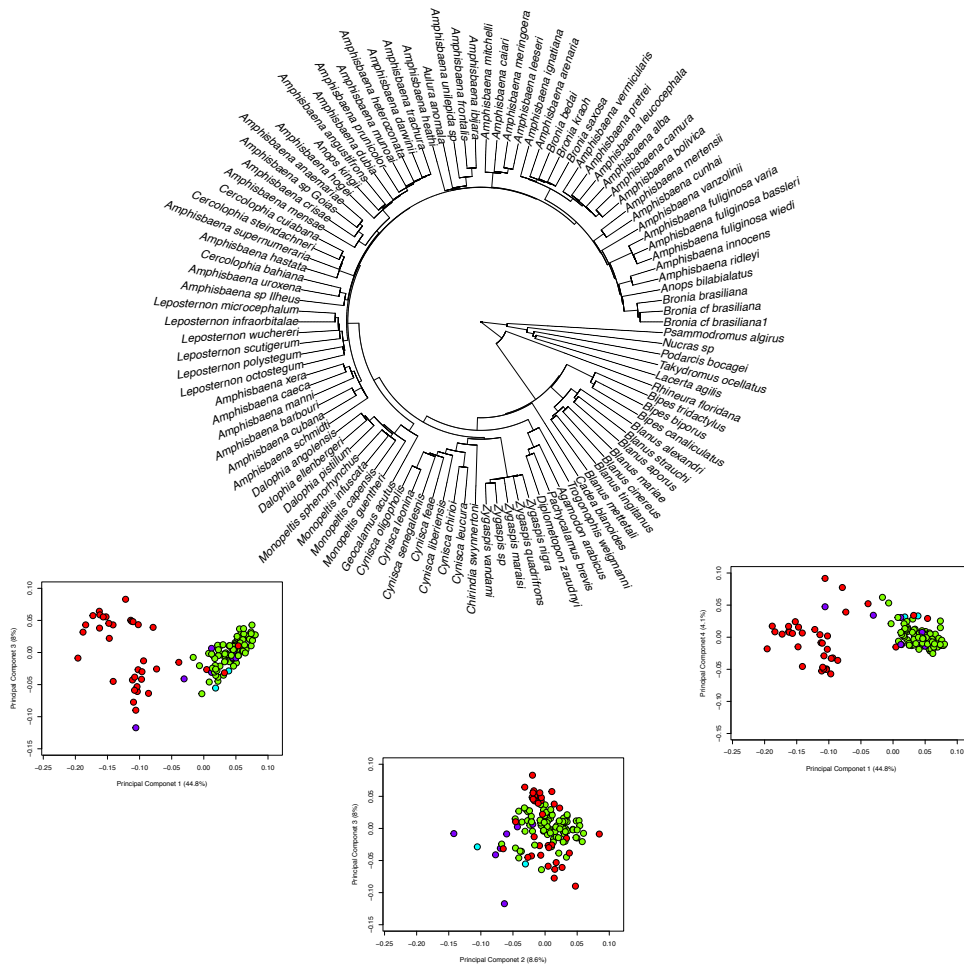
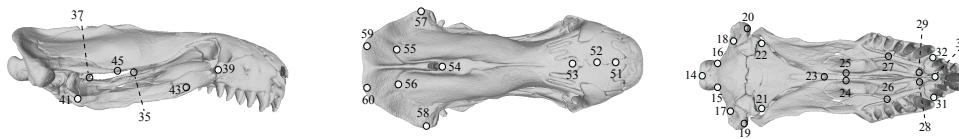


Roberta Graboski Mendes

Phylogeny and evolution of head shape in

Amphisbaenia (Reptilia: Squamata).



São Paulo

2017

Roberta Graboski Mendes

Filogenia e evolução das formas da cabeça em
Amphisbaenia (Reptilia: Squamata).

Phylogeny and evolution of head shape in the
Amphisbaenia (Reptilia: Squamata).

Tese apresentada ao Instituto de
Biotecnologia da Universidade de São
Paulo para obtenção do título de
Doutora em Ciências Biológicas.

Área de Concentração: Zoologia

Orientador(a): Hussam El Dine Zaher

São Paulo, 2017.

RESUMO

Dentre os Squamata, a subordem Amphisbaenia é composta por organismos que apresentam diversas modificações morfológicas adaptadas para hábitos fossoriais. Atualmente, Amphisbaenia possui 192 espécies descritas que são divididas em seis famílias (Amphisbaenidae, Blanidae, Bipedidae, Cadeidae, Rhineuridae e Trogonophidae) que possuem ampla distribuição, ocorrendo na região Neotropical, África subsaariana, partes da região do Mediterrâneo, Baixa Califórnia e Flórida. Apesar do progresso do conhecimento acerca do grupo, o posicionamento filogenético de Amphisbaenia dentro de Squamata, bem como as relações entre as famílias e gêneros ainda permanecem incertos. Muitos trabalhos atribuem as dificuldades para compreensão da origem e evolução das Amphisbaenia à convergência de diversos caracteres morfológicos, como as diferentes formas da cabeça presentes neste grupo. Sendo assim, o presente trabalho visa investigar e contribuir para preencher algumas lacunas sobre o conhecimento do grupo. Para isso, este trabalho fornece uma nova proposta filogenética e taxonômica para Amphisbaenia usando uma amostragem abrangente de táxons e diferentes métodos de sequenciamento (*Sanger e Anchored Phylogenomics*) para compreender as relações entre as famílias e gêneros, bem como inferir o posicionamento filogenético de Amphisbaenia dentro de Squamata. Este trabalho também visa compreender a evolução das formas da cabeça dentro de Amphisbaenia, testando se essas formas possuem relação filogenética, com o ambiente ou se são convergências morfológicas. Para isso foi utilizado tomografia computadorizada de alta resolução, marcos anatômicos (*Landmarks*) e técnicas de morfometria geométrica de 135 espécies de Amphisbaenia.

Palavras chave: Sistemática, Filogenia, Genomics, Squamata, Amphisbaenians.

