clade but did not formally adopt that idea. Because *Ophidia* has been defined explicitly as applying to a less inclusive clade (see below), and because we support the convention of forming the name of the total clade by adding a standard prefix to the name of the crown (see de Queiroz, 2007, and references therein), we use the name *Pan-Serpentes* for the snake total clade. De Queiroz (2007) used the name *Pan-Serpentes* to illustrate some of the advantages of an integrated system of crown and total clade names; however, we are not treating *Pan-Serpentes* as a preexisting name because it was used as a hypothetical example rather than as a nomenclatural proposal (see *ICPN*, Art. 7.2b; Cantino and de Queiroz, 2020).

Lee (1997) defined the name *Pythonomorpha* Cope 1869 as applying to the clade originating in the most recent common ancestor of snakes and mosasauroids (see also Lee, 1998; Lee and Caldwell, 1998, 2000). However, given that snakes were explicitly excluded from *Pythonomorpha* by Cope (1869), it would be more appropriate (*ICPN*, Rec. 11A; Cantino and de Queiroz, 2020) to define that name so that the inclusion of snakes is permitted but not required (e.g., as the smallest clade containing both *Mosasaurus hoffmanni* and *Dolichosaurus longicollis*, which would include snakes in the context of the phylogeny of Lee and Caldwell [2000]). Lee and Caldwell (1998) defined the name *Ophidia* Macartney 1802 as applying to the clade originating in the most recent common ancestor of *Serpentes* and *Pachyrachis problematicus*, to which Lee (1998) added a

qualifying clause that would prevent use of the name *Ophidia* in the context of phylogenies in which any of 25 taxa not normally considered snakes are part of that clade. Those definitions are inappropriate given that the authors equated the name *Ophidia* with the English vernacular name “snakes”, which they intended to refer to a clade composed of organisms that possess most of the diagnostic characters of crown-group snakes (Lee, 2001). According to the stated definition, an extinct species very similar in appearance to *Pachyrachis* but slightly more distantly related to extant snakes would not be part of *Ophidia*, seemingly contrary to the authors’ intent. A more appropriate definition of *Ophidia* would specify the reference of that name using an apomorphy or set of apomorphies.

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