

**Acrodonta** H. Stannius 1856 [J. A. Schulte, II, K. de Queiroz and O. Torres-Carvajal], converted clade name

**Registration Number:** 4

**Definition:** The crown clade originating in the most recent common ancestor of *Agama* (originally *Lacerta*) *agama* (Linnaeus 1758), *Chamaeleo* (originally *Lacerta*) *chamaeleon* (Linnaeus 1758), *Uromastix* (originally *Lacerta*) *aegyptia* (Forskål 1775) and *Leiolepis guttata* Cuvier 1829. This is a minimum-crown-clade definition. Abbreviated definition: min crown  $\nabla$  (*Agama agama* (Linnaeus 1758) & *Chamaeleo chamaeleon* (Linnaeus 1758) & *Uromastix aegyptia* (Forskål 1775) & *Leiolepis guttata* Cuvier 1829).

**Etymology:** Derived from the Greek *akros* (at the top) + *odontos* (tooth), referring to the fact that the marginal teeth of these lizards are attached to the jaws more apically than was the case ancestrally in squamates.

**Reference Phylogeny:** For the purposes of applying our definition, Supplement Figure 1 of Schulte and Moreno-Roark (2010) should be treated as the primary reference phylogeny. *Leiolepis guttata* is not included in that phylogeny but is considered most closely related to *L. guentherpetersi* of the taxa that are included (Grismer and Grismer, 2010; Grismer et al., 2014). Application of our definition in the context of phylogenies inferred by Macey et al. (2000a), Conrad (2008), Gauthier et al. (2012), Pyron et al. (2013), and Reeder et al. (2015) result in the name being applied to a clade of identical composition.

**Composition:** *Acrodonta* is believed to contain at least 692 extant species (Uetz, 2017) distributed

among the following 7 mutually exclusive clades: *Agaminae*, *Amphibolurinae*, *Chamaeleonidae*, *Draconinae*, *Hydrosaurus*, *Leiolepis*, and *Uromastycinae* (Macey et al., 2000b; Schulte et al., 2003). Estes (1982) presented a compilation of the lizard fossil record including *Acrodonta*, and Evans (2003) provided a more recent review; however, those authors did not distinguish clearly between crown and stem, and several of the taxa referred by them to *Acrodonta* appear to be outside of the crown (Conrad, 2008).

**Diagnostic Apomorphies:** The following is a list of some of the more obvious derived characters shared by the members of *Acrodonta* relative to other extant iguanians (though several exhibit homoplasy):

1. Dorsolateral portion of dentary extends well posterior to coronoid apex (Etheridge and de Queiroz, 1988).
2. Splenial reduced or absent (Estes et al., 1988).
3. Maxillae meet anteromedially below palatal portion of premaxilla (Cope, 1864), and are expanded dorsally at the contact (Gauthier et al., 2012).
4. Lacrimal foramen enlarged (Etheridge and de Queiroz, 1988).
5. Pterygoid teeth absent (Estes et al., 1988).
6. All but the most anterior maxillary and dentary teeth relatively apically attached (acrodont), with the spaces between them filled by bone of attachment; those teeth are not replaced (Estes et al., 1988; Gauthier et al., 2012).
7. Number of ossicles in scleral ring reduced to 11 or 12 (Estes et al., 1988).

8. Fracture planes in caudal vertebrae absent (Estes et al., 1988).
9. Dorsal muscles of lower leg innervated by interosseous nerve (Estes et al., 1988).
10. *M. mylohyoideus anterior* in two layers, superficial layer transverse or anteriorly oblique, profound layer directed transversely and obliquely backward (Camp, 1923).
11. Reticular papillae present on fore and hind tongue (Schwenk, 1988).
12. Absence of a recognizable origin for mitochondrial light-strand replication ( $O_L$ ) between the tRNA<sup>Asn</sup> and tRNA<sup>Cys</sup> genes (Macey et al., 1997a, 2000a).
13. A rearrangement of the mitochondrial genome in which the positions of the tRNA<sup>Ile</sup> and tRNA<sup>Gln</sup> genes are switched in order (Macey et al., 1997a,b, 2000a).
14. D-stem replaced by a D-arm replacement loop in the mitochondrial tRNA<sup>Cys</sup> gene (Macey et al., 1997a,c, 2000a).

