

An unpublished manuscript of Alfredo Dugès related to the classification of lizards according to tongue morphology, c. 1898

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ABSTRACT: An unpublished manuscript of Alfredo Dugès was found in Guanajuato, Mexico. This manuscript is interesting in depicting some of the ideas Dugès held about the phylogenetic position of many lizard groups in the nineteenth century, in particular, his conclusion on the phylogenetic position of *Heloderma*, the only known venomous lizard at that time. Dugès's discussion is important in the context of a science dominated by Europeans and North Americans, putting this lizard in a modern phylogenetic context.

KEY WORDS: Reptilia – classification – morphology – Helodermatidae – Americas.

RESUMEN: Un manuscrito inédito de Alfredo Dugès se encontró en Guanajuato, México. Este manuscrito tiene interés ya que representa las ideas de A. Dugès sobre la posición filogenética de varios grupos de lagartijas a la luz del conocimiento en el siglo XIX. Es importante su conclusión sobre la posición filogenética de *Heloderma*, la única lagartija venenosa conocida en ese tiempo. La propuesta de Dugès, es importante en el contexto de la taxonomía del siglo XIX dominada por europeos y norteamericanos. Dugès colocó a estas lagartijas en un contexto filogenético moderno, tal como se les considera actualmente.

PALABRAS CLAVE: Reptilia – clasificación – morfología – Helodermatidae – América.

INTRODUCTION

Alfred Auguste Delscautz Dugès, better known as Alfredo Dugès (Figure 1), was a French-Mexican herpetologist who, according to Smith and Smith (1969), is considered the father of Mexican herpetology. This interesting figure in Mexican science published at least 184 papers and a few books in many disciplines of biology, but particularly in herpetology (94 according to Smith and Smith 1969).

Dugès was born in Montpellier, France, in 1826 and moved to Mexico in 1853. He died in Guanajuato in 1910. His first paper, about the viperids of France, was published in 1850 and he published nine papers before moving to Mexico. However, the majority of his scientific papers were published while Dugès lived in Guanajuato, Mexico, in Spanish,

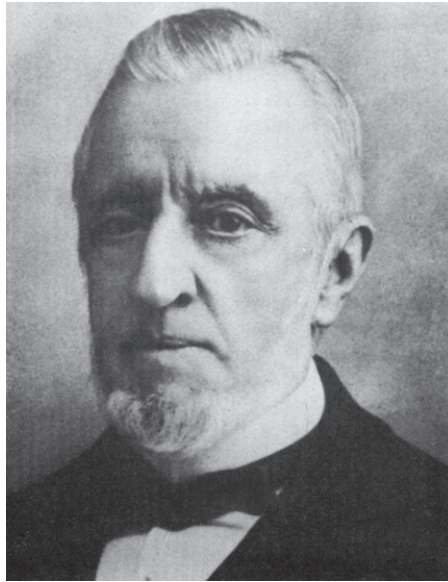


Figure 1. Alfredo Dugès (from Beltrán *et al.* 1990.
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French and English (in decreasing order of frequency). Most of his academic work was done in Mexico, particularly in Guanajuato while he was associated with the Colegio del Estado, now the Universidad de Guanajuato (Lanuza 1924). In this institution he created a small museum that still exists, now named Museo de Historia Natural Alfredo Dugès, and it contains the natural history collections he made during his lifetime, as well as some of his library and notes. Unfortunately, many of Dugès's possessions were dispersed, and some have been lost or stolen from the Museo de Historia Natural Alfredo Dugès.