ABSTRACT

Within the Squamata, the suborder Amphisbaenia consists of a group of legless lizards that have adapted to fossorial life through several morphological changes. Currently, Amphisbaenia comprises 192 described species that are divided into six families (Amphisbaenidae, Blanidae, Bipedidae, Cadeidae, Rhineuridae, and Trogonophidae). The suborder is widely distributed, occurring in the Neotropical region, sub-Saharan Africa, parts of the Mediterranean region, Baja California and Florida. Despite advancements in the knowledge of the group, the phylogenetic position of Amphisbaenia within Squamata and the relationships among its families and genera remains uncertain. Many studies attribute the difficulties in understanding the origin and evolution of the Amphisbaenia to the convergence of the head shapes. Thus, the present study aims to investigate and contribute to fill these gaps in the knowledge of this group. For this, it was provided a new phylogenetic and taxonomic proposal for Amphisbaenia a combination of different approaches for taxon and character methods (Sanger, Anchored Phylogenomics and morphological data) to understand the relationships among families and genera, as well as to infer the phylogenetic position of the Amphisbaenia within Squamata. Additionally, this study aims to understand the evolution of head forms within Amphisbaenia, testing whether these forms have a phylogenetic or environment relationship, and if they are morphological convergences. High-resolution X-ray computed tomography (HRXCT), anatomical landmarks and geometric morphometrics techniques were used to analyze the differences in head shape of 135 species of Amphisbaenia.

Key words: Systematic, Phylogeny, Genomics, Squamates, Amphisbaenians.

GENERAL INTRODUCTION

Squamata (snakes, "lizards", amphisbaenians and mosasaurs) are reptiles with a vast fossil record (Conrad, 2008) and share several morphological characteristics, which support them as a monophyletic clade. Amphisbaenia is classified as a suborder of Squamata, comprising organisms that have strictly fossorial habits. Their anatomy has several modifications for this lifestyle, such as extremely rigid skulls joined by sutures to assist in the excavation, an elongated body, short tail and a unique modification of the inner ear, which detects low frequency sounds (Gans, 1978; Kearney, 2003).

Currently, Amphisbaenia comprises of 193 nominal taxa (Uetz *et al.*, 2017) that are divided into six families (Kearney, 2003; Vidal *et al.*, 2008). Of the six families in Amphisbaenia, four have restricted geographic distributions: Rhineuridae consists of only one extant species distributed in the southeastern United States of America; Bipedidae comprises three species, which are found in southern Baja California, Guerrero, and Michoacán in Mexico; Blanidae comprises seven species distributed in the Mediterranean region (Kearney, 2003; Sindicato *et al.*, 2014); and Cadeidae consists of two species restricted to Cuba (Vidal *et al.*, 2008). The other two families have a widespread distribution: Trogonophidae consists of six species divided into four genera, distributed across the Middle East (including Socotra Island) and North Africa (Gans, 1990; Kearney, 2003); and Amphisbaenidae, which is the most diverse family (174 nominal taxa), has a disjoint distribution, occurring in sub-Saharan Africa, South America and the Caribbean island (Kearney, 2003; Vidal *et al.*, 2008; Montero, 2016; Uetz *et al.* 2017).

Because of the extensive distribution and the cryptic nature of fossorial organisms, Amphisbaenia is often poorly represented in museum collections. Considering these facts, the taxonomy and phylogenetic relationships of this group remains disputing. Furthermore, many

studies attribute the difficulties to understanding their relationships to convergence, i.e. homoplasy, of several morphological characters.

Estes *et al.* (1978) conducted one of the first phylogenetic studies involving large groups of Squamata based on morphological characters including osteology and the anatomy of the soft tissues. The results of this study suggested that Amphisbaenia form a monophyletic clade with Dibamidae and “snakes”. However, due to morphological convergence, the phylogenetic position of this clade was considered uncertain (Estes *et al.*, 1978). Besides, it is noteworthy that in this study, the phylogenetic analysis did not utilize information from fossil records that seems to affect significantly the results of analyses based exclusively on morphological data.

Historically, studies based only on morphological characters grouped Amphisbaenia with Gekkota (Lee 1998; Evans & Barbadillo, 2008), Lacertidae (Schwenk, 1988; Wu, 1996), Scincidae (Conrad, 2008), Dibamidae (Greer, 1985b; Hallermann, 1998; Kearney, 2003; Rieppel & Zaher, 2000a; Lee, 2000; Gauthier *et al.*, 2012) and snakes (Rage, 1982). However, recent studies based on molecular and morphological analyses (total evidence) suggest that Amphisbaenia are related to Lacertidae (Townsend *et al.*, 2004; Vidal & Hedges, 2005; Vidal & Hedges, 2008; Wiens, 2010, 2012; Müller *et al.*, 2011; Streicher & Wiens, 2017).

Similar to the question concerning the affinities of Amphisbaenia within Squamata, phylogenetic analyses of familial and generic relationships are also challenging, and these relationships have been uncertain for more than a century. Morphological studies by Taylor (1951), Vanzolini (1951, 1951b) and Gans (1978, 1974) recognize four families: Amphisbaenidae, Bipedidae, Rhineuridae and Trogonophidae. However, these studies did not employ phylogenetic method to establish the affinities among families. Kearney (2003) analyzed 162 morphological characters, and introduced the first and most complete phylogenetic proposal for Amphisbaenia.

In this study, Amphisbaenia was inferred to be the sister group of Dibamidae, and a new family was described (Blanidae). This study also supported the classical hypothesis of *Bipes* as the sister group of all Amphisbaenians.

With the advent of molecular biology new proposals on the phylogenetic relationships within Amphisbaenia were presented, showing some contrasts among morphological phylogenies. Kearney & Stuart (2004) analyzed two nuclear genes for 18 species of amphisbaenians and found Rhineuridae as sister group to all other Amphisbaenia. These authors also found Bipedidae as sister group of the clade composed by Trogonophidae and Amphisbaenidae. Macey *et al.* (2004) analyzed the complete mitochondrial genome of 12 amphisbaenian species and supported the new hypothesis that Rhineuridae is sister group of all other families, with Bipedidae as sister group of Trogonophidae and Amphisbaenidae. Furthermore, Vidal *et al.* (2008), analyzing 22 taxa mitochondrial mitochondrial and nuclear genes, also corroborated the hypothesis that Rhineuridae is the sister group of the remaining families. Additionally, these authors described a new family (Cadeidae) for the genus *Cadena*, from Cuba.

Although some studies discuss the phylogenetic relationships among Amphisbaenia families, there are few studies that detail the intra-generic and intra-specific relationships. Measey & Tolley (2013) analyzed the phylogenetic relationships within the African radiation of Amphisbaenidae and found the following three main clades: 1) composed by *Geocalamus*, *Dalophia* and *Monopeltis*, 2) composed by *Chirindia* and *Cynisca*, and 3) composed by *Zygaspis*. Furthermore, it was also notable that specimens of *Geocalamus acutus* from Kenya and Tanzania were recovered as highly divergent lineages. In summary, their results showed that the Sub-Saharan species are the sister clade of the South American radiation, and supported the hypothesis of a single origin for South American members. Although the phylogenetic relationships between

African species were well resolved, the phylogenetic tree presented low support for some clades, which probably was a consequence of the limited taxon sampling.

