Comments on the Dentition of the Teiid *Dicrodon* Duméril and Bibron, 1839

Author(s): Santiago Brizuela, Ralf Kosma
Source: South American Journal of Herpetology, 12(3):200-204.
Published By: Brazilian Society of Herpetology
https://doi.org/10.2994/SAJH-D-16-00032.1
URL: http://www.bioone.org/doi/full/10.2994/SAJH-D-16-00032.1

South American Journal of Herpetology, 12(3), 2017, 200–204

Comments on the Dentition of the Teiid *Dicrodon* Duméril and Bibron, 1839

Santiago Brizuela[1,*], Ralf Kosma[2]

1 *Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Departamento de Biología Facultad de Ciencias Exactas y Naturales, Mar del Plata, Argentina. Funes 3250, B7602AYJ Mar del Plata, Argentina.*
2 *Staatliches Naturhistorisches Museum, Niedersächsische Landesmuseen Braunschweig, Abteilung für Paläontologie, Gaußstraße 22, D-38106 Braunschweig, Germany.*
* *Corresponding author. Email: brizuela@mdp.edu.ar*

Abstract. The teiid genera *Dicrodon* and *Teius* possess transverse bicuspid posterior teeth on the dentaries and maxillae. In general, their dentition is considered to be comparable, and little attention has been given to their dental morphology. Here the dentition of *Dicrodon* is described in detail and compared to that of *Teius*. The dentition of *Dicrodon* differs from that of *Teius* in the following characters: both cusps are more concentrically placed (in occlusal view); the lingual cusp is developed on a crescent ridge; the crescent ridge may present mesial and distal protuberances; the lingual cusp is shorter (never as tall) as the labial cusp; and the intercuspid ridge is incomplete (missing in the lingual cusp). These characters allow the dental diagnosis of both genera.

Keywords. Bicuspid; Lizard; Squamata; Teeth; Teiidae; Transverse.

Resumen. Los géneros de la familia Teiidae *Dicrodon* y *Teius* poseen dientes transversalmente bicuspidados tanto en sus dentarios como en sus maxilares. Poca atención ha recibido la morfología dental de estos géneros, y sus denticiones son consideradas en general como comparables. En esta contribución se describe en detalle la dentición de *Dicrodon* y se la compara con la de *Teius*. La dentición de *Dicrodon* difiere de la de *Teius* en los siguientes caracteres: ambas cúspides se encuentra en una posición más concéntrica sobre la base (en vista oclusal); la cúspide lingual se desarrolla sobre un cresta con forma de medialuna; la cresta puede presentar protuberancias mesiales y distales a la cúspide; la cúspide lingual es más baja (nunca tan alta) que la labial; y, la cresta intercuspidal es incompleta (ausente sobre la cúspide lingual). Estas características permiten la diagnosis dental de ambos géneros.

INTRODUCTION

The tooth morphology of both extant and extinct lizards is of great interest for paleoherpetology because one of the most abundant elements of their fossil record are tooth bearing elements (maxillae and mostly dentaries). Extant lizards present important diversity in tooth morphology (e.g., Edmund, 1969; Kosma, 2004), of which we will focus on that of the teiid *Dicrodon* Duméril and Bibron, 1839, represented by the species *D. guttulatum* Duméril and Bibron, 1839. The tooth morphology is described, discussed and compared in particular with that of another teiid genus, *Teius* Merrem, 1820. *Dicrodon* and *Teius* are characterized, among other things, by a particular subpleurodont implantation and heterodonty (e.g., Nydam et al., 2007). The latter stands out by the possession of transverse bicuspid (with labial and lingual cusps) posterior marginal teeth (MacLean, 1974; Presch, 1974). This transverse bicuspid dentition is very distinct among teiids and lizards in general, although a superficially comparable dentition is present in the extinct Polyglyphanodontini Nydam et al., 2007 (*Polyglyphanodon* Gilmore, 1940, *Peneteius* Estes, 1969, and *Dicothodon* Nydam, 1999; Nydam et al., 2007). The other teiids are all more or less heterodont; there are forms with the more common mesiodistally tricuspid teeth as *Ameiva* Meyer, 1795, *Kentropyx* Spix, 1824, *Cnemidophorus* Wagler, 1830, and *Crocodilurus* Spix, 1824 (Presch, 1974), while others like *Tupinambis* Daudin, 1802 present large molariform posterior teeth (Presch, 1974; Dessem, 1985; Brizuela and Albino, 2010). *Dracaena* Daudin, 1802 is particularly remarkable presenting extraordinarily enlarged posterior teeth (Presch, 1974), as does its extinct sister genus *Paradracaena* Sullivan and Estes, 1997.

