

Squamata M. Opperl 1811 [K. de Queiroz and J. A. Gauthier], converted clade name

Registration Number: 101

Definition: The largest crown clade containing *Lacerta agilis* Linnaeus 1758 but not *Sphenodon* (originally *Hatteria*) *punctatus* (Gray 1842). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Lacerta agilis* Linnaeus 1758 \sim *Sphenodon punctatus* (Gray 1842)).

Etymology: Derived from the Latin *squama* (scale) + *-ata* (provided with), thus, “scaled.”

Reference Phylogeny: Figure 1 of Gauthier et al. (2012) is the primary reference phylogeny (see also Estes et al. 1988: Fig. 6; Lee, 1998: Figs. 1–2; Conrad, 2008: Fig. 56); however, our definition has been formulated so that it will apply to a clade of identical composition in the context of phylogenies based on molecular (e.g., Townsend et al., 2004: Fig. 8; Vidal and Hedges, 2005: Fig. 1; Wiens et al., 2010: Fig. 4; Pyron et al., 2013: Fig. 1) and combined morphological and molecular data (Reeder et al., 2015: Fig. 1; Simões et al., 2018: Fig. 2) that differ regarding relationships within *Squamata* (see Composition and Comments). Although *Lacerta agilis* is not included in the primary reference phylogeny, it is most closely related to *Lacerta viridis* of the taxa included in that tree (see Baeckens et al., 2015).

Composition: *Squamata* was hypothesized by Estes et al. (1988; see also Gauthier, 1982) to be composed of two primary extant subclades, *Iguania* and *Scleroglossa*, and those subclades have been corroborated by subsequent analyses based on morphological data (e.g., Lee, 1998; Conrad, 2008; Gauthier et al.,

2012). By contrast, analyses based on DNA-sequence data place the root of the squamatan tree within “*Scleroglossa*,” usually with either *Dibamidae* or *Gekkota*, or a clade composed of both taxa, as the sister to all other squamatans (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2010; Pyron et al., 2013; Reeder et al., 2015). In the context of these alternative hypotheses, the two primary extant subclades are different and in one case have been given the names *Dibamia* and *Bifurcata* (Vidal and Hedges, 2005). *Squamata* is composed of 10,078 currently recognized extant species (Uetz, 2016), thus rivaling *Aves* and surpassing its sister clade, *Sphenodon* (with only one currently recognized extant species), by four orders of magnitude. Somewhat dated lists of extinct species are available for *Serpentes* (Rage, 1984) and for non-*Serpentes*, non-mososaurian *Squamata* (Estes, 1983).

Diagnostic Apomorphies: Gauthier et al. (1988) listed 69 + 5 (addendum) putative synapomorphies of *Squamata* relative to other extant diapsids, which are also diagnostic relative to most other extinct diapsids given that so few potential stem squamatans have been identified (see *Pan-Squamata* in this volume). Estes et al. (1988) added 18 potential synapomorphies that have reversed in some squamatans. Gauthier et al. (2012) listed only 59, including 20 that are shared with the putative stem squamatan *Huehucuetzpalli mixtecus* (see *Pan-Squamata*, this volume), but this lower number reflects the near-absence of soft anatomical characters in their study. Some of the most obvious diagnostic apomorphies are paired male intromittent organs (hemipenes), loss of caruncle (false egg tooth), mobile fronto-parietal

joint (modified in fossorial forms and mosasauroids), embryonic fusion of parietals (reversed in some gekkotans, some xantusiids, and *Sineoamphisbaena hexatabularis*), mobile quadrate with peg-in-socket squamosal-quadrate articulation (lost in chameleons and modified in snakes), pterygoids and vomers separated by palatines (reversed in some amphisbaenians and some polyglyphanodontians), very slender stapes (reversed in some fossorial forms), slender epipterygoid, subdivision of embryonic metotic fissure into vagus (jugular) foramen posteriorly and recessus scalae tympani anteriorly, embryonic or early post-embryonic (dibamids and some xantusiids) fusion of exoccipitals and opisthotics, coronoid eminence formed by coronoid bone only (reversed in some snakes and some amphisbaenians), keeled cervical intercentra, all ribs (including cervicals) single-headed, procoelous vertebrae (reversed in some gekkotans), absence of trunk intercentra (reversed in some gekkotans and full-grown xantusiids), emarginated scapulocoracoid (reversed in *Heloderma*, amphisbaenians, chameleons, some dolichosaurs, some dibamids, some pygopodids), and absence of gastralia.