Mott & Vieites (2009) investigated the phylogenetic relationships within the South American species. In this study, representatives were included from each amphisbaenian family, except Cadeidae, and from each Neotropical genus except *Mesobaena*. The results of this study suggest that Neotropical species form a monophyletic group. However, *Amphisbaena*, *Bronia* and *Cercolophia* were recovered as non monophyletic. The exception was *Leposternon* that was monophyletic in their study, but was also positioned within *Amphisbaena*. Moreover, the monophyly of *Anops* was not tested, because only one species (*A. kingii*) was represented in the phylogeny. Considering these results, the authors suggested that the morphological characters that define the South American groups represent adaptive convergences, and that the Brazilian genera of Amphisbaenia should be considered, by nomenclatural priority, as belonging to a single genus *Amphisbaena*. Contrary to Mott and Vieites (2009), Ribeiro *et al.* (2011), described a South American species, and revalidated the genus *Leposternon*, stating that the taxonomic changes on the Neotropical amphisbaenids were precipitated due to the low bootstrap supports and little morphological evidences. Although plausible, Ribeiro *et al.* (2011) considered that the decision to synonymize the genus *Leposternon* to *Amphisbaena* needed more evidence.

Many of these studies attribute the difficulties to understand the origin and evolution of Amphisbaenia to convergence, i.e. homoplasy, of several morphological characters. Although these species are poorly studied, some of their adaptations to live underground are well known. Such adaptations include blindness, elongated body and reduction or absence of limbs. The absence of limbs is often understood as the results of the use of their heads to burrow through the soil (Gans, 1978). Although environmental features (e.g. microhabitats, temperature, etc.) are key

factors driving diversity and phenotypic diversification in many vertebrates (e.g. Stayton, 2003), in fossorial organisms these factors have been imposed by the burrowing lifestyle.

According to Gans (1974), the different morphological skull shapes in Amphisbaenia are correlated with the digging behavior, which is related to fossorial habits. Some taxa such as *Anops* and *Mesobaena* have a head with a characteristically keel-headed shape, in which the skull is dorsolaterally depressed. The *Leposternon* and *Rhineura* genera share the same head form called shovel-headed shape, with a flat nose and a sharp craniofacial angle. Another form found in Amphisbaenia is the spade-headed shape, present in Trogonophidae family, where the sharp craniofacial angle is achieved through a separate underlying arrangement of bones and overlapping scales on the head. Other species of Amphisbaenia exhibit a general round-headed shape, whereas the *Amphisbaena* and *Zygaspis* genera have a robust and rounded skull.

According Gans (1974, 1978), the head shapes are related to the distribution of Amphisbaenia. Gans (1978) suggests that the taxa which are shovel-headed shape from Africa, North America and South America, as well as those with a keel-headed shape from Africa and South America, could have evolved locally from taxa with the rounded generalized form (round-headed shape). Kearney (2003) using morphological data concluded that the Amphisbaenia with the keel-headed and shovel-headed shape form a monophyletic group, but these groups were considered tentative, given the possibility that this character is functionally correlated (Gans, 1974). However, Kearney & Stuart (2004) and Mott & Vieites (2009), based on their results, stated that the cranial morphotypes are a result of morphological convergence. Furthermore, Kearney & Stuart (2004) emphasized that the different forms of the head would be related to the geographic distribution of these taxa, as suggested by Gans (1978). Hoogmoed *et al.* (2009) described a new species of Amphisbaenia from South America, and suggested that the head shape of *Mesobaena*

rhachicephala does not fit to any of the categories suggested by Gans (1974). This result highlights the importance to study the forms of the head of Amphisbaenia, and also indicates that there is more variation within the suborder than the four morphotypes already described in previous studies.

Despite the advances made by previous studies, the taxonomy and phylogenetic relationships of amphisbaenids remains uncertain. Given the continuing inconsistencies between the morphological classification (e.g., Kearney, 2003) and molecular phylogenies (e.g., Kearney & Stuart, 2004; Mott & Vieites, 2009) of Amphisbaenia, the first chapter of my thesis aims to investigate and contribute to fill the knowledge gap about the systematics of this group. Therefore, I am providing a new phylogenetic and taxonomic proposal for Amphisbaenia and inferring the phylogenetic position of Amphisbaenia within Squamata. I am using a combination of different sets of evidence and phylogenetic approaches. These approaches comprise an exploration of two distinct methods for phylogenetic inference (concatenation and species tree) using Sanger (mitochondrial and nuclear genes) and Anchored Phylogenomics methods. Additionally, it was performed a total evidence analysis combining a morphological matrix with Anchored Phylogenomic data. I also performed species tree methods to overcome potential gene/species tree conflicts, using ASTRAL, MPEST and STAR. Based on the phylogenetic results, I am revising the classification of Amphisbaenia, with special attention to morphological diagnoses for particular clades. As a result, I am describing two new families in Africa, and two new subfamilies of Amphisbaenidae from the Neotropical region. Also, I am resurrecting one genus for Africa and one subfamily for South American, and I am providing a taxonomic discussion regarding the South American groups.

Additionally, to understand the diversity of cranial morphology in *Amphisbaenia*, I am answering three main questions in the second chapter of my thesis: 1) Are CSDG morphologically distinct? 2) Do CSDG differ considering soil use? 3) Is the general cranial shape variation related with type of soils? To answer these questions, I used high-resolution computed tomography (HRXCT), phylogenetic inference and landmark-based on Geometric Morphometrics methods. To achieve these objectives I applied the following steps: first, I tested the shape divergence between CSDG using principal components and phylomorphospace analysis; second, I checked morphological disparity between CSDG using disparity analysis; and third, I used geographic distribution of *Amphisbaenians* and geo-referenced soil maps to correlate CSDG and general cranial shape variation with type of soils using phylogenetic generalized least squares (GLS) ANOVA and Partial Least Squares (PLS) analysis. These analyses showed that there is two statically significant separated cranial shape based in CSDG: 1) composed by shovel-headed group, and 2) composed by keel-headed, round-headed and spade-headed groups. Furthermore, our results showed that extant *Amphisbaenians* form a multi-starburst pattern in cranial phylomorphospace, and there is criss-crossing of branches within major clades indicated a consistent with mostly homoplastic shape evolution. Also, we found a stronger correlation between general shape and type of soil, this result indicates that of cranial diversity in *Amphisbaenians* is associate with borrowing habits.

