

Amphisbaenia J. E. Gray 1844 [M. Kearney and K. de Queiroz], converted clade name

Registration Number: 10

Definition: The largest crown clade containing *Amphisbaena fuliginosa* Linnaeus 1758 (*Amphisbaenidae*) but not *Lacerta agilis* Linnaeus 1758 (*Lacertidae*) and *Teius* (*Lacerta*) *teyou* (Daudin 1802) (*Teioidea*) and *Dibamus novaeguineae* Duméril and Bibron 1839 (*Dibamidae*) and *Coluber constrictor* Linnaeus 1758 (*Serpentes*). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Amphisbaena fuliginosa* Linnaeus 1758 ~ *Lacerta agilis* Linnaeus 1758 & *Teius teyou* (Daudin 1802) & *Dibamus novaeguineae* Duméril and Bibron 1839 & *Coluber constrictor* Linnaeus 1758).

Etymology: Derived from the Greek *amphi-* (on both sides, double) + *baeno* (walk, go, pass), thus, “moving both backwards and forwards.”

Reference Phylogeny: Figure 1 of Gauthier et al. (2012) should be treated as the primary reference phylogeny, although similar relationships have been supported by molecular phylogenetic analyses of both amphisbaenians (Macey et al., 2004; Vidal et al., 2008; Longrich et al., 2015) and squamates (Townsend et al., 2004; Vidal and Hedges, 2005; Pyron et al., 2013). Although not included in the reference phylogeny, the specifier *Lacerta agilis* is most closely related to *Lacerta viridis* among the included taxa (e.g., Godinho et al., 2005).

Composition: *Amphisbaenia* contains 193 currently recognized extant species (Uetz, 2017), which have been referred to the following mutually exclusive clades: *Rhineuridae*, *Bipedidae*, *Blanidae*, *Cadeidae*, *Trogonophidae*,

and *Amphisbaenidae* (Kearney, 2003a; Vidal et al., 2008). A list of extinct species was provided by Estes (1983), though several taxa have been described subsequently (e.g., Charig and Gans, 1990; Gans and Montero, 1998; Smith, 2009; Augé, 2012; Longrich et al., 2015). Apart from *Sineoamphisbaena hexatabularis* and *Crythiosaurus mongoliensis*, all fossils previously referred to *Amphisbaenia* that were included in the analysis of Kearney (2003a; *Listromycter leakeyi*, *Lophocranium rusingense*, and various rhineurids) were inferred to be part of the crown clade. Only a few of the currently known fossils (e.g., *Chthonophis subterraneus*, *Oligodontosaurus*) are outside of the total clades of the previously mentioned amphisbaenian subgroups (Longrich et al., 2015). Although some North American fossil amphisbaenians possess seemingly ancestral characters (e.g., a complete postorbital bar) not seen in any living amphisbaenians (see e.g., Berman, 1972, 1973, 1976), current phylogenetic inferences (e.g., Kearney, 2003a; Hembree, 2007; Gauthier et al., 2012; Longrich et al., 2015) place those fossils in the stem group of *Rhineura* and thus within the crown clade *Amphisbaenia*. In the context of some molecular phylogenies (e.g., Vidal and Hedges, 2004; Wiens et al., 2012), in which *Lacerta* is as or more closely related to *Amphisbaena* than is *Rhineura*, *Rhineura* and its fossil relatives are not part of *Amphisbaenia* according to our definition.

Diagnostic Apomorphies: Kearney (2003a) listed 17 putative synapomorphies of *Amphisbaenia* relative to other extant and extinct squamates (see also Gans, 1978; Estes et al., 1988; Gauthier et al., 2012). Some of the most obvious diagnostic apomorphies are: eyes reduced or

absent, body scales arranged in rings (annuli), enlarged median premaxillary tooth, elongated postorbital region of skull, braincase enclosed anteriorly by enlarged orbitosphenoid(s), absence of suborbital fenestra, absence of epipterygoid, anteriorly elongated extracolumella with distal connections to the dermis, loss of external hind limbs (vestigial femora present internally in *Bipes* and *Blanus*), reduction of right lung (the left lung is reduced in most other elongate squamates), short tail with caudal autotomy septum confined to a single vertebra and lacking regeneration.