MATERIALS AND METHODS

Specimens from the following institutional collections were studied under a stereomicroscope: AMNH, American Museum of Natural History, USA; BMNH, British Museum of Natural History, UK; IFSZ, Internationales Forschungszentrum für systematische Zoologie der Humboldt-Universität, Germany; QCAZR, Museo de Zoología, Escuela de Biología, Pontificia Universidad Católica del Ecuador, sección Reptiles, Ecuador; SDS, San Diego Natural History Museum, USA; UNMdP-O, Colección Herpetológica, sección Osteología, Universidad Nacional de Mar del Plata, Argentina; UNNE, Universidad Nacional del Nordeste, Resistencia y Corrientes, Argentina; USNM, United States National Museum (Smithsonian Institution), USA; ZFMK, Zoologisches Forschungsinstitut und

Submitted: 15 July 2016
Accepted: 04 July 2017
Handling Editor: Taran Grant
doi: 10.2994/SAJH-D-16-00032.1

Museum Alexander Koenig, Germany. Standard digital camera and scanning electron microscope (Laboratorio de Microscopia de la Universidad Nacional de Mar del Plata) were used to figure most important dental characters. Dental terminology follows that of Edmund (1969) and suggestions of Smith and Dodson (2003), and when necessary reference to the terminology of Richter (1994) is also made. Roman numerals are used to identify absolute tooth positions. There is disagreement (see Zaher and Rieppel, 1999 and Caldwell et al., 2003) regarding tooth implantation at the histological level. Here, implantation is described at a gross morphology level following Presch (1974).

The systematics of Teiidae Gray, 1827 has been recently modified, with new genera proposed and others resurrected (Harvey et al., 2012; Goicoechea et al., 2016). These studies are not osteologically based and many taxa are not supported by osteological and/or dental characters. Considering the latter and the intended goal of this contribution (which is an aid for paleoherpetology) we follow the teiid systematics of Nydam et al. (2007).

RESULTS

All marginal tooth-bearing bones (premaxilla, maxillae, and dentaries) present subpleurodont implantation, with tooth bases attached to both a horizontal shelf (supradental shelf in maxilla and premaxilla, subdental shelf in dentary) and a vertical parapet. No pterygoid teeth were observed. The amount of cementum on the marginal teeth varies among teiids (Presch, 1974). In this case the cementum is very abundant, completely covering tooth bases. The enamel is smooth, with no marked striae, except for the labial part of the carina intercuspidalis (sensu Richter, 1994) in the posterior teeth. High magnification demonstrates an apical cusp striation (Kosma, 2004). Tooth replacement in adults is present (contra MacLean, 1974) (Fig. 1A, C, E) and replacements are always lingual to functional teeth.

The premaxilla presents nine functional tooth positions. The teeth are conical and tall, the more central teeth with apical mesiodistal compression, the more external (i.e., closer to the maxillae) are distally more conical and posteriorly curved.