In addition to the two chapters of my thesis, I am also including in the appendix two manuscripts written in collaboration with other colleagues. Both manuscripts are descriptions of new *amphisbaenian* species, where we also highlight some taxonomic gaps about the South American diversity of *amphisbaenids*. The first manuscript, entitle: “A new four-pored *Amphisbaena* Linnaeus, 1758 (*Amphisbaenia*, *Amphisbaenidae*) from Brazilian Amazon”, was

already accepted in Zootaxa, and the second, entitle: “A New Species of the *Amphisbaena* (Squamata, Amphisbaenidae) from the Brazilian Cerrado with a Key for the Two-Pored Species”, was already submitted to Zootaxa.

CONCLUSION

For more than a century, the phylogenetic position in Squamata diversity, taxonomic status and phylogenetic relationships among genera and species of Amphisbaenians remains uncertain. Within the vertebrate radiation, organisms with underground lifestyle are difficult to observe, and many aspects of their evolutionary biology remain poorly understood. The cryptic nature of fossorial organisms results in a clear underestimation of their diversity. Traditionally, many studies attribute the difficulties to understanding the phylogenetic relationships and affinities of Amphisbaenia to convergence, i.e. homoplasy, of several morphological characters.

The phylogenetic study, based in morphological and molecular datasets showed that there are a high diversity of families and genera for Amphisbaenians. As a result of this thesis, I described two new families in Africa, and two new subfamilies of Amphisbaenidae from the Neotropical region. Also, I resurrected one genus for Africa and one subfamily for South American, and I provided a taxonomic discussion regarding the South American groups.

Despite is known that cranial shapes are considered as homoplastic, many taxonomic studies still using this morphological character to define groups. Some studies tried to correlate the cranial variation with geography or phylogeny (Kearney, 2003; Mott & Vieites, 2009; Measey & Tolley, 2013). The present study suggested that these groups defined by cranial variation do not reflect the biogeographical distribution neither the phylogenetic relationship. Frequently, studies attribute morphological convergences to adaptations (Harvey & Pagel, 1991), and many homoplastic characters may be associated with ecological and environmental variables instead of phylogenetic relationships. The comparative methods analysis of this thesis also showed a stronger correlation of shape and soil types. However, to completely understand the evolutionary mechanisms that promote the cranial diversity, the results presented here need to be integrated and

correlated with other refined ecological information from the soil types (e.g. temperature, humidity, texture, etc.) to test the adaptive factors that specifically constrained the evolution of skull shapes.

Although this thesis showed the most complete taxon sampling, several information about morphological diversity, phylogenetic relationships among species and new taxonomic rearrangements, the diversity of many families remains uncertain. As an example, there are many species that are just know by type series (e.g. *Baikia africana*). Also, some species has a restrict distribution, and occurring in areas of difficult access (e. g. *Mesobaena huebneri*, occurs in an isolate area of Amazon forest). Fortunately, phylogenetic and taxonomic studies will become increasingly workability for Amphisbaenians and a comprehensive understanding of evolutionary and diversification processes are in progress.

REFERENCES

- Adams, D.C. & Felice, R. 2014. Assessing phylogenetic morphological integration and trait covariation in morphometric data using evolutionary covariance matrices. *Plos One*, 9 (4): e94335
- Adams, D.C., Collyer, M.L., Kaliontzopoulou, A., Sherratt, E. 2017. Geomorph: Software for geometric morphometric analyses. R package version 3.0.4. Available at <http://cran.r-project.org/web/packages/geomorph/index.html>.
- Albert, E.M., Zardoya, R., García-París, M. 2007. Phylogeographical and speciation patterns in subterranean worm lizards of the genus *Blanus* (Amphisbaenia: Blanidae). *Molecular Ecology*, 16 (7): 1519-1531.
- Albert, E.V. & Fernández, A. 2009. Evidence of cryptic speciation in a fossorial reptile: description of a new species of *Blanus* (Squamata: Amphisbaenia: Blanidae) from the Iberian Peninsula. *Zootaxa*, 2234: 56- 68.
- Baird, S.F. 1858. Description of new genera and species of North American lizards in the museum of the Smithsonian Institution. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1858: 253- 256. [p. 255; *Lepidosternon floridanum*]
- Bates, M., Branch, W., Bauer, A.M., Burger, M., Marais, J., Alexander, G., Villiers, M.S. 2014. Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. Edition Suricata, Publisher South Africa National Biodiversity Institute (SANBI).
- Bell, T. 1827. Description of a new species of *Anolius*, and a new species of Amphisbaena; collected by W.S. MacLeay, Esq. in the Island of Cuba. *Journal of Zoology (London)* 3 (10, art. 26): 235- 236. [fig. 2]

- Bivand, R. & Lewin-Koh, N. 2017. mapproj: tools for reading and handling spatial objects. R package version 0.8-25. Available at: <http://CRAN.R-project.org/package=mapproj>.
- Bivand, R., Keitt, T. & Rowlingson, B. 2017. rgeos: bindings for the geospatial data abstraction library. R package version 0.8-10. Available at: <http://CRAN.R-project.org/package=rgeos>.
- Bivand, R., Rundel, C., 2017. rgeos: Interface to Geometry Engine – Open Source (GEOS). R Package Version 0.3-26. Available at: <http://CRAN.R-project.org/package=rgeos>.
- Bonnaterre, l’A.J.P. 1789. Tableau encyclopédique et méthodique des trois règnes de la nature. Erpétologie. Paris: Panckoucke. [p. 68; *Bipes canaliculatus*, see Vanzolini 1977: 8]
- Bookstein, F. L. 1996. Biometrics, biomathematics and the morphometric synthesis. Bulletin of Mathematical Biology, 58 (2), 313- 365.
- Boulenger, G.A. 1885. Catalogue of the lizards in the British Museum (Natural History). Vol. 2, Second edition. London, xiii+497 pp.
- Boulenger, G.A. 1907c. Second report on the reptiles and batrachians collected in South Africa by Mr. C.H.B. Grant, and presented to the British Museum by Mr. C.D. Rudd. Proceedings of the Zoological Society of London, 1907: 478- 487. [p. 485; *Monopeltis granti*]
- Branch, W.R., Rödel, M.O., Marais, J. 2003. Herpetological survey of the Niassa Game Reserve, northern Mozambique - Part I: Reptiles. Salamandra, 41 (4): 195-214.
- Broadley, D. G., Gans, C & Visser, J. 1976. Studies on amphisbaenians (Amphisbaenia, Reptilia). 6. The genera *Monopeltis* and *Dalophia* in southern Africa. Bulletin of the American Museum of Natural History, 157 (5): 313- 485.