Additional apomorphies of *Acrodonta* have been summarized by Estes et al. (1988), Conrad (2008), and Gauthier et al. (2012).

### Synonyms:

The following are approximate synonyms:

Agamoïdes of Blainville (1822), partial (see Comments);

Acrodontes of Fitzinger (1843), partial (see Comments);

*Chamaeleonidae* of Frost and Etheridge (1989);  
*Chamaeleonoidea* of Vidal and Hedges (2009).

If *Agamidae*, as traditionally circumscribed, were to be found to be paraphyletic relative to *Chamaeleonidae* (see Comments), then *Agamidae* and its synonyms would also be partial synonyms of *Acrodonta*.

**Comments:** From the early nineteenth to the mid twentieth centuries, many systematists separated the highly modified chamaeleonids from the agamids, often grouping the latter with iguanids and various other “lizards” (e.g., Cuvier, 1817, 1829; Merrem, 1820; Gray, 1825, 1845; Latreille, 1825; Wagler, 1828, 1830; Bonaparte, 1831, 1850; Wiegmann, 1834; Duméril and Bibron, 1834–1854; Gravenhorst, 1843; Jones, 1847–1849; Duméril and Duméril, 1851; Stannius, 1856; Strauch, 1887; Haeckel, 1895; Hay, 1902; Williston, 1904, 1925; Camp, 1923; Nopcsa, 1923; Romer, 1933, 1945). This tendency reached its extreme in the taxonomies of Haworth (1825) and Boulenger (1884; 1885–1887), who placed chamaeleons in a taxon separate from one including all other limbed squamates (both taxa under various names). Nonetheless, at least some authors during this period grouped chamaeleonids with agamids (or at least some of them) to the exclusion (for the most part) of iguanids (e.g., Blainville, 1822, see also 1835; Fitzinger, 1826, 1843). Perhaps the closest early (i.e., nineteenth century) approximations (in terms of composition) to the clade here named *Acrodonta* were Blainville’s (1822) taxon *Agamoïdes* and Gray’s (1827) unnamed group for those lizards with slightly notched tongues and “Teeth simple, marginal, entire” (p. 57). Blainville’s *Agamoïdes* contained *Agama*, *Chamaeleo*, and *Draco* but also the iguanid *Basiliscus*; Gray’s unnamed group was made up of agamids and chamaeleonids, although the former included *Zonurus* (= *Cordylus*), which is now considered distantly related.

Camp (1923) presented an early phylogeny of lizards with a clade corresponding to *Acrodonta* as recognized here, although he did not recognize it taxonomically. Instead, he grouped *Agamidae* with *Iguanidae* in a paraphyletic *Iguania*, assigning *Chamaeleonidae* to the mutually exclusive taxon *Rhipoglossa*. McDowell and Bogert (1954) placed chamaeleonids within *Iguania* but did

not group them specifically with agamids. Based on an explicit phylogenetic analysis, Estes et al. (1988) inferred a clade composed of agamids and chamaeleonids, which has been corroborated by subsequent analyses based on morphological (e.g., Frost and Etheridge, 1989; Lee, 1998; Conrad, 2008; Gauthier et al., 2012), molecular (e.g., Macey et al., 2000b; Townsend et al., 2004, 2011; Hugall et al., 2007; Schulte and Moreno-Roark, 2010; Pyron et al., 2013), and combined morphological and molecular data (e.g., Macey et al., 1997a; Reeder et al., 2015).