The maxilla has 17–20 functional tooth positions. Up to tooth X teeth are unicuspid, conical and posteriorly curved (Fig. 1A). The five anterior-most teeth are taller than the following teeth and their apical end presents a more pronounced posterior curvature. In some specimens, the last of the unicuspid teeth is much larger and robust than those preceding it. Tooth XI is bicuspid; the main cusp is the labial one which occupies most of the apical end of the tooth. The accessory cusp is located lingually in a more anterior position than the apex of the main cusp. There is no complete intercuspid ridge (carina intercuspidalis sensu Richter, 1994); only the lingual face of the labial cusp presents a marked crest. Posterior to the lingual (accessory) cusp, a shallow, concave surface is developed. The following teeth are all robust, transversely expanded, and bicuspid. The lingual cusp is always shorter and situated in the middle of a marked crest of crescent shape that limits the lingual side of the occlusion surface, accompanying the base of the labial cusp (see dentary tooth; Fig. 1G, H). This crest, the crescent ridge, is irregular and can present mesial and distal protuberances. Both lingual and labial cusps present wear facets at their apices.

The dentary dentition is similar (but with more teeth: 21–22) (Fig. 1C). The 14 anterior teeth are unicupsid and the rest are bicuspid. As in the maxillae, the transition from a unicuspid to bicuspid condition is very short. It occurs between tooth positions XIV and XV, and involves up to two teeth in which the lingual cusp is more anteriorly displaced. The following teeth present a main labial cusp, lingual to which is the crescent ridge where the lingual cusp develops (Fig. 1G, H). Mesial and distal protuberances are observed on the crescent ridge as in the teeth of the maxillae.

DISCUSSION

Transverse bicuspid posterior marginal teeth are present in two teiid genera, *Dicrodon* and *Teius*. Presch (1974) briefly described the dentition of both genera, pointing out several differences. One of these differences is that the lingual cusp in *Dicrodon* is never as tall as the labial cusps, while the cusps can be of almost equal size in *Teius* (Brizuela and Albino, 2009) (Fig. 1I). Another difference noted by Presch (1974) is the presence of a complete intercuspid ridge (carina intercuspidalis sensu Richter, 1994) in *Teius* and not in *Dicrodon* where a crest is only observed on the lingual side of the labial cusp (Fig. 1G, H, I). Presch (1974: 347) mentions the possible biconodont structure of the lingual cusp of *Dicrodon,* according to this contribution this would correspond to the protuberances develop mesially and distally on the crescent ridge, that can be up to four (Kosma, 2004). In this study additional characters are recognized that allow the distinction of the dentition of these two genera. In occlusal view the cusps of *Dicrodon* are more concentrically placed while in *Teius* they are continuous with the labial and lingual tooth walls (Fig. 1G, I). Moreover, in *Dicrodon* the lingual cusp sits on a crescent ridge, a configuration which is not observed in *Teius* where shelves (mesial and distal) are observed (Brizuela and Albino, 2009; Fig. 1G, I). All these characters allow clear and confident differentiation of both genera based on the morphology of posterior teeth.

To date, the fossil record of these genera is scarce, restricted to a few mentions of undescribed Pliocene–Recent