Synonyms: Numerous approximate synonyms of *Squamata* match the modern concept to various degrees in terms of composition. *Squamosa* of Latreille (1825, except for the inclusion of caecilians), *Saurophidia* of Blainville (1835), *Reptilia* of Bonaparte (1840, 1841), *Streptostylica* of Stannius (1856) and Cope (1900), *Lepidosauria* and *Diplophalli* of Haeckel (1866, inclusion of *Sphenodon* unclear), *Pholidota* of Haeckel (1895), *Sauria* of Gadow (1898, 1901), and *Lyognathi* and *Lyognatha* of Jaekel (1911) refer to a taxon of more or less identical composition.

Sauria of MaCartney (1802) and others (some of whom included crocodylians), *Saurii* of Kuhl (1820) and others, *Gradientia* of Merrem

(1820) and Haworth (1825), *Sauri* of Gray (1825), *Pedata*, *Tetrapoda*, and *Communipedis* of Haworth (1825), *Saurae* of Gray (1827) and Wagler (1828), *Lacertae* of Wagler (1830) and others, *Lacertiformes* of Bonaparte (1831), *Lacertina* of Müller (1831), *Squamati* of Wiegmann (1834), *Saures* of Swainson (1839), *Lacertilia* of Owen (1842 [including *Rhynchosaurus articeps*], 1866) and others, *Saura* of Gray (1845), *Lacertia* of Owen (1845), *Kionocrania* of Stannius (1856) and Huxley (1886), *Lepidota* of Jan (1857), *Autosaurii* of Gegenbaur (1859), *Autosauria* of Haeckel (1866), *Lacertilia vera* of Boulenger (1884, 1885–7), *Eusauri* of Gadow (1898), *Autosauri* of Gadow (1898, 1901), *Lacerti* of Jaekel (1911), *Lacertosauria* of Tornier (1913), and *Lacertidae* of Nopcsa (1923) are partial as well as approximate synonyms that refer to taxa that exclude various highly modified squamates, such as snakes, amphisbaenians, other serpentiform species, and chameleons (in various combinations).

Other partial (and approximate) synonyms were used for a paraphyletic group made up of *Iguania* and *Gekkota*, which is associated with the same ancestor as *Squamata* on the reference phylogeny (but not on some of those based on molecular data—see Reference Phylogeny). These include *Pachyglossi* of Bonaparte (1840), *Amblyglossae* of Fitzinger (1843), *Pachyglossae* of Gray (1845), *Ascalabota* of Camp (1923), and *Iguaniformes* of Hay (1930), although Gray's (1845) *Pachyglossae* might alternatively be considered a partial synonym of *Lepidosauria* given that it included *Sphenodon punctatus*. Still other partial synonyms were used for a doubly paraphyletic group that excluded both *Autarchoglossa* and *Chamaeleonidae*; these include *Ascalabotae* of Merrem (1820), *Ascolabata* of Gray (1825), *Inextensilinguis* of Haworth (1825), *Pachyglossae* of Weigmann (1834), and *Pachyglossa* of Strauch (1887; who also included *Xenosaurus* and *Heloderma*).

Comments: Many eighteenth and early nineteenth century naturalists based their primary groupings within ectothermic tetrapods (*Amphibia* of some authors, *Reptilia* of others) on mode of locomotion, separating the slitherers with small or no limbs (*Serpentes*, *Ophidia*, and variants of those names) from the limbed-propelled walkers and crawlers (*Gradientia*, *Reptilia*, and variants of those names). Thus, squamates with well-developed limbs (“typical lizards”) were commonly grouped with crocodylians and sometimes with turtles and even salamanders and frogs, rather than with snakes, while those with long bodies and reduced limbs (e.g., *Anguis*, *Amphisbaena*, and sometimes even the amphibian *Caecilia*) were considered “snakes” (e.g., Linnaeus, 1758; Laurenti, 1768; Scopoli, 1777). The “lizards” (under various names) were first separated from turtles (e.g., Brongniart, 1800; Cuvier, 1800; Daudin, 1802–1803) and later from crocodylians (e.g., Blainville, 1816, 1822; Merrem, 1820; Gray, 1825). Derivation of snakes from within “lizards” was inferred by several authors (e.g., Haeckel, 1866; Camp, 1923; McDowell and Bogert, 1954), and the formal abandonment of the paraphyletic group “lizards”, by that time usually referred to as either *Sauria* or *Lacertilia*, was proposed by Estes et al. (1988). Although the paraphyly of “lizards” (relative to both snakes and amphisbaenians) is now highly corroborated and widely acknowledged, the group continues to be treated as a taxonomic unit, although no longer given a formal name (e.g., Vitt and Caldwell, 2014; Pough et al., 2016; Crother, 2017).