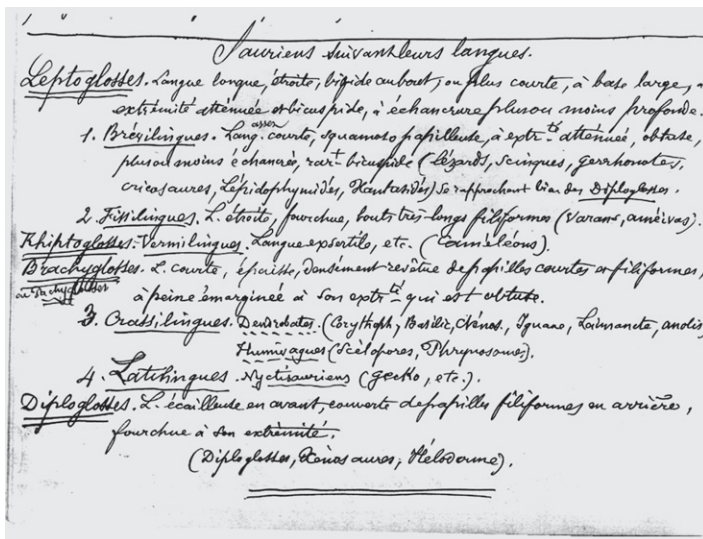
During the course of an investigation about the life and contributions of Alfredo Dugès, we visited the historic site called Alhóndiga de Granaditas, now converted into a historical museum, in the city of Guanajuato. In the archives of Alhóndiga de Granaditas we found a notebook that Dugès had labeled “Un buen libro” (“A good book”). In this notebook are drafts of 30 of his publications as well as an unpublished note (on pages 38–39), written in French and entitled “Sauriens suivant leurs langues” (“Lizards according to their tongues”). Dugès dated most of the manuscripts in the notebook; however this particular draft is not dated. Fortunately, we are able to date this unpublished work fairly precisely to 1898 because it is bracketed by two notes that were published with known dates: the preceding one, entitled “*Geatractus*, gen. nov.” is dated 1898 and was published in *La Naturaleza*¹ (Dugès 1898a); the succeeding manuscript, entitled “Chilacayote monstruoso” (“A monstrous chilacayote”), was published 1898 (Dugès 1898b). Although it seems unlikely, there is some indication in the contents of the note that suggests it may have been written in 1900 or slightly thereafter (see discussion, pp 251–252).

The unpublished manuscript referred to here comprises only two paragraphs. The first paragraph describes the different kinds of lizard tongues known to Dugès, and the second presents a classification of different North American genera, with special reference to *Heloderma* (see transcription below).

Our consideration of the manuscript and a comparison with others in the same notebook, leads us to believe that this note was not intended for publication. On most of the manuscripts in the notebook, Dugès added a note with the name of the journal to which each one was sent for publication. In addition, the manuscript described here has several errors and misspellings of scientific names.

“SAURIENS SUIVANT LEURS LANGUES”

Below the photographs of the paragraphs from Dugès’s manuscript, the French text is translated, line by line, into English.



[p. 38]

Lizards according to their tongues.

Leptoglossa. Tongue long, narrow, bifid at the end, or shorter, broad at the base, the tip is attenuated and bicuspid, with a notch more or less deep.

1. Brevilingua. Tongue very short, squamose-papillae, attenuated at the end, blunt, more or less notched, rarely \pm bicuspid (lacertids², skinks, gerrhonotes, cricosaurs, lepidophymids, xantusiids) it often approaches the Diploglossans.

2. Fissilingua. Tongue narrow, forked, the tip very long filiform (varanids, ameivas)

Rhiptoglossa. Vermilingua. Projectile tongue, etc. (chameleons).

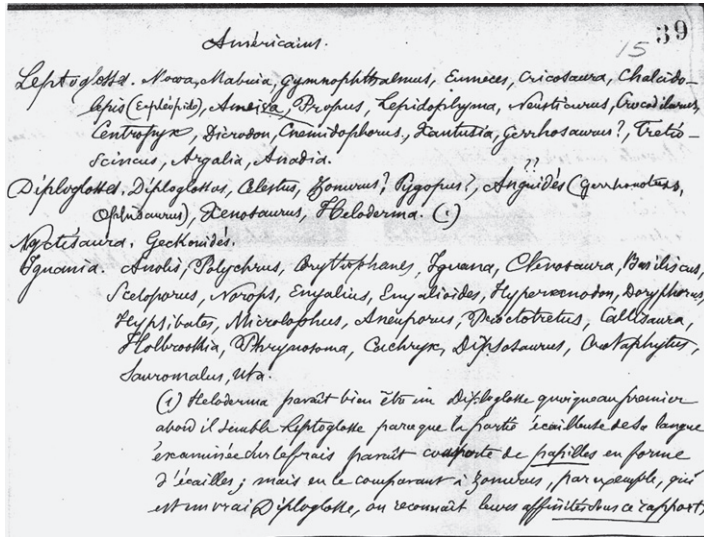
Brachyglossa. or Pachyglossa. Tongue short, thick densely covered with short filiform papillae, just barely trimming the margins of the tip—which is blunt.