- Colli, G.R., Fenker, J., Tedesco, L.G., Barreto-Lima, A., Mott, T., Ribeiro, S.L.B. 2016. In the depths of obscurity: Knowledge gaps and extinction risk of Brazilian worm lizards (Squamata, Amphisbaenidae). *Biological Conservation*, 204: 51- 62.
- Conrad, J.C. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History*, 310, 182 pp.
- Cope, E.D. 1861. Some remarks defining the following species of Reptilia Squamata. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 13: 75-77.
- Cuvier, G. 1829. *Le règne animal, distribué d'après son organisation, nouv. ed.* Paris: Deterville. [p. 73]
- Duméril, A.M.C. & Bibron, G. 1839. *Erpétologie générale ou Histoire naturelle complète des reptiles. Errata. De l'ordre des Lézards ou des Sauriens.* Ed. Roret. Paris. 5: i- viii 1 1 + 1- 856. [*Amphisbaena leucura*, *A. macrural*, *Lepidosternon phocaena*; pp. 484–485, pl. viii].
- Edmund, A.G. 1969. Dentition. In Gans, C. A., Bellairs, A. d'A and Parsons T.S. (editors), *Biology of the Reptilia* 1 (4): 117- 200. London: Academic Press. [pp. 171- 172]
- Estes, R., Queiroz, K. & Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: Estes, R. & Pregill, G.K. (Eds.). *Phylogenetic relationships of the lizard families: Essays commemorating Charles L. Camp.* Stanford University, Stanford, pp. 119- 281.
- Evans, S.E. & Barbadillo, L.J. 1998. An unusual lizard (Reptilia: Squamata) from the Early Cretaceous of Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, 124: 235-265.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39: 783- 791.
- Fitzinger, L.J.F.J. 1843. *Systema reptilium. Fasciculus primus Amblyglossae.* Vienna: Baumüller and Seidel. [p. 22]

- Futuyma, D.J. 1986. *Evolutionary Biology*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
- Futuyma, D.J. 1998. *Evolutionary Biology*. 3rd ed. Sinauer Associates, Sunderland, Massachusetts. (dated 1998, published 1997)
- Gans, C. & Alexander, A. A. 1962. Studies on the amphisbaenids (Amphisbaenia; Reptilia). 2. On the amphisbaenids of the Antilles. *Bulletin of the Museum of Comparative Zoology*, 128 (3): 65- 158.
- Gans, C. & Kraklau, D. M. 1989. Studies on amphisbaenians (Reptilia) 8. Two genera of small species from East Africa (*Geocalamus* and *Loveridgea*). *American Museum Novitates* 2944: 1- 28. [all; *Geocalamus acutus*, *G. modestus*, *Loveridgea ionidesii*, *L. phylofiniens*]
- Gans, C. & Lehman, G. C. 1973. Studies on amphisbaenians (Amphisbaenia: Reptilia. 5. The species of *Monopeltis* from north of the river Zaire. *Occasional Papers, Museum of Zoology, University of Michigan*, 669: 1- 34. [all; *Monopeltis galeata*, *M. guentheri*, *M. jugularis*, *M. schoutedeni*]
- Gans, C. & Montero, R. 2008. An Atlas of Amphisbaenian Skull Anatomy. In: Gans, C., Gaunt A. S. & Adler, K. (Eds.), *Biology of Reptilia*. Vol 21. The Skull and Appendicular Locomotor Apparatus of Lepidosauria. Society for the Study of Amphibians and Reptiles, Ithaca, New York, pp. 621- 738.
- Gans, C. 1960. Studies on amphisbaenids (Amphisbaenia: Reptilia). 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bulletin of the American Museum of Natural History*, 119 (3): 129- 204. [all; *Agamodon anguliceps*, *A. arabicus*, *A. compressus*, *Diplometopon zarudnyi*, *Pachycalamus brevis*, *Rhineura floridana*, *Trogonophis wiegmanni*]

- Gans, C. 1974. *Biomechanics: An Approach to Vertebrate Biology*. J.B. Lippincott Company, Philadelphia, 261pp.
- Gans, C. 1978. The characteristics and affinities of the Amphisbaenia. *Transactions of the Zoological Society of London*, 34: 347- 416.
- Gans, C. 1987. Studies on amphisbaenians (Reptilia). 7. The small round-headed species (*Cynisca*) from western Africa. *American Museum Novitates*, 2896: 1- 84.
- Gans, C. 1990. Patterns in amphisbaenian biogeography: a preliminary analysis. In: Peters, G. & Hutterer, R. (Eds.). *Vertebrate in the tropics: Proceedings of the International Symposium of Vertebrate Biogeography and Systematics in the tropics*. Alexander Zoological Research Institute and Zoological Museum, Bonn, pp. 133- 143.
- Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behlke, A.D.B. 2012. Assembling the Squamate tree of life: Perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History*, 5 (1): 3-308.
- Goloboff, P.A, Farris, J., Nixon, K. (2008). T.N.T, a free program for phylogenetics analysis. *Cladistics*, 24: 774-786.
- Goloboff, P.A. & Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32 (3): 221-238.
- Gray, J.E. 1844. Catalogue of the tortoises, crocodiles, and amphisbaenians in the collection of the British Museum. *British Museum of Natural History (London) 1844*: 80 pp. [p. vi, vii, viii, 2, 68- 74]
- Gray, J.E. 1865. A revision of the genera and species of amphisbaenians with the descriptions of some new species now in the collection of the British Museum. *Proceedings of the Zoological Society of London*, 1865: 442- 455.

- Greer, A. 1985. The relationships of the lizard genera *Anelytropsis* and *Dibamus*. *Journal of Herpetology*, 19: 116- 156.
- Grismer, 2002. *Amphibians and Reptiles of Baja California, Including Its Pacific Islands and the Islands in the Sea of Cortés*. University of California. 413pp.
- Günther, C.A.L.G. 1880. Description of new species of reptiles from eastern Africa. *Annals and Magazine of Natural History*, ser. 5, 6 (33): 234- 238. [p. 234]
- Günther, C.A.L.G. 1881. Description of the amphisbaenians and ophidians collected by Prof. I. Bayley Balfour in the island of Socotra. *Proceedings of the Zoological Society of London* 1881: 461- 462. [pp. 461- 462]
- Gunz, P., Mitteroecker, P., Neubauer, S., Webber, G.W., Bookstein, F.L, 2009. Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57 (1): 48-62.
- Hallermann, J. 1998. The ethmoidal region of *Dibamus taylori* (Squamata: Dibamidae), with a phylogenetic hypothesis of dibamid relationships within Squamata. *Zoological Journal of the Linnean Society*, 122: 385- 426.
- Hallowell, E. 1852. Description of new species of Reptilia from western Africa. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 64: 62- 65. [pp. 62- 63; *Phractogonus galeatus*].
- Hijmans, R.J. *et al.*, 2016. Raster: Geographic Data Analysis and Modeling. R package version 2.5-8. Available at: <http://cran.rproject.org/web/packages/raster>
- Hipsley, C. A & Müller, J. 2017. Developmental dynamics of ecomorphological convergence in a transcontinental lizard radiation. *Evolution*, 71 (4): 936- 948.