The name *Acrodonta* was coined by Stannius (1856; see also Jan, 1857) for a group composed of what are now considered agamids but not chamaeleonids, although earlier authors had used a similar name (*Acrodontes*) for a group of similar composition (Duméril and Bibron, 1834–1854; Duméril and Duméril, 1851) or one composed of chameleons and arboreal (but not terrestrial) agamids (Fitzinger, 1843). Cope (1864) applied the name *Acrodonta* to a group composed of *Chamaeleonidae*, *Agamidae*, and *Hattereriidae* (*Sphenodon*, which is now considered distantly related), although he did not recognize that taxon in some subsequent works (e.g., Cope, 1875, 1900) and removed chamaeleonids from it in others (e.g., Cope, 1889). In the twentieth century, the name *Acrodonta* was seldom used until it was applied by Estes et al. (1988), using an explicit phylogenetic definition, to the crown clade composed of agamids and chamaeleonids, and it has been widely used for that clade in subsequent works (e.g., Macey et al., 1997a, 2000a,b; Lee, 1998; Frost et al., 2001; Schulte et al., 2003; Townsend et al., 2004, 2011; Conrad, 2008; Gauthier et al., 2012; Reeder et al., 2015). Because alternative names for this clade (see synonyms) have been used rarely, selection of the name *Acrodonta* for the clade in question would seem uncontroversial (except for the possibility of using that name for a more inclusive apomorphy-based or

total clade). Use of *Chamaeleonidae* for the clade here named *Acrodonta* (Frost and Etheridge, 1989) is at odds with the most common uses of both names (*Acrodonta* for the clade in question and *Chamaeleonidae* for a less inclusive clade). Moreover, the authors of that proposal subsequently used *Acrodonta* for the clade in question (Frost et al., 2001). The name *Chamaeleonoidea* Fitzinger 1826 sensu Vidal and Hedges (2009), but not sensu Gauthier et al. (2012), seems to be a redundant and thus unnecessary name that refers to a clade of identical composition to *Acrodonta*. Given the possibility of agamid paraphyly relative to chamaeleonids (e.g., Estes et al., 1988; Frost and Etheridge, 1989; Conrad, 2008; Schulte and Moreno-Roark, 2010; Gauthier et al., 2012), if *Agamidae* were to be considered a synonym of *Acrodonta*, the latter name should have precedence based on a closer match in terms of hypothesized composition. However, that situation could be avoided by defining the name *Agamidae* using a definition analogous to the one used for the name *Iguanidae* (this volume)—that is, the most inclusive crown clade containing *Agama agama* (Linnaeus 1758) but not *Iguana iguana* (Linnaeus 1758) (*Iguanidae*) and *Chamaeleo chamaeleon* (Linnaeus 1758) (*Chamaeleonidae*). Under that definition, the names *Acrodonta* and *Agamidae* could never be considered synonyms, because *Acrodonta* refers to a clade that necessarily includes *Chamaeleo chamaeleon*, whereas *Agamidae* would refer to a clade that necessarily excludes that taxon.

## Literature Cited

- de Blainville, H. D.. 1822. *De L'organisation des Animaux ou Principes D'anatomie Comparée*. F. G. Levrault, Paris.
- de Blainville, H. 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* 4:1–64.