3. Crassilingua. Dendrobates (Corythophanes, Basiliscus, Ctenosaura, Iguana, Lamantus, Anolis Humivagues (Sceloporus, Phrynosoma).

4. Latilingua. Nyctisaurians (gecko, etc.).

Diploglossa. Tongue scaly at the front, covered with filiform papillae on the back, forked at the tip.

(Diploglossus, Xenosaurus, Heloderma)



Americans

[p. 39]

Leptoglossa. Mocoa, Mabuia, Gymnophthalmus, Eumeces, Cricosaura, Chalcidolepis (Eupleopide), Ameiva, Propus, Lepidophyma, Neusticurus, Crocodilurus, Centropyx, Dicrodon, Cnemidophorus, Xantusia, Gerrhosaurus?, Tretioscincus, Argalia, Anadia.

Diploglossa, Diploglossus, Celestus, Zonurus?, Pygopus?, Anguoids?? (Gerrhonotus, Ophisaurus), Xenosaurus, Heloderma. (1)

Nyctisaura. Geckonids.

Iguania. Anolis, Polychrus, Corythophanes, Iguana, Ctenosaura, Basiliscus, Sceloporus, Norops, Enyalius, Enyalioides, Hyperanodon, Doryphorus, Hypsibates, Microlophus, Aneuporus, Proctotretus, Callisaura, Holbrookia, Phrynosoma, Cachryx, Dipsosaurus, Crotaphytus, Sauromalus, Uta.

(1) *Heloderma* seems to be a Diploglossan that at first sight seems leptoglossan because the scaly part of the tongue examined in a freshly killed specimen appears to be covered with papillae in the form of scales; but in comparison with *Zonurus*, for example, which is a true Diploglossan, its affinities are recognized in this report.

DISCUSSION

Lizard tongues are immensely variable in size, shape and superficial form – much more so than in other groups of tetrapods (Schwenk 1988, 2000a, 2000b). This phenotypic diversity was noted as early as the fifth century BC by Aristotle (Smith and Ross 1910: 508; 1912: 660, 690) and was further described by subsequent, important anatomists, such as Antoine Dugès (1827), Cuvier (1835), Duvernoy (1836) and Owen (1866). Herpetologists recognized the systematic significance of this variation early on and included lingual characters as a core component of the first, formal systems of lizard classification (for example, Oppel 1811;

Wagler 1830; Wiegmann 1834; Duméril and Bibron 1836, 1837, 1839). Indeed, modern systematists have continued to regard the lizard tongue as a rich source of phylogenetically informative characters (for example, Camp 1923; Estes *et al.* 1988; Schwenk 1988; Lee 2000, 2005). Given the centrality of lingual form in lizard classifications, especially in the nineteenth century, it is not surprising that Alfredo Dugès made notes about such a classification in his notebook. Although he did not publish his classification, it is likely that he used it in guiding his own work.

In comparing Dugès's classification with earlier schemes, we found that it does not represent an original contribution, although it has some novel elements. First, it appears that Dugès's classification is a hybrid between two important, earlier classifications by Wiegmann (1834) and Cope (1864, 1875; updated in 1900). Dugès's classification is based primarily on that of Wiegmann (1834) and includes all of Wiegmann's major taxa (note that the names of these taxa, *Leptoglossa*, *Pachyglossa*, *Rhaptoglossa*, and *Brachyglossa* are based on tongue form). However, to this framework Dugès added the primary taxon *Diploglossa*, a group introduced by Cope (1864). Second, Dugès replaced Wiegmann's (1834) pachyglossan "Fam. *Ascalabotae*" (*Gekkonidae* in modern usage) with Gray's (1845) name, *Nyctisaura*, also used by Cope (1864, 1875). Finally, based on his own, original observations, Dugès placed *Heloderma* (the Gila monster and Mexican beaded lizard, family *Helodermatidae*) within the *Diploglossa* (also following Cope (1864, 1883)) and not in the *Leptoglossa*, as had Wiegmann (1834) and Fitzinger (1843). We return to this latter point below.