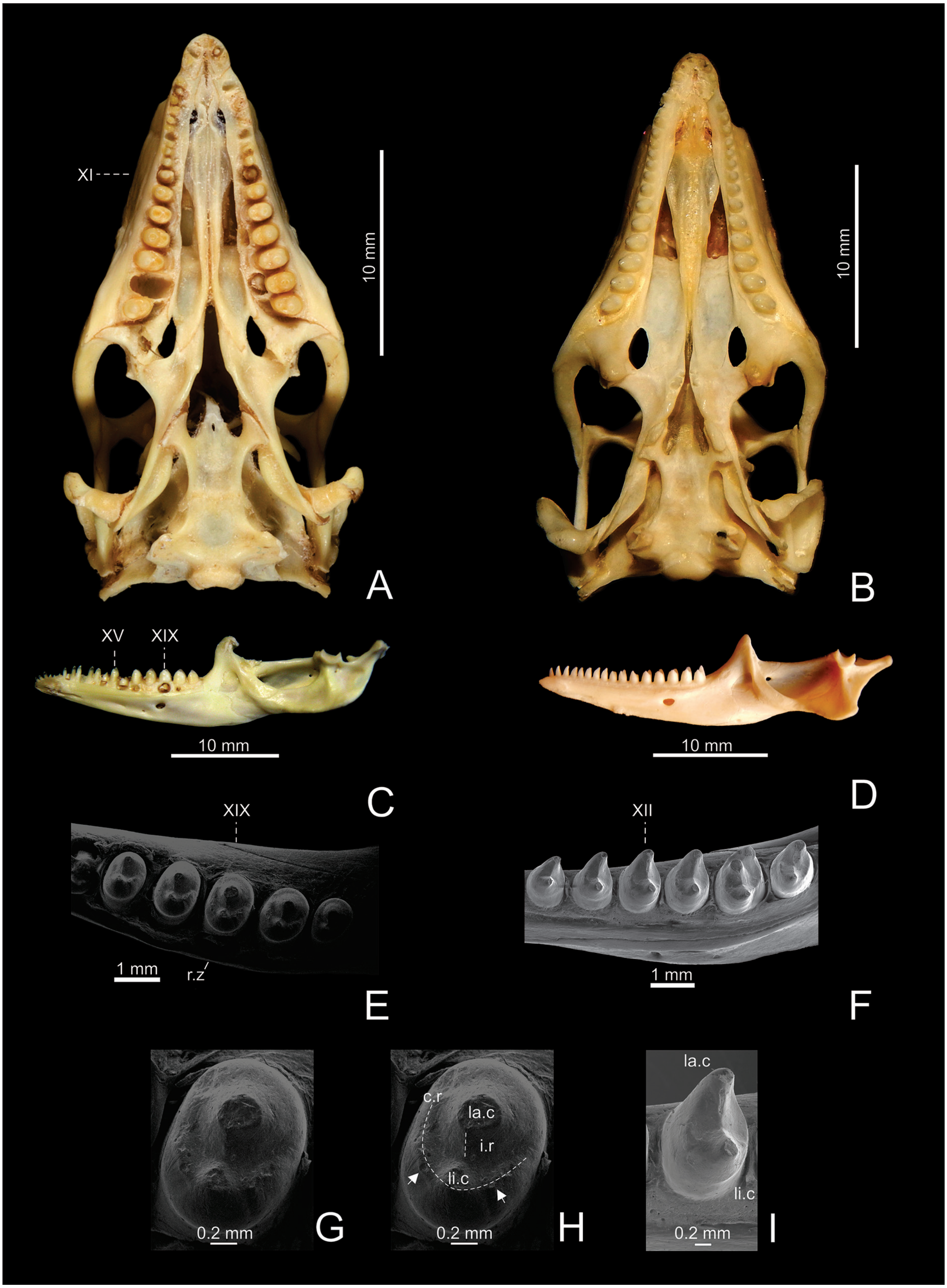

Figure 1. Dental series of *Dicrodon* and *Teius*. Ventral views of the skulls of **(A)** *Dicrodon guttulatum* (SDS 30842) and **(B)** *Teius teyou* (UNMdP-O 16); medial views of the right hemimandibles of **(C)** *Dicrodon guttulatum* (QCAZR 2139) and **(D)** *Teius teyou* (UNMdP-O 16); closeup of dentary dentition of **(E)** *Dicrodon guttulatum* (QCAZR 2139) and **(F)** *Teius teyou* (UNNE 8715); **(G, H)** occlusal view of tooth XIX of *Dicrodon guttulatum* (QCAZR 2139); **(I)** occlusal views of bicuspid tooth XII of *Teius teyou* (UNNE 8715). Abbreviations: la.c, labial cusp; li.c, lingual cusp; c.r, crescent ridge; i.r, intercuspid ridge; r.z, replacement zone. Arrows indicate crescent ridge protuberances. (Fig. F and I courtesy of Tropical Zoology).

material from Ecuador, Brazil and Argentina (Hoffstetter, 1970; de Queiroz, 2004; Brizuela and Cruz, 2013). This is unexpected, since they are considered to have differentiated during the Paleogene (Giugliano et al., 2007), and their particular dentitional characteristics would make these genera easily identifiable. The data presented here will be useful in the generic determination of these lizards fossils.