Synonyms: *Amphisbaenoidea* (e.g., of Fitzinger, 1826; Müller, 1831; Stannius, 1856; Günther, 1867; Camp, 1923), approximate.

Amphisboena of Gray (1831), approximate.

Annulati (e.g., of Wiegmann, 1834; Fitzinger, 1843; Cope, 1900), approximate.

Amphisbaenae (e.g., of Wiegmann, 1834; Parker, 1868; Huxley, 1886), approximate.

Saurophidii of Bonaparte (1840) but not of Bonaparte (1841), which included *Chalcides*, approximate.

Cancellata of Gravenhorst (1843), partial (*Bipes* excluded).

Annulata of Gravenhorst (1843), partial (*Amphisbaena* and *Blanus* excluded).

Ophiosauri of Cope (1864), approximate.

Glyptodermata of Haeckel (1866), approximate.

Annulata (e.g., of Haeckel, 1866, as synonym; Gegenbaur, 1878, as synonym; Romer, 1956, 1966), approximate.

Opheosauri of Cope (1875, 1889), approximate.

Ophisauri of Cope (1875; attributed to Merrem), approximate.

Amphisbaenida (e.g., of Gegenbaur, 1878; Strauch, 1887), approximate.

Amphisbaenidae (e.g., of Boulenger, 1884, 1885–1887; Fürbringer, 1900; Gadow, 1901; Hay, 1902, 1930; Camp, 1923; Williston, 1925; Romer, 1933, 1945, 1956, 1966; Vanzolini, 1951; McDowell and Bogert, 1954), approximate.

Glyptoderma of Haeckel (1895), approximate.

Amphisbaenoida of Huxley (1886), approximate.

Amphisbaenomorpha of Fürbringer (1900), approximate.

Amphisbenidae of Nopcsa (1908), approximate.

Comments: Many early naturalists used the presence versus absence of limbs as the basis of major groups within *Reptilia*, and consequently, they placed the limbless amphisbaenians (e.g., *Amphisbaena*) within the serpents ≈ ophidians (e.g., Linnaeus, 1758; Shaw, 1802; Merrem, 1820). *Bipes* (*Chirotes*), which possesses forelimbs but not hindlimbs, was placed either within the saurians ≈ lacertilians (e.g., Daudin, 1802–1803; Oppel, 1811; Cuvier, 1817), within the serpents ≈ ophidians (e.g., Blainville, 1816, 1822), or in a separate taxon (e.g., *Saurophidii*, *Ophiosauri*) that was apparently considered intermediate between the two (e.g., La Cépède, 1788–1789; Wagler, 1828, 1830; Gray, 1831). However, even those early authors (e.g., Blainville, 1816, 1822) who considered both *Bipes* and *Amphisbaena* to be snakes did not group them together within the snake taxon. The first author to recognize a taxon composed only of species that are now considered amphisbaenians appears to have been Fitzinger (1826), who placed *Amphisbaena* and *Bipes*, along with the recently described *Leposternon*, in his (Familia) *Amphisbaenoidea*. This grouping was soon followed by other authors (e.g., Gray, 1831, 1844; Müller, 1831; Wiegmann, 1834), though often under different names (see Synonyms), and by the end of

the nineteenth century, most authors recognized a group similar to the modern concept of *Amphisbaenia* (e.g., Haeckel, 1895; Gadow, 1898, 1901; Cope, 1900; Fürbringer, 1900).

Amphisbaenians are highly modified for burrowing and share several associated derived features supporting monophyly of the group (see Diagnostic Apomorphies), including several that are not shared by other burrowing squamates (e.g., the arrangement of scales in annuli, a solid skull with bony enclosure of the braincase anteriorly, unique modifications of the extracolumella). Moreover, monophyly of *Amphisbaenia* has been supported by the results of explicit phylogenetic analyses based on both morphological (Kearney, 2003a; Gauthier et al., 2012) and molecular data (Kearney and Stuart, 2004; Townsend et al., 2004; Pyron et al., 2013). Nevertheless, some molecular studies have indicated that *Amphisbaenia* may be paraphyletic or polyphyletic, with *Rhineura* more closely related to *Lacerta* than to *Amphisbaena* (Vidal and Hedges, 2004) or outside of a clade containing both *Amphisbaena* and *Lacerta* (Wiens et al., 2012).