- Hoogmoed, M., Pinto, R.R., Rocha, W.A., Pereira, E.G. 2009. A new species of *Mesobaena metens*, 1925 (Squamata: Amphisbaenidae) from Brazilian Guiana, with a key to the Amphisbaenidae of the Guianan region. *Herpetologica*, 65 (4): 436.
- Katoh, S. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. (outlines version 7). *Molecular Biology and Evolution*, 30, 772-780.
- Kaup, J.J. 1830. *Trogonophis*. Eine neue Amphibiengattung, den Amphisbaenen zunächst verwandt. *ISIS von Oken* 23: columns 880- 881. [pl. 8, figs. a and t].
- Kearney, M. & Stuart, B.L. 2004. Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones. *Proceedings of the Royal Society of London B*, 271: 1677- 1683.
- Kearney, M. 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. *Herpetological Monographs*, 17: 1-74.
- Kearse, M.; Moir, R.; Wilson, A.; Stones-Havas, S.; Cheung, M.; Sturrock, S.; Buxton, S.; Cooper, A.; Markowitz, S.; Duran, C.; Thierer, T.; Ashton, B.; Mentjies, P.; Drummond, A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28 (12), 1647-1649.
- Lakjer, T. 1927. Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Sauropsiden. *Zoologisches Jahrbuch, Abteilung für Anatomie und Ontogenie der Thiere* 49: 57- 356. [pp. 158- 172, 231- 232, 234- 235, 237, 239- 240, 255- 256, 259- 260, 264- 266, 268, 271- 272, 274, 326; figs. 54- 57, 59- 60, 97, 129, 264- 266, 268, 271-

272, 274; *Amphisbaena alba*, *A. fuliginosa*, *A. vermicularis*, *Lepidosternon microcephalum*, *L. scutigerum*, *Trogonophis wieganni*]

- Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., Calcott, B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular biology and evolution*, 34 (3): 772- 773.
- Lanza, B. 1990. Amphibians and reptiles of the Somali Democratic Republic: check list and biogeography. *Biogeographia*, 14: 407-465.
- Latreille, P.A. 1802. Serpents. In C.S. Sonnini and P.A. Latreille (editors), *Histoire naturelle des reptiles*, vol. 2. Paris. [pp. 235, 332]
- Lee, M.S.Y. & Caldwell, M.W. 2000. Adriosaurus and the affinities of mosasaurs, dolichosaurs, and snakes. *Journal of Paleontology*, 74: 915- 937.
- Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biological Journal of the Linnean Society*, 65: 369-453.
- Lemmon, A.R., Emme, S.A., Lemmon, E.M. 2012. Anchored hybrid enrichment for massively high-throughput phylogenomics. *Systematic Biology*, 61 (5): 727- 44.
- Lewis, P.O. 2001. A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. *Systematic Biology*, 50 (6): 913- 925.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classe, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* Tomus I. Editio decima, reformata, Salvii, L., Holmiæ, 824 pp.
- Liu, L & Edwards, S. 2010. A maximum pseudo-likelihood approach for estimating species trees under the coalescent model. *BMC Evolutionary Biology*, 10: 302.

- Liu, L., Yu, L., Pearl, D.K., Edwards, S.V. 2009. Estimating Species Phylogenies Using Coalescence Times among Sequences. *Systematic Biology*, 58 (5): 468- 477.
- Losos, J.B. & Mahler, D.L. 2011. Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation, in: Bell, M., Futuyma, D., Eanes, W., Levinton, J. (Eds.), *Evolution since Darwin: the first 150 years*. Sinauer, Sunderland, pp. 381-420.
- Macey, J.R., Papenfuss, T.J., Kuehla, J.V., Fourcadea, H.M. & Boorea, J.L. 2004. Phylogenetic relationships among amphisbaenian reptiles based on complete mitochondrial genomic sequences. *Molecular Phylogenetics and Evolution*, 33: 22- 31.
- Machado, D.J. 2015. YBYRÁ facilitates comparison of large phylogenetic trees. *BMC Bioinformatics*, 16: 204. Available at: <https://gitlab.com/MachadoDJ/ybyra>.
- Maddison W.P. 1991. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. *Systematic Zoology*, 40: 304- 314
- Maisano, J.A., Kearney, M. & Rowe, T. 2006 Cranial anatomy of the spade-headed amphisbaenian *Diplometopon zarudnyi* (Squamata, Amphisbaenia) based on high-resolution X-ray computed tomography. *Journal of Morphology*, 267, 70- 102.
- Mané, Y. & Trape, J.F. 2015. Note sur une collection d'amphisbènes (Squamata, Amphisbaenidae) d'Afrique occidentale. *Bulletin de la Société Herpétologique de France*, 154, p. 35-60
- Marcy, A.E., Hadley, E.A., Sherratt, E., Garland, K., Weisbecker, V. 2016. Getting a head in hard soils: Convergent skull evolution and divergent allometric patterns explain shape variation in a highly diverse genus of pocket gophers (*Thomomys*). *BMC Evolutionary Biology*, 16 (1): 207