Two other authors also discussed the position of *Heloderma*: Bocourt (1878) and Boulenger (1885). Bocourt (1878) made an extensive discussion of the taxonomic position of *Heloderma*, reviewing and discussing previous works. He concluded that *Heloderma* belongs to a different group of lizards, and concurred with Wiegmann (1834) placing it in the *Trachydermy*. This family he divided in two subfamilies using the presence of grooved teeth. In the first group (*Glyphodonta*) Bocourt placed *Heloderma*, and in the second (*Aglyphodonta*) *Xenosaurus*, *Lepidophyma*, *Xantusia* and *Cricosaura*. Dugès's classification differs more widely from that proposed by Boulenger (1885) who considered tongue morphology as well as other osteological characters to make his classification of lizards. *Helodermatids* are placed in the suborder *Lacertilia* in group B, organisms with flattened tongues, smooth or with villose papillae. All lizard families recognized by Boulenger were placed by him in this suborder except *Chamaeleontidae* placed in the suborder *Rhaptoglossa*.

A few other observations are pertinent. In the first part of the manuscript, Dugès provided a short description of the tongues in each of the higher taxa he used in his classification. He also assigned specific taxa to each of the groups in order to exemplify the lizards that possessed each kind of tongue. He recognized four principal groups of lizards (*Leptoglossa*, *Rhaptoglossa*, *Brachyglossa* or *Pachyglossa*, and *Diploglossa*). Dugès followed Wiegmann (1834) by including the subtaxa ("sections") for each major group: *Leptoglossa* includes sections *Brevilingua* and *Fissilingua*; *Rhaptoglossa* includes section *Vermilingua*; and *Brachyglossa/Pachyglossa* includes sections *Crassilingua* and *Latilingua*. Also following Wiegmann (1834), Dugès subdivided the section *Crassilingua* into *Dendrobates* and *Humivagues*. As noted above, Dugès adopted Gray's (1845) name *Nyctisaura*, instead of Wiegmann's (1834) *Ascalabotae* for species in the *Latilingua*.

Dugès identified a number of lizard families within each of his major taxa. We clarify their content here with the modern names. Within the *Brevilingua* (*Leptoglossa*), Dugès included: *Lacertidae*², *Scincidae*, *Gerrhosauridae*, and *Xantusiidae*; within *Fissilingua*

(Leptoglossa): Varanidae and Teiidae; within Vermilingua (Rhiptoglossa): Chamaeleonidae; within Dendrobates (Brachyglossa, Crassilingua): Corytophanidae, Iguanidae and Polychrotidae. Note that many species in these latter families have arboreal habits, as suggested by the name Dendrobates (from the ancient Greek, δένδρος (tree) and βατες (roam)). Similarly Humivagues (Brachyglossa, Crassilingua) includes the Phrynosomatidae, most species of which have terrestrial habits, as the word Humivagues suggests (from Latin, *humus* (ground, earth, soil) and *vagus* (wandering, roaming)). The Nyctisaura (Brachyglossa, Latilingua) includes the Gekkonidae in which most species are nocturnal, as implied by the name (from the Greek νυκτος (night) and σαυρος (lizard, reptile)). Finally, within Diploglossa, Dugès included Xenosauridae and Helodermatidae.