Thought distinct, both *Dicrodon* and *Teius* share similar implantation and transverse bicuspid tooth morphology, which raises several questions. Considering diet, most *Dicrodon* species are considered herbivores (*D. guttulatum* and *D. holmbergi* Schmidt, 1957) and only *D. heterolepis* Tschudi, 1845 is insectivorous (Hardeman, 2010; van Leeuwen et al., 2011). Whereas most *Teius* (*T. oculatus* D'Orbigny and Bibron, 1837 and *T. suquiensis* Avila and Martori, 1991) are insectivorous (Acosta et al., 1991; Ávila et al., 1992; Cappellari et al., 2007) and in the case of *T. teyou* Daudin, 1802 can additionally ingest fruits of *Ziziphus mistol* (Cei, 1993; Varela and Bucher, 2002), of which it is a legitimate seed disperser. Therefore, the transverse bicuspid posterior teeth are adequate for both insectivores and herbivores, suggesting that phylogenetic constraint might be involved. The question then would be if the teeth (and the particular subpleurodont implantation with abundant cementum) of *Dicrodon* are homologous with those of *Teius,* i.e., did they arise once among teiids or do they have independent origins? Nydam et al. (2007) conducted an osteologically based phylogenetic analysis of Teioidea and Borioteiioidea Nydam et al., 2007 (Polyglyphanodontia) and recover *Dicrodon* as a sister taxon to *Teius* and both as sister taxa to the rest of the Teiinae. In this scenario transverse bicuspid teeth are synapomorphic to both *Dicrodon* and *Teius*. This is also consistent with Harvey et al. (2012) combined (combined allozyme, mtDNA, and 10 morphological characters) analysis in which *Dicrodon* and *Teius* are sister taxa although nested among the other teiines. This is not the case in other phylogenetic hypothesis in which *Dicrodon* and *Teius* (or *Teius* and *Dicrodon*) are recovered as stem to the rest of the Teiinae (Reeder et al., 2002; Giugliano et al., 2007; Goicoechea et al., 2016), in these hypotheses transverse bicuspid teeth would be homoplastic among *Dicrodon* and *Teius*. More work is needed to resolve these issues.

ACKNOWLEDGMENTS

We thank O. Torres-Carvajal and F. Ayala (both from Pontificia Universidad Católica del Ecuador) for the loan of a *Dicrodon guttulatum* specimen. We are grateful to I. Olivares (Museo de La Plata, Argentina) and M. Oppedisano (Universidad Nacional de Mar del Plata, Argentina) for facilitating bibliography and aid in obtaining electron microscope images respectably. We also thank R. Nydam (Midwestern University, USA) for his valuable comments on the manuscript. We want to express our gratitude to the curators of the abovementioned institutions for giving us access to the material under research, in particularly B.D. Hollingsworth (San Diego Natural History Museum) and G. Schneider (Museum of Zoology, University of Michigan) who additionally facilitated images for this work.

REFERENCES

Avila L.J., Martori R.A. 1991. A unisexual species of *Teius* Merrem 1820 (Sauria Teiidae) from central Argentina. *Tropical Zoology* 4:193–201.

Acosta J.C., Ávila L., Martori R.A. 1991. Ecología trófica de *Teius oculatus* (Sauria: Teiidae) en el sur de la provincia de Córdoba (Argentina). Composición, varación anual y estacional de la dieta. *Cuadernos de Herpetología* 6:12–22.

Ávila L.J., Acosta J.C., Martori, R.A. 1992. Corposición, variación anual y estacional de la dieta de *Teius* suquiensis (Sauria: Teiidae) en la provincia de Córdoba (Argentina). *Cuadernos de Herpetología* 7:5–13.