Despite the long history of treating “lizards” and snakes as separate taxa, a close relationship between them has also been recognized for a long time. The first author to recognize and name a taxon composed exclusively of “lizards” (including amphisbaenians) and snakes appears to have been Blainville (1816), who used the

French vernacular name *Bispeniens* in reference to the hemipenes, which are still considered diagnostic (see Diagnostic Apomorphies). The taxon was recognized inconsistently under a variety of names by nineteenth century authors (e.g., Blainville, 1822, 1835; Latreille, 1825; Haworth, 1825; Fitzinger, 1826; Gray, 1831a; Bonaparte, 1840, 1841, 1850; Stannius, 1856; Zittel, 1887–1890; Cope, 1889; Haeckel, 1895), but during the twentieth century it was recognized more consistently under the name *Squamata* (e.g., Cope, 1900; Hay, 1902; Williston, 1917, 1925; Camp, 1923; Nopcsa, 1923; Romer, 1933, 1945, 1956, 1966; Gans, 1978; Estes, 1983; Estes et al., 1988; Lee, 1998), a use that continues in the present century (e.g., Conrad, 2008; Wiens et al., 2010; Gauthier et al., 2012). Several early explicit phylogenetic analyses based on morphology supported squamate monophyly (e.g., Rage, 1982; Benton, 1985; Gauthier et al., 1988; Evans, 1988), a result that has been corroborated by subsequent molecular and combined morphological and molecular studies (e.g., Townsend et al., 2004; Hugall et al., 2007; Albert et al., 2009; Reeder et al., 2015; Simões et al., 2018).

The name *Squamata* was first used by Oppel (1811), who applied it to a group composed of “lizards” (including crocodylians) and snakes. Crocodylians (*Loricata*), were removed from *Squamata* by Merrem (1820; see also Blainville, 1816), thus more closely approximating the modern composition of the taxon, and this proposal was followed by most subsequent authors who recognized a taxon designated by that name (e.g., Haworth, 1825; Fitzinger, 1826; Gray, 1831a; Bonaparte, 1841 [as a synonym]; Gravenhorst, 1843 [though he excluded snakes]; Gray, 1844, 1845 [though he excluded amphisbaenians]; Bonaparte, 1850). When *Sphenodon punctatus* (tuatara) was first described (Gray, 1831b), it was considered an agamid “lizard” and thus implicitly part of *Squamata*.

Cope (1864) separated *Sphenodon* (= *Hatteria*) from *Agamidae* as *Hatteriidae*, and Günther (1867) further separated it from all “lizards” (*Lacertilia*) as *Rhynchocephalia*, though both authors retained *Sphenodon* within *Squamata*. Cope (1875) increased the separation further still by including extinct taxa (*Protorosauridae* and *Rhynchosauridae*) within *Rhynchocephalia*, not recognizing *Squamata*, and placing turtles between *Rhynchocephalia* and “lizards” (and snakes) in his taxonomy. However, he later (Cope, 1889) recognized *Squamata* as a group including “lizards” and snakes but excluding *Sphenodon*, and this arrangement has been adopted by most authors since the beginning of the twentieth century (e.g., Cope, 1900; Williston, 1917, 1925; Nopcsa, 1923; Romer, 1933, 1945, 1956, 1966; McDowell and Bogert, 1954; Gans, 1978; Estes, 1983; Estes et al., 1988; Lee, 1998, 2005; Conrad, 2008).