In the nineteenth century there was considerable confusion and disagreement about the taxonomic position of *Heloderma* and other members of the lizard group known today as the Anguimorpha (including variously Shinisauridae, Xenosauridae, Anguidae, Helodermatidae, Lanthanotidae, Varanidae and sometimes snakes; see McDowell and Bogert 1954; Estes *et al.* 1988; Schwenk 1988; Lee 1997, 2000, 2005; Norell and Gao 1997; Gao and Norell 1998; Townsend *et al.* 2004). A notable feature of Dugès's classification is his placement of *Heloderma* within the Diploglossa, a taxon that does not appear in Wiegmann (1834) (who placed *Heloderma* and Anguidae within his Leptoglossa; see above). In this, Dugès seems to follow Cope (1864), who first named the taxon Diploglossa, including within it Helodermatidae, Anguidae and Gerrhonotidae (the latter now included within Anguidae). In a revised classification, Cope (1900) removed *Heloderma* from the Diploglossa and placed it within its own suborder, but it is unclear whether Dugès saw this later revision or not (see below). Finally, Dugès also included within his Diploglossa *Xenosaurus*, a genus that was not known to Wiegmann in 1834 (the first species was described in 1856 by Gray under the genus *Cubina* and the genus was named in 1861 by Peters). Cope (1864) thought that *Xenosaurus* was a diploglossan, but did not include it within his classification, a conclusion he confirmed in his 1900 revision.

Although the evidence indicates that Dugès's classificatory note was written between 1898 and 1899, there is a possibility that it was written later (in 1900 or later). This conflict arises because of two genera Dugès included within the group Diploglossa on the second page of his note: *Zonurus* (*Cordylus* in modern nomenclature) and *Pygopus* (families Cordylidae and Pygopodidae, respectively), each being marked with a question mark. Their presence here is noteworthy for two reasons. First, both are Old World taxa and would seem to be out of place in a section labelled "Américains" (presumably intended as a list of New World taxa known to Dugès). Second, both genera were placed within Diploglossa for the first time by Cope in 1900. Cope (1864), in contrast, included both genera within Leptoglossa. Furthermore, both genera lack the trait of a retractile foretongue, the character on which the name Diploglossa is based (McDowell and Bogert 1954; Schwenk 1988), and both are universally excluded from the Diploglossa (for example, Anguimorpha) as presently understood (Estes *et al.* 1988; Schwenk 1988; Gao and Norell 1998; Townsend *et al.* 2004; Vidal and Hedges 2005; Kumazawa 2007; Conrad 2008). Thus, Dugès's inclusion of *Zonurus* and *Pygopus* in Diploglossa seems surprising unless he had seen a copy of Cope (1900), which would suggest that he wrote his note a year or two later than we believe (therefore in 1900 or later). However, Cope died in 1897 and according to Camp (1923), Cope's (1900) manuscript was edited and published posthumously. It is possible that an earlier version of Cope's manuscript circulated among herpetologists, including Dugès, before 1900. During the course of our research on Dugès's correspondence, we found several

letters exchanged between Dugès and Cope, although we did not find any in relation to this issue. Alternative explanations, less likely, include the possibility that Dugès identified *Zonurus* and *Pygopus* as diploglossans based on his own original observations, or that he saw such a classification in a source we have not discovered.

The last paragraph of Dugès's note is important because it indicates original observations to support his taxonomic placement of *Heloderma* within Diploglossa. By comparing the tongue of a freshly killed specimen of *Heloderma* with that of *Zonurus* (*Cordylus*), Dugès concluded that *Heloderma* was appropriately included within the Diploglossa, as suggested by Cope (1864; *contra* Cope 1900) and not the Leptoglossa, as suggested by Wiegmann (1834; his Trachydermi). This paragraph suggests that Dugès's classification may be based, in some cases, on his own observations and independent judgments, and not just on work published by others. His inclusion of *Heloderma* in Diploglossa is correct by modern standards. However, it is ironic in that it was based on comparison with *Cordylus*, which he considered to be a "true" diploglossan, although we now recognize that they are not phylogenetically related and does not belong in the group (nor does *Pygopus*). Any similarity in tongue form between *Heloderma* and *Cordylus* is purely superficial (Schwenk 1988).