- Martín, J., Polo-Cavia, N., Gonzalo, A., López, P., Civantos, E. 2011. Structure of a Population of the Amphisbaenian *Trogonophis wiegmanni* in North Africa. *Herpetologica* 67 (3): 250-257.
- Martins, E. P. 1999. Estimation of ancestral states of continuous characters: a computer simulation study. *Systematic Biology*, 48:642-650.
- Measey, J. & Tolley, K.A. 2013. A molecular phylogeny for sub-Saharan amphisbaenians. *African Journal of Herpetology*, 62 (2): 100- 108.
- Meyer, M. & Kircher, M. 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harbor Protocols*.
- Mirarab, S. & Warnow, T. 2015. ASTRAL-II: coalescent-based species tree estimation with many hundreds of taxa and thousands of genes. *Bioinformatics*, 31: i44- i52.
- Montero, R. & Gans, C. 1999. The head skeleton of *Amphisbaena alba* Linneaus. *Annals-Carnegie Museum Pittsburgh*, 68: 15- 79.
- Montero, R. 2016. On the Validity of Several Argentinian Species of *Amphisbaena* (Squamata, Amphisbaenidae). *Journal of Herpetology*, 50 (4): 642- 653.
- Mott, T. & Vieites, D.R. 2009. Molecular phylogenetics reveals extreme morphological homoplasy in Brazilian worm lizards challenging current taxonomy. *Molecular Phylogenetics and Evolution*, 51: 190- 200.
- Müller, J., Hipsley, C. A., Head, J., Kardjilov, N., Hilger, A., Wuttke, M., Reisz, R. R. 2011. Eocene lizard from Germany reveals amphisbaenian origins. *Nature*, 473: 364- 367.
- Noonan, B.P. & Chippindale, P.T. 2006. Dispersal and vicariance: The complex evolutionary history of boid snakes complex. *Molecular Phylogenetics and Evolution*, 40: 347- 358.

- Oelrich, T.M. (1956) The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Miscellaneous Publication of the Museum of Zoology University of Michigan, 94, 1122.
- Papenfuss, T.J. 1982. The ecology and systematics of the amphisbaenian genus *Bipes*. Occasional Papers of the California Academy of Science, ser. 4, 136: 1- 42. [all; *Bipes biporus*, *B. canaliculatus*, *B. tridactylus*]
- Parker, H.W. 1942. The lizards of British Somaliland. Bulletin of the Museum of Comparative Zoology Harvard, 91 (1): 1- 101. [pp. 56- 59; *Amphisbaena knighti*]
- Pebesma, E. & Bivand, R. 2017. S Classes and Methods for Spatial Data: the sp Package. Vignette in R package sp, R package 1.2-5. Available at: <https://cran.r-project.org/web/packages/sp/>.
- Peters, W.C.H. 1880. Über neue oder weniger bekannte Amphibien des Berliner Zoologischen Museums. (*Elapomorphus erythronotus*, *Hylomantis fallax*, *Leptocalamus drilineatus*, *Monopeltis (Phractogonus) jugularis*, *Xenodon punctatus*.) Monatsberichte der Berliner Akademie der Wissenschaften 1880: 217- 224. [pp. 219- 220, pl.]
- Peters, W.C.H. 1882. Über eine neue Art und Gattung der Amphisbaenoiden, *Agamodon anguliceps*, mit eingewachsenen Zähnen, aus Barava (Ostafrika) und über die zu den Trogonophides gehörigen Gattungen. Sitzungsber. Königl. Preuss. Akad. Wiss. (Berlin) 1882 (26): 579-584
- Pook, C.E., Wüster, W., Thorpe, R.S. 2000. Historical biogeography of the western rattlesnake (Serpentes: Viperidae: *Crotalus viridis*), inferred from mitochondrial DNA sequence information. Molecular Phylogenetics and Evolution, 15: 269-282.

- Price, S.A., Holzman, R., Near, T.J., Wainwright, P.C. 2011. Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecology Letters*, 14, 462-469.
- Pyron, R.A. 2017. Novel Approaches for Phylogenetic Inference from Morphological Data and Total-Evidence Dating in Squamate Reptiles (Lizards, Snakes, and Amphisbaenians). *Systematic Biology*, 66 (1): 28- 56.
- Pyron, R.A., Burbrink, F.T. 2012. Extinction, ecological opportunity, and the origins of a global snake diversity. *Evolution* 66, 163-178.
- Rage, J.C. 1982. La phylogenie des Lepidosauriens (Reptilia): une approche cladistique. *Comptes Rendus de l'Academie des Sciences Paris*, 284: 1765-1768.
- Rambaut, A.; Drummond, A.J. (2007). Tracer v 1.4. Available at: <http://beast.bio.ed.ac.uk/Tracer>.
- Razzetti, E., Sindaco, R., Grieco, C., Pella, F., Ziliani, U., Pupin, F. Riservato, E., Pellitteri-Rosa, D., Butikofer, L., Suleiman, A.S., Al-Aseily, B., Carugati, C., Boncompagni, E., Fasola, M. 2011. Annotated checklist and distribution of the Socotran Archipelago Herpetofauna (Reptilia). *Zootaxa*, 2826: 1- 44.
- Reeder, T.W., Townsend, T.M., Mulcahy, D.G., Noonan, B., Wood Jr., Perry, Sites, J.W., Wiens, J.J. 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. *Plos One*, 10(3): e0118199
- Ribeiro, S., Nogueira, C., Cintra, C.E.D., Jr Silva, N.J., Zaher, H. 2011. Description of a new pored *Leposternon* (squamata, Amphisbaenidae) from The Brazilian Cerrado. *South American Journal of Herpetology*. 6(3): 177-188.

- Rieppel, O. & Zaher, H. 2000. The intramandibular joint in squamates and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. *Fieldiana (Geology)*, New Series, 43: 1- 69.
- Rieppel, O. 1981. The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *Journal of Zoology (London)*, 195: 493- 528. [pp. 495, 523- 525]
- Rohlf, F. J. e Slice, D. 2001. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology*, 39 (1): 20- 59.
- Rokyta D.R., Lemmon A.R., Margres M.J. & K. Aronow 2012. The venom-gland transcriptome of the eastern diamondback rattlesnake (*Crotalus adamanteus*). *BMC Genomics*, 13: 312.
- Romer, A.S. 1956. *Osteology of the reptiles*. Chicago: University of Chicago Press. [pp. 119, 121- 124, 229, 245, 255, 270- 271, 285, 311, 340, 412, 417, 438, 443, 563- 565]
- Ruane, S, Torres-Carvajal, O., Burbrink, F.T. 2015. Independent Demographic Responses to Climate Change among Temperate and Tropical Milksnakes (Colubridae: Genus *Lampropeltis*). *Plos One*, 10 (6): e0128543
- Sakamoto, M. & Ruta, M. 2012. Convergence and divergence in the evolution of cat skulls: Temporal and spatial patterns of morphological diversity. *Plos One*, 7 (7): e39752.
- Schettino, L.R., Mancina, C.A., González, V.R. 2013. Reptiles of Cuba: Checklist and Geographic distribution. *Smithsonian Herpetological Information Service*, 144: 1- 96.
- Schwartz, A., and R.W. Henderson. 1991. *Amphibians and reptiles of the West Indies: descriptions, distributions and natural history*. Gainesville: University of Florida Press. [pp. 555- 564; *Amphisbaena caeca*, *A. caudalis*, *A. cubana*, *A. fenestrata*, *A. gonavensis*, *A. innocens*, *A. manni*, *A. schmidtii*, *A. xera*, *Cadea blanooides*, *C. palirostrata*]