Squamata is clearly the most appropriate name for the clade in question. Other candidate names (see Synonyms) either have seldom been used since the eighteenth century (e.g., *Saurophidia*, *Streptostylica*, *Lyognathi*), are more appropriately applied to different clades (e.g., *Pholidota*, *Reptilia*, *Lepidosauria*), or were used (most commonly) for a paraphyletic group associated with the same ancestor (e.g., *Sauria*, *Lacertilia*) and thus do not correspond as closely in terms of composition (*Squamata* itself was used in this way by Gravenhorst, 1843, and Haeckel, 1866). Moreover, the name *Squamata* has previously been defined phylogenetically as designating the same (crown) clade to which it is applied here (Estes et al., 1988; Lee, 1998), although it has sometimes been applied implicitly to a more inclusive clade (see Conrad, 2008; Simões et al., 2018). We have defined the name using a maximum crown clade definition in the interest of presenting a simple definition (one with few specifiers) that will nevertheless apply to the same clade in the context of major differences between

the internal relationships in phylogenies based on morphological (e.g., Estes et al., 1988; Lee, 1998; Conrad, 2008; Gauthier et al., 2012; but see Simões et al., 2018) versus molecular (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2010; Pyron et al., 2013; see also Reeder et al., 2015) data (see Composition).

Despite these striking disagreements, data from both DNA sequences and phenotypic sources strongly support many of the same crown squamatan subclades: traditional *Anguimorpha* plus *Serpentes*, *Dibamidae*, *Gekkota*, *Iguania*, *Lacertoidea* (including *Amphisbaenia*), and *Scincoidea*. Estimating the timing of their divergence is complicated because their interrelationships are in dispute and their early fossil records are sparse. A single partial, but articulated, specimen from the mid-Triassic (~240 Ma), *Megachirella wachtleri* (Renesto and Posenato, 2003), has recently been inferred to be a stem squamatan (Simões et al., 2018). It is the only potential pan-squamatan known from the Triassic or Early Jurassic. Otherwise, the oldest pan-squamatan fossils that might be referable to the total clades of any of the crown squamatan subclades are mainly partial jawbones known from ~167 Ma (Bathonian, Middle Jurassic; e.g., Caldwell et al., 2015). Relatively intact, or at least associated, remains of stem-members of three of them (*Gekkota*, *Scincoidea*, *Anguimorpha*) are known from ~150 Ma (Kimmeridgian, Late Jurassic; e.g., Evans, 2003). Apart from *Dibamidae*, which has no fossil record, most of the rest are diverse and disparate by ~75 Ma (Campanian, Late Cretaceous; e.g., Gao and Norell, 2000). Crown squamatans appear to have been the dominant lepidosaurs in terrestrial ecosystems since the Early Cretaceous (e.g., Evans and Matsumoto, 2015; and references therein), while rhynchocephalians predominated during the early Mesozoic (e.g., Cocude-Michel, 1963; Hsiou et al., 2015; and references therein; see also *Lepidosauria*, this volume).