- Bonaparte, C. L. 1831. *Saggio di una Distribuzione Metodica Degli Animali Vertebrati*. Antonio Boulzaler, Roma.
- Bonaparte, C. L. 1850. *Conspectus Systematum Herpetologiae et Amphibiologiae*. E. J. Brill, Lugduni Batavorum (Leiden).
- Boulenger, G. A. 1884. Synopsis of the families of existing *Lacertilia*. *Ann. Mag. Nat. Hist.* 14:117–122.
- Boulenger, G. A. 1885–1887. *Catalogue of the Lizards in the British Museum (Natural History)*. Taylor & Francis, London.
- Camp, C. L. 1923. Classification of the lizards. *Bull. Am. Mus. Nat. Hist.* 48:289–481.
- 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. Based on the specimens contained in the U.S. National Museum. *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. U.S. Natl. Mus.* 1898:153–1270.
- Cuvier, G. 1817. *Le Règne Animal Distribué D'après Son Organization, Pour Servir de Base a L'histoire Naturelle des Animaux et D'introduction a L'anatomie Comparée, Tome 2: Les Reptiles, Les Poissons, Les Mollusques, et Les Annélides*. Déterville, Paris.
- Cuvier, G. 1829. *Le Règne Animal Distribué D'après Son Organisation, Pour Servir De Base a L'histoire Naturelle des Animaux et D'introduction a L'anatomie Comparée, Tome 2: Chez Déterville, Paris*.
- Duméril, A. M., and G. Bibron. 1834–1854. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Roret, Paris.
- Duméril, M. C., and A. M. Duméril. 1851. *Catalogue Méthodique de la Collection des Reptiles*. Gide et Baudry, Paris.
- Estes, R. 1982. *Sauria Terrestria, Amphisbaenia. Handbuch der Paläoherpetologie, Vol. 10* 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.
- Etheridge, R., and K. de Queiroz. 1988. A phylogeny of *Iguanidae*. Pp. 283–367 in *Phylogenetic Relationships of the Lizard Families* (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, CA.
- Evans, S. 2003. At the feet of the dinosaurs: the early history and radiation of lizards. *Biol. Rev.* 78:513–551.
- 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 Museums zu Wien*. J. G. Heubner, Vienna.
- Fitzinger, L. I. 1843. *Systema Reptilium. Fasciculus Primus. Amblyglossae*. Baumüller and Seidel, Vienna.
- Forskål, P. 1775. *Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium, Quae in Itinere Orientale Observavit Petrus Forsskål. Post Mortem Auctoris Editit C. Niebuhr, Adjuncta est Materia Medica Kahirina Atque Tabula Maris Rubri Geographica*. Heineck and Faber, Copenhagen.
- Frost, D. R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (*Reptilia: Squamata*). *Misc. Publ. Nat. Hist. Mus. Univ. Kans.* 81:1–65.
- Frost, D. R., R. Etheridge, D. Janies, and T. Titus. 2001. Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the *Iguania (Squamata: Iguania)*. *Am. Mus. Novit.* 3343:1–38.
- 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.
- Gravenhorst, J. L. C. 1843. *Vergleichende Zoologie*. Graß, Barth & Comp., Breslau.

- Gray, J. E. 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. *Ann. Philos.* 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.* 2:54–58.
- Gray, J. E. 1845. *Catalogue of the Specimens of Lizards in the Collection of the British Museum*. Edward Newman, London.
- Grismer, J. L., A. M. Bauer, L. L. Grismer, K. Thirakhupt, A. Aowphol, J. R. Oaks, P. L. Wood, C. K. Onn, N. Thy, M. Cota, and T. Jackman. 2014. Multiple origins of parthenogenesis, and a revised species phylogeny for the Southeast Asian butterfly lizards, *Leiolepis*. *Biol. J. Linn. Soc.* 113:1080–1093.
- Grismer, J. L., and L. L. Grismer. 2010. Who's your mommy? Identifying maternal ancestors of asexual species of *Leiolepis* Cuvier, 1829 and the description of a new endemic species of asexual *Leiolepis* Cuvier, 1829 from Southern Vietnam. *Zootaxa* 2433:47–61.
- Haeckel, E. 1895. *Systematische Phylogenie der Wirbelthiere* (Vertebrata). Georg Reimer, Berlin.
- Haworth, A. H. 1825. A binary arrangement of the Class Amphibia. *Philos. Mag.* 65:372–373.
- Hay, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bull. U.S. Geol. Surv.* 179:1–868.
- 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.
- Jan, G. 1857. *Indice Sistematico dei Rettili ed Anfibi Esposti nel Museo Civico di Milano*. Luigi di Giacomo Priola, Milano.
- Jones, T. R. 1847–1849. *Reptilia*. Pp. 264–325 in *The Cyclopaedia of Anatomy and Physiology* (R. B. Todd, ed.). Longman, Brown, Green, Longmans, & Roberts, London.
- Latreille, M. 1825. *Familles Naturelles du Règne Animal, Exposées Succinctement et dans un Ordre Analytique, avec l'indication de leurs Genres*. J.-B. Baillière, Paris.
- 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.
- Linnaeus, C. 1758. *Systema Naturae Per Regna Trium Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 10th edition. Laurentii Salvii, Holmiae (Stockholm).
- Macey, J. R., A. Larson, N. B. Ananjeva, and T. J. Papenfuss. 1997a. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *J. Mol. Evol.* 44:660–674.
- Macey, J. R., A. Larson, N. B. Ananjeva, Z. Fang, and T. J. Papenfuss. 1997b. Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Mol. Biol. Evol.* 14:91–104.
- Macey, J. R., A. Larson, N. B. Ananjeva, and T. J. Papenfuss. 1997c. Replication slippage may cause parallel evolution in the secondary structures of mitochondrial transfer RNAs. *Mol. Biol. Evol.* 14:30–39.
- Macey, J. R., J. A. Schulte, II, and A. Larson. 2000a. Evolution and phylogenetic information content of mitochondrial genomic structural features illustrated with acrodont lizards. *Syst. Biol.* 49:257–277.
- Macey, J. R., J. A. Schulte, II, A. Larson, N. B. Ananjeva, Y. Wang, R. Pethiyagoda, N. Rastegar-Pouyani, and T. J. Papenfuss. 2000b. Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. *Syst. Biol.* 49:233–256.
- McDowell, S. B., and C. M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizard. *Bull. Am. Mus. Nat. Hist.* 105:1–142.
- Merrem, B. 1820. *Versuch eines Systems der Amphibien. Tentamen Systematis Amphibiorum*. Johann Christian Krieger, Marburg.
- Nopcsa, F. 1923. *Die Familien der Reptilien*. Gebrüder Borntraeger, Berlin.
- 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.