In the last section of his note, on the second page, Dugès seems to have intended to apply his classification to the American lizards that he was familiar with. Apparently this section is incomplete because he did not include all of the taxa mentioned in the first (classification) section of his note. As noted previously, it is unclear why Dugès included here several Old World taxa, including *Zonurus*, *Pygopus* and Gerrhosauridae. It is also noteworthy that he used the name Iguania in place of Crassilingua (Brachyglossa/Pachyglossa). Iguania is a name often used by other workers (like Duméril and Bibron 1837) for most of the same species, but it does not accord with the first section of Dugès's note.

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NOTES

¹ *La Naturaleza* was the most important scientific journal published in Mexico during the late nineteenth and early twentieth centuries (Beltrán 1948; Smith 1942).

² In the original document, Dugès uses the word "lézard" which nowadays is translated as lizard. However, in the context of the manuscript, it clearly refers specifically to lizards of the family Lacertidae.

REFERENCES

- BELTRÁN, E., 1948 *La Naturaleza*. Periódico científico de la Sociedad Mexicana de Historia Natural. 1869–1914. *Revista de la Sociedad Mexicana de Historia Natural* 9: 145–174.
- BELTRÁN, E., A. JÁUREGUI DE C. y R. CRUZ, 1990 *Alfredo Dugès*. Guanajuato.
- BOCOURT, M. F., 1878 *Études sur les reptiles. Mission Scientifique au Mexique et dans l'Amérique Centrale*. Feuille 36. Paris.

- BOULENGER, G. A., 1885 *Catalogue of the lizards in the British Museum (Natural History)*. Second edition. London. 2 volumes.
- CAMP, C. L., 1923 Classification of the lizards. *Bulletin of the American Museum of Natural History* **43**: 289–481.
- CONRAD, J. L., 2008 Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* **310**: 1–182.
- COPE, E. D., 1864 On the characters of the higher groups of Reptilia Squamata – and especially of the Diploglossa. *Proceedings of the Academy of Natural Sciences of Philadelphia* **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. *Bulletin of the United States National Museum* **1**: 1–104.
- COPE, E. D., 1883 Notes on the geographical distribution of Batrachia and Reptilia in Western North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* **35**: 10–35.
- COPE, E. D., 1900 Crocodylians lizards and snakes of North America. *Reports of the United States National Museum* **1898**: 153–1270.
- CUVIER, G., 1835 *Leçons d'anatomie comparée*. Volume 4, part 1. Second edition. Paris.
- DUGÈS, Alfredo, 1898a Un nuevo género de ofidio. *La Naturaleza*, series 2, **3**: 52.
- DUGÈS, Alfredo, 1898b Un chilacayote monstruoso. *Memorias de la Sociedad Científica Antonio Alzate* **12**: 91–93.
- DUGÈS, Antoine, 1827 Recherches anatomiques et physiologiques sur la déglutition dans les reptiles. *Annales des sciences naturelles* **12**: 337–395.
- DUMÉRIL, A. M. C. and BIBRON, G., 1836 *Erpétologie générale ou histoire naturelle complète des reptiles*. Volume 3 (1836). Paris.
- DUMÉRIL, A. M. C. and BIBRON, G., 1837 *Erpétologie générale ou histoire naturelle complète des reptiles*. Volume 4. Paris.
- DUMÉRIL, A. M. C. and BIBRON, G., 1839 *Erpétologie générale ou histoire naturelle complète des reptiles*. Volume 5. Paris.
- DUVERNOY, G. L., 1836 Mémoire sur quelques particularités des organes de la déglutition de la classe des oiseaux et des reptiles, pour servir de suite à un premier mémoire sur la langue. *Comptes rendus Académie des Sciences, Paris* **2** (supplement): 1–24.
- ESTES, R., DE QUEIROZ, K. and GAUTHIER, J., 1988 Phylogenetic relationships within Squamata, pp 119–281 in ESTES, R. and PREGILL, G. (editors), *Phylogenetic relationships of the lizard families, Essays commemorating Charles L. Camp*. Stanford.
- FITZINGER, L. J. F. J., 1843 *Systema reptilium. Fasciculus primus. Amblyglossae*. Vienna. (Facsimile edition, 1973. Society for the Study of Amphibians and Reptiles.).
- GAO, K. and NORELL, M. A., 1998 Taxonomic revision of Carusia (Reptila: Squamata) from the Late Cretaceous of the Gobi Desert, and phylogenetic relationships of anguimorphan lizards. *American Museum novitates* no. 3230: 1–51.
- GRAY, J. E., 1845 *Catalogue of the specimens of lizards in the collection of the British Museum*. London.
- GRAY, J. E., 1856 Notice of a new species of nocturnal lizard from Mexico. *Annals and magazine of natural history* **18**: 270–271.
- KUMAZAWA, Y., 2007 Mitochondrial genomes from major lizard families suggest their phylogenetic relationships and ancient radiations. *Gene* **388**: 19–26.
- LANUZA, A., 1924 *Historia del Colegio del Estado de Guanajuato*. Guanajuato. (Facsimile edition, 1998.)
- LEE, M. S. Y., 1997 The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical transactions of the Royal Society: biological sciences* **352**: 53–91.
- LEE, M. S. Y., 2000 Soft anatomy, diffuse homoplasy, and the relationships of lizards and snakes. *Zoologica scripta* **29**: 101–130.
- LEE, M. S. Y., 2005 Squamate phylogeny, taxon sampling, and data congruence. *Organisms, diversity and evolution* **5**: 25–45.
- MCDOWELL, S. B. and BOGERT, C. M., 1954 The systematic position of *Lanthanotus* and the affinities of the anguimorphan lizards. *Bulletin of the American Museum of Natural History*. **105**: 1–142.