Literature Cited

- Albert, E. M., D. San Mauro, M. Garcia-Paris, L. Ruber, and R. Zardoya. 2009. Effect of taxon sampling on recovering the phylogeny of squamate reptiles based on complete mitochondrial genome and nuclear gene sequence data. *Gene* 441:12–21.
- Baeckens, S., S. Edwards, K. Huyghe, and R. Van Damme. 2015. Chemical signaling in lizards: an interspecific comparison of femoral pore numbers in *Lacertidae*. *Biol. J. Linn. Soc.* 114:44–57.
- Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zool. J. Linn. Soc.* 84:97–164.
- de Blainville, H. M. D.. 1816. Prodrome d'une nouvelle distribution systématique du règne animal. *Bull. Sci. Soc. Philom. Paris* 8:113–124.
- de Blainville, H. M. D.. 1822. *De L'organisation des Animaux ou Principes d'anatomie Comparée*. F. G. Levrault, Paris.
- de Blainville, H. M. D.. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. *Nouv. Ann. Mus. Hist. Nat. Paris* 4:233–296 + 4 plates.
- Bonaparte, C. L. 1831. *Saggio di Una Distribuzione Metodica Degli Animali Vertebrati*. Antonio Boulzaler, Roma.
- Bonaparte, C. L. 1840. Prodromus systematis herpetologiae. *Nuovi Ann. Sci. Nat. Bologna* 4:90–101.
- Bonaparte, C. L. 1841. A new systematic arrangement of vertebrated animals. *Trans. Linn. Soc. Lond.* 18:247–304.
- Bonaparte, C. L. 1850. *Conspectus Systematum Herpetologiae et Amphibiologiae*. E. J. Brill, Lugduni Batavorum.
- Boulenger, G. A. 1884. Synopsis of the families of existing *Lacertilia*. *Ann. Mag. Nat. Hist., Ser. 5* 14:117–122.
- Boulenger, G. A. 1885–1887. *Catalogue of the Lizards in the British Museum (Natural History)*, Vols. 1–3. Trustees of the British Museum, London.
- Brongniart, A. 1800. Essai d'une classification naturelle des reptiles. Iere Partie. Etablissement des ordres. *Bull. Sci. Soc. Philom. Paris* 2(35):81–82.
- Caldwell, M. W., R. L. Nydam, A. Palci, and S. Apesteguía. 2015. The oldest known snakes from the Middle Jurassic—Lower Cretaceous provide insights on snake evolution. *Nat. Commun.* 6:5996.
- Camp, C. L. 1923. Classification of the lizards. *Bull. Amer. Mus. Nat. Hist.* 48:289–481.
- Cocude-Michel, M. 1963. Les rhynchocephales et les sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Nouv. Arch. Mus. Hist. Nat. Lyon* 7:1–187.
- Conrad, J. L. 2008. Phylogeny and systematics of *Squamata (Reptilia)* based on morphology. *Bull. Am. Mus. Nat. Hist.* 310:1–182.
- Cope, E. D. 1864. On the characters of the higher groups of *Reptilia Squamata*—and especially of the *Diploglossa*. *Proc. Acad. Nat. Sci. Phila.* 16:224–231.
- Cope, E. D. 1875. Check-list of North American *Batrachia* and *Reptilia*; with a systematic list of the higher groups, and an essay on geographical distribution. *Bull. U.S. Natl. Mus.* 1:1–104.
- Cope, E. D. 1889. Synopsis of the families of *Vertebrata*. *Am. Nat.* 23:849–877.
- Cope, E. D. 1900. The crocodylians, lizards, and snakes of North America. *Annu. Rep. Board Regents Smithsonian. Inst.* 1898:155–1270 + 36 plates.
- Crother, B., ed. 2017. *Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, Which Comment Regarding Confidence in Our Understanding*. Society for the Study of Amphibians and Reptiles, Herpetological Circular No. 43.
- Cuvier, G. 1800. *Leçons D'anatomie Comparée*. Tome I. Baudouin, Paris.
- Daudin, F. M. 1802–1803. *Histoire Naturelle, Générale et Particulière des Reptiles*. F. Dufart, Paris.
- Estes, R. 1983. *Sauria terrestria*, Amphisbaenia. *Handbuch der Paläoherpetologie*. Teil 10A. Gustav Fischer, Stuttgart.

- Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within *Squamata*. Pp. 119–281 in *Phylogenetic Relationships of the Lizard Families* (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, CA.
- Evans, S. E. 1988. The early history and relationships of the *Diapsida*. Pp. 221–260 in *The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds* (M. J. Benton, ed.). Systematics Association Special Volume No. 35A. Clarendon Press, Oxford.
- Evans, S. E. 2003. At the feet of the dinosaurs: the early history and radiation of lizards. *Biol. Rev.* 78(4):513–551.
- Evans, S. E., and R. Matsumoto. 2015. An assemblage of lizards from the early cretaceous of Japan. *Palaeontol. Electron.* 18.2.36A:1–36.
- Fitzinger, L. I. 1826. *Neue Classification der Reptilien Nach Ihren Natürlichen Verwandtschaften. Nebst Einer Verwandtschafts-Tafel Und Einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologischen Museum's zu Wien*. J. G. Heubner, Wien.
- Fitzinger, L. I. 1843. *Systema Reptilium. Fasciculus Primus, Amblyglossae*. Braumüller et Seidel, Vindobonae.
- Gadow, H. 1898. *A Classification of Vertebrata Recent and Extinct*. Adam and Charles Black, London.
- Gadow, H. 1901. *Amphibia and Reptiles. The Cambridge Natural History*, Vol. 8. Macmillan, London.
- Gans, C. 1978. The characteristics and affinities of the *Amphisbaenia*. *Trans. Zool. Soc. London* 34:347–416.
- Gao, K., and M. A. Norell. 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bull. Am. Mus. Nat. Hist.* 249:1–118.
- Gauthier, J. A. 1982. Fossil *Xenosauridae* and *Anguinae* from the Lower Eocene Wasatch Formation, southcentral Wyoming, and a revision of the *Anguioidea*. *Contr. Geol. Univ. Wyoming* 21:7–54.
- Gauthier, J., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of *Lepidosauromorpha*. Pp. 15–98 in *Phylogenetic Relationships of the Lizard Families* (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, CA.
- Gauthier, J. A., M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke. 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bull. Peabody Mus. Nat. Hist.* 53:3–308.
- Gegenbaur, C. 1859. *Grundzüge der Vergleichenden Anatomie*. Wilhelm Englemann, Leipzig.
- Gravenhorst, J. L. 1843. *Vergleichende Zoologie*. Breslau, Graf, Barth und Comp.
- Gray, J. E. 1825. A synopsis of the genera of *Reptiles* and *Amphibia*, with a description of some new species. *Ann. Philos., Ser. 2* 10:193–217.
- Gray, J. E. 1827. A synopsis of the genera of saurian reptiles in which some new genera are indicated, and the others reviewed by actual examination. *Philos. Mag., Ser. 2* 2: 54–58.
- Gray, J. E. 1831a. A synopsis of the species of the class *Reptilia*. Pp. 1–110 in *The Animal Kingdom Arranged in Conformity with Its Organization, by the Baron Cuvier, with Additional Descriptions of all the Species Hitherto Named, and of Many Not Before Noticed, by Edward Griffith and Others. Vol. 9: The Class Reptilia. Appendix* (E. Griffith, ed.). Whittaker, Treacher, and Co., London.
- Gray, J. E. 1831b. Note on a peculiar structure in the head of an *Agama*. *Zool. Misc.* 1831:13–14.
- Gray, J. E. 1842. Descriptions of two hitherto unrecorded species of reptiles from New Zealand; presented to the British Museum by Dr. Dieffenbach. *Zool. Misc.* 1842:72.
- Gray, J. E. 1844. *Catalogue of the Tortoises, Crocodiles, and Amphisbaenians in the Collection of the British Museum*. Trustees of the British Museum, London.
- Gray, J. E. 1845. *Catalogue of the Specimens of Lizards in the Collection of the British Museum*. Trustees [of the British Museum], London.
- Günther, A. 1867. Contribution to the anatomy of *Hatteria* (*Rhynchocephalus*, Owen). *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 157:595–629.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen: Allgemeine Grundzüge der Organischen Formen-Wissenschaft, Mechanisch*