- Reeder, T. W., T. M. Townsend, D. G. Mulcahy, B. P. Noonan, P. L. Wood, J. W. Sites, and J. J. Wiens. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. *PLOS ONE* 10(3): e0118199.
- Romer, A. S. 1933. *Vertebrate Paleontology*. 1st edition. University of Chicago Press, Chicago, IL.
- Romer, A. S. 1945. *Vertebrate Paleontology*. 2nd edition. University of Chicago Press, Chicago, IL.
- Schulte, II, J. A., and F. Moreno-Roark. 2010. Live birth among iguanian lizards predates Pliocene–Pleistocene glaciations. *Biol. Lett.* 6:216–218.
- Schulte, II, J. A., J. P. Valladares, and A. Larson. 2003. Phylogenetic relationships within *Iguanidae* inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. *Herpetologica* 59:399–419.
- Schwenk, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. Pp. 569–598 in *Phylogenetic Relationships of the Lizard Families* (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, CA.
- Stannius, H. 1856. *Handbuch der Zootomie (zweiter Theil). Die Wirbelthiere. Zweites Buch, Zootomie der Amphibien*. Verlag von Veit & 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. Petersburg*. 7(35)2:1–72.
- Townsend, T., 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.
- Townsend, T. M., D. G. Mulcahy, B. P. Noonan, J. W. Sites, Jr., C. A. Kuczynski, J. J. Wiens, and T. W. Reeder. 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Mol. Phylogenet. Evol.* 61:363–380.
- Uetz, P., ed. 2017. The Reptile Database, Version October 2017. Available at <http://www.reptile-database.org>.
- Vidal, N., and S. B. Hedges. 2009. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *C. R. Biol.* 332:129–139.
- 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 Klassifikation der Säugethiere und Vögel. Ein Beitrag zur Vergleichenden Zoologie*. J. G. Cotta'schen, Munich, Stuttgart, and Tübingen.
- Wiegmann, A. F. A. 1834. *Herpetologia Mexicana, seu Descriptio Amphibiorum Novae Hispanae quae Itineribus Comitibus de Sack, Ferdinandi Deppe et Chr. Guil. Schiede. Pars Prima, Saurorum Species Amplectens*. C. G. Lüderitz, Berlin.
- Williston, S. W. 1904. The relationships and habits of the mosasaurs. *J. Geol.* 12:43–51.
- Williston, S. W. 1925. *The Osteology of the Reptiles*. Harvard University Press, Cambridge, MA.

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