Although the amphisbaenian taxon has, over the years, been treated by various authors as separate from “lizards” (e.g., Wiegmann, 1834; Bonaparte, 1840; Gray, 1844; Hoffstetter, 1955; Kuhn, 1961; Halstead Tarlo, 1968; Gans, 1978), explicit phylogenetic analyses based on both morphological (e.g., Estes et al., 1988; Lee, 1998; Kearney, 2003a; Gauthier et al., 2012) and molecular (e.g., Kearney and Stuart, 2004; Townsend et al., 2004; Vidal and Hedges, 2005; Pyron et al., 2013) data strongly support the nesting of amphisbaenians within “lizards”. The relationships of amphisbaenians to other “lizards” inferred from morphological data have been considered suspect because of the repeated evolution of body elongation and limb loss within *Squamata* (e.g., Estes et al., 1988; Lee, 1998; Kearney, 2003a; Gauthier et al., 2012). Those

inferred from molecular data indicate deep nesting of amphisbaenians within *Squamata* close to lacertids (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Pyron et al., 2013).

Selection of the name *Amphisbaenia* for the clade in question is relatively straightforward, as this name has been applied most frequently to that clade during roughly the last 60 years (e.g., McDowell and Bogert, 1954; Gans, 1967, 1978, 2005; Underwood, 1971; Estes, 1983; Estes et al., 1988; Kearney, 2003a). Other names that have been applied to this group (see Synonyms) have been used rarely after 1900, with the exceptions of *Amphisbaenidae* (e.g., Vanzolini, 1951; McDowell and Bogert, 1954; Romer, 1956) and *Annulata* (e.g., Romer, 1956; Wu et al., 1993). The name *Amphisbaenidae*, however, is now most commonly applied to a subgroup of amphisbaenians (e.g., Gans, 1967, 1978, 2005; Underwood, 1971; Kearney, 2003a). The name *Annulata* is almost certainly less commonly used than is *Amphisbaenia* (though frequency of use is difficult to assess using automated searches because *annulata* is also commonly used as a species name); moreover, it has been applied by Lee (1998) to a more inclusive putative clade composed of amphisbaenians, dibamids, and the extinct *Sinoamphisbaena hexatabularis*.

The name *Amphisbaenia* was defined phylogenetically by Estes et al. (1988) as the name of a crown clade, and our proposed definition is intended to associate the name with the same clade. Our definition has been formulated so that it will refer to a taxon of identical composition under an alternative hypothesis of relationships (Kearney, 2003a: Fig. 31), which differs in placing *Bipes* rather than *Rhineura* as the sister group to other extant amphisbaenians. It has also been formulated as a maximum-crown-clade definition so that it will restrict the name to the larger of the two extant clades (and the one that includes *Amphisbaena*) in the context of phylogenetic hypotheses in which the species

traditionally included in *Amphisbaenia* form a paraphyletic or polyphyletic group (e.g., Vidal and Hedges, 2004; Wiens et al., 2012). Our definition differs in the second respect from the minimum-clade (node-based) definition of Estes et al. (1988), which would result in the fully limbed *Lacerta* (and presumably other lacertids) being included in *Amphisbaenia* in the context of the aforementioned phylogenetic hypotheses. We consider that outcome less consistent with the historical concept of the taxon than the exclusion of *Rhineura*. Because the inferred closest extant relatives of amphisbaenians differ between analyses based on morphological characters (e.g., Kearney, 2003a,b; Gauthier et al., 2012), which infer dibamids and snakes, and those based on molecular sequences (e.g., Townsend et al., 2004; Vidal and Hedges, 2004; Wiens et al., 2012), which infer lacertids and teioids, we have included external specifiers representing each of those taxa in our definition.

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