Brizuela S., Albino A.M. 2009. The dentition of the Neotropical lizard genus *Teius* Merrem 1820 (Squamata Teiidae). *Tropical Zoology* 22:183–193.

Brizuela S., Albino A.M. 2010. Variaciones dentarias en *Tupinambis merianae* (Squamata, Teiidae). *Cuadernos de Herpetología* 24:5–16.

Brizuela S., Cruz L.E. 2013. Escamosos (Squamata) de la Formación Brochero, Plioceno, de la provincia de Córdoba (Argentina). XXVI Jornadas Argentinas de Paleontología de Vertebrados (La Rioja). *Ameghiniana* 50:9–10.

Caldwell M.W., Budney L.A., Lamoureux D.O. 2003. Histology of tooth attachment tissues in the Late Cretaceous mosasaurid *Platecarpus*. *Journal of Vertebrate Paleontology* 23:622–630. DOI

Cappellari L.H., Lema T. de, Prates P. Jr., Duarte da Rocha C.F. 2007. Diet of *Teius oculatus* (Sauria, Teiidae) in southern Brazil (Dom Feliciano, Rio Grande do Sul). *Iheringia, Série Zoologia* 97:31–35. DOI

Cei J.M. 1993. Reptiles del Noroeste, Nordeste y Este de la Argentina. Herpetofauna de las selvas subtropicales, Puna y Pampas. *Museo Regionale di Scienze Naturali Torino, Monografia* 14:1–949.

Daudin F.M. 1802. Histoire Naturelle, Générale et Particulière des Reptiles; ouvrage faisant suit à l'Histoire naturell générale et particulière, composée par Leclerc de Buffon; et rédigee par C.S. Sonnini, membre de plusieurs sociétés savantes, Tome Troisième. F. Dufart, Paris. DOI

de Queiroz A.N. 2004. Étude des vertébrés du site archéologique Rs-Tq-58, Montenegro, RS, Brésil: aspects archéozoologiques et taphonomiques. Pp. 153–176, in Goñalons G.L.M. (Ed.), Zooarchaeology of South America. Archaeopress, Oxford.

Dessem D. 1985. Ontogenetic changes in the dentition and diet of *Tupinambis* (Lacertilia: Teiidae). *Copeia* 1985:245–247.

D'Orbigny A., Bibron G. 1837. Voyage dans l'Amérique Méridionale, Tome 5, 1re Partie: Reptiles. Chez V. Levrault, Paris. DOI

Duméril A.M.C., Bribon G. 1839. Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Tome Cinquième. Librarie Encyclopédique Roret, Paris. DOI

Edmund A.G. 1969. Dentition. Pp. 117–200, in Gans C., Bellairs A.d'A., Parsons T.S. (Eds.), Biology of the Reptilia, vol. 1. Academic Press, New York.

Estes R. 1969. Relationships of two Cretaceous lizards (Sauria, Teiidae). *Breviora* 317:1–8.

Gilmore C.W. 1940. New fossil lizards from the Upper Cretaceous of Utah. *Smithsonian Miscellaneous Collections* 99:1–3.

Giugliano L.G., Garcia Collevatti R., Colli G.R. 2007. Molecular dating and phylogenetic relationships among Teiidae (Squamata) inferred by molecular and morphological data. *Molecular Phylogenetics and Evolution* 45:168–179. DOI

Goicoechea N., Frost D.R., De la Riva I., Pellegrino K.C.M., Sites J.W. Jr., Rodrigues M.T., Padial, J.M. 2016. Molecular systematics of teioid lizards (Teioidea/Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similarity-alignment. *Cladistics* 32:624–671. DOI

Gray J.E. 1827. Synopsis of the genera of saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. *Philosophical Magazine* 2:54–58. DOI

Hardeman D.W. Jr. 2010. Ecomorphology of the lizards in the genus *Dicrodon*. Ph.D. Dissertation, Texas A&M University, USA.

Harvey M.B., Ugueto G.N., Gutberlet R.L. Jr. 2012. Review of teiid morphology with a revised taxonomy and phylogeny of the Teiidae (Lepidosauria: Squamata). *Zootaxa* 3459:1–156.