- Schwenk, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. Pp. 569- 598. In R. Estes and G. Pregill (Eds.), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford University Press, Stanford, California.
- Sherratt, E.**, Gower, D.J., Klingenberg, C.P., Wilkinson, M. 2014. Evolution of cranial shape in caecilians (Amphibia: Gymnophiona). *Evolutionary Biology*, 41 (4): 528-545.
- Sidlauskas, B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: A phylomorphospace approach. *Evolution*, 62 (12), 3135- 3156.
- Sindaco, R., Kornilios, P., Sacchi, R., Lymberakis, P. 2014. Taxonomic reassessment of *Blanus trauchi* (Bedriaga, 1884) (Squamata: Amphisbaenia: Blanidae), with the description of a new species from south-east Anatolia (Turkey). *Zootaxa*, 3795 (3): 311- 326.
- Sindaco, R. & Jeremcenko, V.K. 2008. *The reptiles of the Western Palearctic*. Edizioni Belvedere, Latina (Italy), 579 pp.
- Smith, A. 1848. *Illustrations of the zoology of South Africa*. London, 1838- 1849. [pl. 67; see Kirby, 1965; Waterhouse, 1880].
- Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22: 2688-2690.
- Stamatakis, A., 2014. RAxML-Version 8: A tool for Phylogenetic Analysis and Post- Analysis of Large phylogenies. *Bioinformatics*, 9: 1312- 1313.
- Stayton, C. T. 2003. Functional and morphological evolution of herbivory in lizards. *Integrative and Comparative Biology*, 43(6), 913.
- Streicher, J.W. & Wiens, J.J. 2017. Phylogenomics analysis of more than 4000 nuclear loci resolve the origin of snakes among lizards. *Biology Letters*, 12: 20170393.

- Taylor, 1951. Concerning Oligocene amphisbaenid reptiles. University of Kansas Science Bulletin, 34: 521- 579.
- Thomas, R. & Hedges, S.B. 2006. Two new species of *Amphisbaena* (Reptilia: Squamata: Amphisbaenidae) from the Tiburon Peninsula of Haiti. Caribbean Journal of Science, 42 (2), 208- 219.
- Townsend, T.M., Larson, A., Louis, E., 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.
- Uetz, P., Goll, J., Hallerman, J. (2017). The TIGR Reptile Database. Available at: <http://www.reptile-database.org>.
- Vandelli, D. 1797. Florae, et Faunae Lusitanicae Specimen. Memorias de la Academia Real de Ciencias (Lisboa) 1: 37- 79. [pp. 69- 70]
- Vanzolini, P.E. 1951a. Evolution, adaptation and distribution of the amphisbaenid lizards (Sauria: Amphisbaenidae). Thesis, Harvard University.
- Vanzolini, P.E. 1951b. A systematic arrangement of the family Amphisbaenidae (Sauria). Herpetologica, 7: 113- 123.
- Vidal, N. & Hedges, S.B. 2005. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. Comptes Rendus Biologies, 328: 1000- 1008.
- Vidal, N., Azvolinsky, A., Cruaud, C. & Hedges, S.H. 2008. Origin of tropical American burrowing reptiles by transatlantic rafting. Biology Letters, 4: 115-118.

- Wagler, J. 1824. *Serpentum Brasiliensium species novae, ou histoire naturelle des espèces nouvelles de Serpens*. In: Spix, J. *Animalia nova sive species novae*. Typis Francisci Seraphi Hübschmann, Monaco, pp. 1- 7.
- Wagler, J.G. 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vōgel*. Munich: J.G. Cotta. [pp. 196- 197; *Amphisbaena, Blanus, Chirotes, Lepidosternon*]
- Webster, A.J. & Purvis, A. 2002. Testing the accuracy of methods for reconstructing ancestral states of continuous characters. *Proceedings of the Royal Society B*, 269 (1487): 143- 149.
- Wiens, J.J., Hutter, C.R., Mulcahy, D.G., Noonan, B.P., Townsend, T.M, Sites Jr., J.W., Reeder, T.W. 2012. Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. *Biology Letters*, 8 (6): 1043-1046.
- Wiens, J.J., Kuczynski, C.A., Townsend, T., Reeder, T. W., Mulcahy, D. G., Sites Jr, J. W. (2010). Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. *Systematic Biology*, 59: 674- 688.
- Wiley, D. F., Amenta, N., Alcantara, D. A., Ghosh, D., Kil, Y. J., Delson, E., et al. 2007. *Landmark Editor version 3.6*: Institute for analysis and visualization.
- Witte, G.F. & Laurent, R.F. 1942. Contribution à la systématique des Amphibaenidae du Congo Belge. *Revue Zoologique et Botanique Africaine* 36(1): 67- 86. [all]
- Witte, G.F. 1922. Description de reptiles nouveaux du Congo Belge. *Revue Zoologique Africaine* 10: 66- 71. [pp. 66- 69; *Monopeltis lujae, M. truncata, M. vanderysti*]
- Witte, G.F. 1933a. Reptiles récoltés au Congo Belge par le Dr. Schouteden et par M. G.-F. de Witte. *Annales de le Museum Congo Belge, Série. Zoologie*, 1, 3(2): 53- 100. [pp. 72- 73; *Amphisbaena quadrifrons, Monopeltis guentheri, M. schoutedeni*]

Wu, X.C., Brinkman, D.B., Russell, A.P. 1996. *Sineoamphisbaena hexatabularis*, an amphisbaenian (Diapsida: Squamata) from the Upper Cretaceous red beds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. Canadian Journal of Earth Sciences, 33: 541- 577.

Zangerl, R. 1944. Contributions to the osteology of the skull of the Amphisbaenidae. American Midland Naturalist 31(2): 417- 454. [all; *Amphisbaena cubana*, *A. fuliginosa*, *Bipes biporus*, *Chirindia ewerbecki*, *Geocalamus acutus*, *Leposternon microcephalum*, *Monopeltis capensis*, *Rhineura floridana*, *Trogonophis wiegmanni*]

Zelditch, M.L., D.L. Swidersky, H.D. Sheets, and W.L. Fink. 2012. Geometric morphometrics for biologists: a primer. Elsevier Academic Press, New York.