- NORELL, M. A. and GAO, K., 1997 Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi Desert, and the recognition of a new clade of lizards. *American Museum novitates* no. 3211: 1–25.
- OPPEL, M., 1811 *Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrum einer Naturgeschichte derselben*. Munich.
- OWEN, R., 1866 *On the anatomy of vertebrates*. Volume 1. *Fishes and reptiles*. London.
- PETERS, W. C. H., 1861 Eine neue Gattung von Eidechsen, *Xenosaurus fasciatus* aus Mexico. *Monatsbericht der königlichen Akademie des Wissenschaften, Berlin* **1861**: 453–454.
- SCHWENK, K., 1988 Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny, pp 569–598 in ESTES, R. and PREGILL, G. (editors), *Phylogenetic relationships of the lizard families, Essays commemorating Charles L. Camp*. Stanford.
- SCHWENK, K., 2000a An introduction to tetrapod feeding, pp 21–61 in SCHWENK, K. (editor), *Feeding: form, function and evolution in tetrapod vertebrates*. San Diego.
- SCHWENK, K., 2000b Feeding in lepidosaurs, pp 175–291 in SCHWENK, K. (editor), *Feeding: form, function and evolution in tetrapod vertebrates*. San Diego.
- SMITH, H. M., 1942 The publication dates of “La Naturaleza”. *Lloydia* **5**: 95–96.
- SMITH, H. M. and SMITH, R. B., 1969 *Early foundations of Mexican herpetology, an annotated and indexed bibliography of the herpetological publications of Alfredo Dugès, 1826–1910*. Urbana.
- SMITH, J. A. and ROSS, W. D., 1910 *The works of Aristotle translated into English*. Volume 4. *Historia animalium* (translated by D’A. W. Thompson). Oxford.
- SMITH, J. A. and ROSS, W. D., 1912 *The works of Aristotle translated into English*. Volume 5. *De partibus animalium* (translated by W. Ogle). Oxford.
- TOWNSEND, T. M., LARSON, A., LOUIS, E. and MACEY, J. R., 2004 Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic biology* **53**: 735–757.
- VIDAL, N. and HEDGES, S. B., 2005 The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes rendus biologiques* **328**: 1000–1008.
- WAGLER, J., 1830 *Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel*. Munich.
- WIEGMANN, A. F. A., 1834 *Herpetología Mexicana seu descriptio amphibiorum Novae Hispaniae. Pars prima. Saurorum species*. Berlin. (Facsimile reprint, 1969).

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