- Begründet Durch die von Charles Darwin Reformirte Descendenz-Theorie. Band 2: Allgemeine Entwicklungsgeschichte der Organismen.* G. Reimer, Berlin.
- Haeckel, E. 1895. *Systematische Phylogenie. Dritter Theil: Systematische Phylogenie der Wirbelthiere* (Vertebrata). Georg Reimer, Berlin.
- Haworth, A. H. 1825. A binary arrangement of the class *Amphibia*. *Philos. Mag. J.* 65:372–373.
- Hay, O. P. 1902. *Bibliography and Catalogue of the Fossil Vertebrata of North America*. United States Geological Survey, Washington, DC.
- Hay, O. P. 1930. *Second Bibliography and Catalogue of the Fossil Vertebrata of North America*. Carnegie Institution, Washington, DC.
- Hsiou, A. S., M. A. G. De França, and J. Ferigolo. 2015. New data on the *Clevosaurus* (*Sphenodontia: Clevosauridae*) from the Upper Triassic of southern Brazil. *PLOS ONE* 10(9):e0137523.
- Hugall, A. F., R. Foster, and M. S. Y. Lee. 2007. Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG-1. *Syst. Biol.* 56:543–563.
- Huxley, T. H. 1886. *A Manual of the Anatomy of Vertebrated Animals*. D. Appleton, New York.
- Jaekel, O. 1911. *Die Wirbeltiere: Eine Übersicht Über Die Fossilen und Lebenden Formen*. Gebrüder Borntraeger, Berlin.
- Jan, G. 1857. *Cenni sul Museo Civico di Milano ed Indice Sistemático dei Rettili ed Anfibi Esposti nel Medesimo*. Luigi di Giacomo Priola, Milano.
- Kuhl, H. 1820. Beiträge zur Kenntnifs der Amphibien. Pp. 75–131 in *Beiträge zur Zoologie Vergleichenden Anatomie*. Hermannschen Buchhandlung, Frankfurt am Main.
- Latreille, P. A. 1825. *Familles Naturelles du Règne Animal, Exposées Succinctement et dans un Ordre Analytique, avec L'indication de Leurs Genres*. J. B. Baillièrre, Paris.
- Laurenti, J. N. 1768. *Specimen Medicum, Exhibens Synopsis Reptilium Emendatam cum Experimentis circa Venena et Antidota Reptilium Austriacorum*. Joan. Thom. Nob. de Trattner, Viennae.
- Lee, M. S. Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol. J. Linn. Soc.* 65:369–453.
- Lee, M. S. Y. 2005. Molecular evidence and marine snake origins. *Biol. Lett* 1(2):227–230.
- Linnaeus, C. 1758. *Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 10th edition. Laurentii Salvii, Holmiae (Stockholm).
- MacCartney, J. 1802. Scientific names [see p. vi] in Cuvier, G. 1802. *Lectures on Comparative Anatomy*. Translated by William Ross under the inspection of James MacCartney. T. N. Longman and O. Rees, London.
- McDowell, Jr., S. B., and C. M. Bogert. 1954. The systematic position of *Lanthanotus borneensis*, and the affinities of the anguinomorph lizard. *Bull. Am. Mus. Nat. Hist.* 105:1–142.
- Merrem, B. 1820. *Versuch Eines Systems der Amphibien*. Johann Christian Krieger, Marburg.
- Müller, J. 1831. Beiträge zur Anatomie und Naturgeschichte der Amphibien. *Z. Physiol.* 4:190–275.
- Nopcsa, F. 1923. *Die Familien der Reptilien. Fortschritte der Geologie und Palaeontologie, Heft 2*. Gebrüder Borntraeger, Berlin.
- Oppel, M. 1811. *Die Ordnungen, Familien, und Gattungen der Reptilien, als Prodrom Einer Naturgeschichte Derselben*. Joseph Lindauer, München.
- Owen, R. 1842. Report on British fossil reptiles, part II. *Rep. Br. Assoc. Adv. Sci.* 11:60–204.
- Owen, R. 1845. Description of certain fossil crania, discovered by A. G. Bain, Esq., in sandstone rocks at the south-eastern extremity of Africa, referable to a different species of an extinct genus of *Reptilia* (*Dicynodon*), and indicative of a new tribe or sub-order of *Sauria*. *Trans. Geol. Soc. Lond.* 7:59–84 + 4 plates.
- Owen, R. 1866. *On the Anatomy of Vertebrates. Vol. 1: Fishes and Reptiles*. Longmans, Green, and Co., London.
- Pough, F. H., R. M. Andrews, M. L. Crump, A. D. Savitsky, K. D. Wells, and M. C. Brandley. 2016. *Herpetology*. 4th edition. Sinauer, Sunderland, MA.

- Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of *Squamata*, including 4161 species of lizards and snakes. *BMC Evol. Biol.* 13:93.
- Rage, J.-C. 1982. La phylogénie des lépidosauriens (*Reptilia*): une approche cladistique. *C. R. Acad. Sci. Paris* 284:1765–1768.
- Rage, J.-C. 1984. Serpentes. *Handbuch der Paläoherpetologie*, Teil 11. Gustav Fischer, Stuttgart.
- Reeder, T. W., T. M. Townsend, D. G. Mulcahy, B. P. Noonan, P. L. Wood, Jr., J. W. Sites, Jr., and J. J. Wiens. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. *PLOS ONE* 10: e0118199.
- Renesto, S., and R. Posenato. 2003. A new lepidosauromorph reptile from the Middle Triassic of the Dolomites. *Riv. Ital. Paleo. Strat.* 109:463–474.
- Romer, A. S. 1933. *Vertebrate Paleontology*. University of Chicago Press, Chicago, IL.
- Romer, A. S. 1945. *Vertebrate Paleontology*. 2nd edition. University of Chicago Press, Chicago, IL.
- Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, IL.
- Romer, A. S. 1966. *Vertebrate Paleontology*. 3rd edition. University of Chicago Press, Chicago, IL.
- Scopoli, I. A. 1777. *Introductio ad Historiam Naturalem Sistens Genera Lapidum, Plantarum, et Animalium Hactenus Detecta, Characteribus Essentialibus Donata, in Tribus Divisa, Subinde ad Leges Naturae*. Wolfgangum Gerle, Pragae.
- Simões, T. R., M. W. Caldwell, M. Tałanda, M. Bernardi, A. Palci, O. Vernygora, F. Bernardini, L. Mancini, and R. L. Nydam. 2018. The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature* 557:706–709.
- Stannius, H. 1856. *Handbuch der Zootomie. Zweiter Theil. Die Wirbelthiere. Zweites Buch. Zootomie der Amphibien*. Veit and Comp., Berlin.
- Strauch, A. 1887. Bemerkungen über die Geckoniden-Sammlung im zoologischen Museum der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. *Mem. Acad. Imp. Sci. St.-Petersb. Ser.* 7 35:1–72.
- Swainson, W. W. 1839. *The Natural History of Fishes, Amphibians, & Reptiles, or Monocardian Animals. Vol. II: The Cabinet Cyclopaedia; Natural History; Conducted by Dionysius Lardner*. Longman, Orme, Brown, Green, and Longmans, and John Taylor, London.
- Tornier, G. 1913. *Reptilia*. Pp. 315–376 in *Handwörterbuch der Naturwissenschaften, Achter Band* (E. Korschelt, ed.). Gustav Fischer, Jena.
- Townsend, T. M., A. Larson, E. Louis, and J. R. Macey. 2004. Molecular phylogenetics of *Squamata*: the position of snakes, amphisbaenians and dibamids, and the root of the squamate tree. *Syst. Biol.* 53:735–757.
- Uetz, P., ed. 2016. Species numbers (as of August 2016). The Reptile Database. Available at <http://www.reptile-database.org/>.
- Vidal, N., and S. B. Hedges. 2005. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *C. R. Biol.* 328:1000–1008.
- Vitt, L. J., and J. P. Caldwell. 2014. *Herpetology, an Introductory Biology of Amphibians and Reptiles*. 4th edition. Academic Press, London.
- Wagler, J. 1828. Vorläufige Übersicht des Gerüsts, so wie Ankündigung seines Systema Amphibiorum. *Isis von Oken* 21:859–861.
- Wagler, J. 1830. *Natürliches System der Amphibien, mit Vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur Vergleichenden Zoologie*. J. G. Cotta'schen, München, Stuttgart und Tübingen.
- Wiegmann, A. F. A. 1834. *Herpetologia Mexicana, seu Descriptio Amphibiorum Novae Hispaniae, quae Itineribus Comitum de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense Pervenerunt. Pars Prima, Saurorum Species Amplectens, Adiecto Systematis Saurorum Prodromo, Additisque Multis in Hunc Amphibiorum Ordinem Observationibus*. C. G. Lüderitz, Berolini.
- Wiens, J. J., C. A. Kuczynski, T. Townsend, T. W. Reeder, D. G. Mulcahy, and J. W. Sites, Jr. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. *Syst. Biol.* 59:674–688.

Williston, S. W. 1917. The phylogeny and classification of reptiles. *J. Geol.* 25:411–421.

Williston, S. W. 1925. *The Osteology of the Reptiles*. Harvard University Press, Cambridge, MA.

Zittel, K. A. 1887–1890. *Handbuch der Palaeontologie. I. Abteilung. Palaeozoologie. III. Band. Vertebrata* (Pices, Amphibia, Reptilia, Aves). R. Oldenbourg, München und Leipzig.

History; Smithsonian Institution; Washington, DC 20560-0162, USA. Email: dequeirozk@si.edu.

Jacques A. Gauthier; Department of Geology and Geophysics; Yale University; 210 Whitney Avenue, New Haven, CT 06520-8109, USA. Email: jacques.gauthier@yale.edu.

Authors

Kevin de Queiroz; Department of Vertebrate Zoology; National Museum of Natural

Date Accepted: 18 July 2018

Primary Editor: Philip Cantino