Hoffstetter R. 1970. Vertebrados Cenozoicos del Ecuador. IV Congreso Latino Americano de Zoología (Caracas), Actas 2:955–970.

Kosma R. 2004. The dentitions of recent and fossil scincomorphan lizards (Lacertilia, Squamata) – systematics, functional morphology, paleoecology. Ph.D. Dissertation, Universität Hannover, Germany.

MacLean W.P. 1974. Feeding and locomotor mechanisms of teiid lizards: functional morphology and evolution. *Papéis Avulsos de Zoologia, Museu de Zoologia da Universidade de São Paulo* 27:179–213.

Merrem B. 1820. Versuch eines Systems der Amphibien I (Tentamen Systematis Mmphibiorum). Krieger J.C., Marburg.

Meyer F.A.A. 1795. Synopsis reptilium: novam ipsorum sistens generum methodum: nec non *Gottingensium huius* ordinis animalium enumerationem. Vandenhoek et Ruprecht, Gottingae. DOI

Nydam R.L. 1999. Polyglyphanodontinae (Squamata: Teiidae) from the medial and Late Cretaceous: new taxa from Utah, U.S.A. and Baja California del Norte, Mexico. *Utah Geological Survey Miscellaneous Publication* 99-1:303–317.

Nydam R.L., Eaton J.G., Sankey J. 2007. New taxa of transversely-toothed lizards (Squamata: Scincomorpha) and new information on the evolutionary history of "teiids". *Journal of Paleontology* 81:538–549. DOI

Presch W. 1974. A survey of the dentition of the macroteiid lizards (Teiidae: Lacertilia). *Herpetologica* 30:344–349.

Reeder T.W., Cole C.J., Dessauer H.C. 2002. Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. *American Museum Novitates* 3365:1–61. DOI

Richter A. 1994. Lacertilia aus der Unteren Kreide von Uña und Galve (Spanien) und Anoual (Marokko). *Berliner geowissenschaftliche Abhandlungen Reihe E (Paläobiologie)* 14:1–147.

Schmidt K.P. 1957. Notes on lizards of the genus *Dicrodon*. *Fieldiana. Zoology* 39:65–71.

Smith J.B., Dodson P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23:1–12. DOI

Spix J.B. von. 1824. Animalia nova sive species novae lacertarum quas in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspicius Maximiliani Josephi I Bavariae Regis suscepto collegit et descripsit Dr. J.B. de Spix. Typis Franc. Seraph. Hubschmanni, Monachii. DOI

Sullivan R.M., Estes R. 1997. A reassessment of the Tupinambinae. Pp. 100–112, in Kay R.F., Madden R.H., Cifelli R.L., Flynn J.J. (Eds.), Vertebrate Paleontology in Neotropics. Smithsonian Institution Press, Washington, D.C.

Tschudi J.J. von. 1845. Reptilium conspectum quae in Republica Peruana reperiuntur et pleraque observata vel collecta sunt in itinere a Dr. J.D. de Tschudi. *Archiv für Naturgeschichte* 11:150–168.

van Leeuwen J.P., Catenazzi A., Holmgren M. 2011. Spatial, ontogenetic, and sexual effects on the diet of a teiid lizard in arid South America. *Journal of Herpetology* 45:472–477.

Varela R.O., Bucher E.H. 2002. The lizard *Teius teyou* (Squamata: Teiidae) as a legitimate seed disperser in the Dry Chaco Forest of Argentina. *Studies on Neotropical Fauna and Environment* 37:115–117. DOI

Wagler J.G. 1830. Natürliches System der Amphibien: mit vorangehender Classification der Säugethiere und Vögel: ein Beitrag zur vergleichenden Zoologie. J.G. Cotta'scchen Buchhandlung, München, Stuttgart und Tübingen. DOI

Zaher H., Rieppel O. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. *American Museum Novitates* 3271:1–19.