

FOSSILS OF CICHLID FISHES FROM THE MIOCENE AND PLEISTOCENE OF COSTA RICA

FÓSILES DE PECES CICLIDOS DEL MIOCENO Y PLEISTOCENO DE COSTA RICA

Spencer G. Lucas^{1*}, Asher J. Lichtig¹, Kenneth Pérez² y Guillermo E. Alvarado³

¹New Mexico Museum of Natural History, 1801 Mountain Road NW,
Albuquerque, NM 87104-1375 USA

²Consulting geologist, Costa Rica

³Centro de Investigaciones Geológicas, Universidad de Costa Rica, Costa Rica

*Autor para contacto: spencer.lucas@state.nm.us

(Recibido: 16/03/2017 aceptado: 10/05/2017)

ABSTRACT: We document fossils of cichlid fishes from Costa Rica, the first fossil record of cichlids in Central America. These fossils are from shallow marine strata of Late Miocene age at the Proyecto Hidroeléctrico Reventazón and lake deposits of Middle Pleistocene age at San Miguel de Turrúcares. The occurrence of a Late Miocene cichlid in marine sediments in Costa Rica indicates a likely marine dispersal of cichlids from South America to Central America, and it also fits with the idea that cichlids crossed shallow marine waters during the Miocene to achieve their current distribution. The freshwater Middle Pleistocene cichlid fossils from San Miguel de Turrúcares indicate that, at least by the Middle Pleistocene, cichlids inhabited freshwater habitats in Costa Rica, as they now do across much of Central America.

Keywords: Cichlidae, fishes, Costa Rica, Miocene, Pleistocene, paleobiogeography.

RESUMEN: El presente trabajo documenta restos fósiles de peces cíclidos de Costa Rica, constituyendo el primer registro fósil de cíclidos en América Central. Estos fósiles provienen de rocas sedimentarias marinas de ambiente poco profundo, posiblemente del Mioceno Superior, hallados en el Proyecto Hidroeléctrico Reventazón, así como de depósitos lacustres continentales del Pleistoceno Medio en San Miguel de Turrúcares. La ocurrencia de cíclidos miocénicos en sedimentos marinos en Costa Rica indica una posible dispersión marina de los cíclidos desde América del Sur a América Central y se ajusta a la idea de que migraron en el Mioceno y cruzaron las aguas marinas poco profundas para lograr su distribución actual. Los fósiles de cíclidos de Pleistoceno Medio de agua dulce de San Miguel de Turrúcares indican que, al menos para el Pleistoceno Medio, los cíclidos colonizaban hábitats de agua dulce, como ahora lo hacen en gran parte de América Central.

Palabras clave: Cíclidos, peces fósiles, Costa Rica, Mioceno, Pleistoceno Medio, paleobiogeografía.

INTRODUCTION

Today, cichlids are a diverse family of perch-like fishes that live in Central and South America, the West Indies, Africa, Madagascar, the Middle East, Sri Lanka and coastal India. There are at least 1300 species of living cichlids, and their fossil record extends back to the Eocene (e.g., Casciotta y Arratia, 1993; Murray, 2001a, b; Malabarba et al., 2006). In the New World, fossil cichlids are known from the Miocene of Argentina, the Miocene of Hispaniola (Haiti) and the Eocene and Pliocene of Brazil (Woodward, 1898, 1939; Schaeffer, 1947; Bardack, 1961; Casciotta and Arratia, 1993; Murray, 2001b). No cichlid fossils have been documented from Central America, although diverse cichlids now live in that region (e. g., Miller, 1966; Myers, 1966). The closest fossil cichlid to Central America is one known from Haiti. Thus, Cockerell (1923) named a new species *Cichlasoma* (now *Nandopsis*) *woodringi* from Las Caholas, Haiti. The age of this fossil is usually listed as Pliocene, but associated fossil plants indicate a Miocene age (Cooke et al., 1943; Bowin, 1975; Graham, 1990; Chakrabarty, 2006b).

It is thus of some importance to document here the first known fossils of Central American cichlids, from Costa Rica (Fig. 1). These fossils are from a Late Miocene marine deposit and a Middle Pleistocene nonmarine deposit, and do shed some light on ideas about cichlid paleobiogeography in the New World.

MIOCENE CICHLIDS GEOLOGICAL CONTEXT

The Late Miocene fossil cichlids were discovered in the area of the Proyecto Hidroeléctrico Reventazón in a block from the filling of the entrance of a tunnel that was removed as part of construction. The approximate location using the system of coordinates of the Costa Rica Transverse Mercator 2005 (CRTM05) is 1113789.5 North and 546569.8 East (Fig. 1).

Because the fossils were not found in situ in an outcrop, we have identified and correlated the

lithology of the fossil-bearing rocks with that of equivalent outcrops. The blocks in which the fossils were found correspond lithologically to lenses of bioclastic limestones with a significant content of macrofossils (mollusks and echinoderms). Stratigraphically, these lenses of limestone are found within the sandstones and greenish shales of the Río Banano Formation (Taylor, 1975). Similar lenses have been observed in the Palomo, Lajas and Carazo gullies, sites that served as sources of materials from which the blocks with fossils are believed to have originated. The limestone beds seen in the field around the reservoir of the Reventazón Hydroelectric Power Plant display the characteristic lithologies of the Río Banano Formation. Ideas about its age have varied from Middle Miocene to Early Pleistocene, but in the area of study a Late Miocene age is most likely (Pizarro, 1993; Cassell y Sen Gupta, 1989 a,b; Espinoza, 2012). More precision is not possible at the moment.

MIOCENE CICHLIDS--DESCRIPTION

The cichlid fossils are in nine pieces that represent at least one individual. They include one specimen from the posterior of the head to the caudal fin rays, two specimens that include only the vertebral column, two with only scales, two with the vertebral column and scales, and two with scales and indeterminate other remains.

The most complete specimen (Fig. 2) is moderately deep bodied with relatively large ctenoid scales throughout the anterior two-thirds of the body. The ctenoid scales are approximately 9 mm high and 6 mm long with a radial pattern of lines toward their anterior ends. The pelvic fins are large, with the first rays approximately 32 mm long and 3 mm in diameter. The pectoral fins are absent and are inferred to be anterior to the preserved portion of the specimen. The caudal fin is composed of at least 9 nearly parallel rays at least 35 mm long. The centra appear to become longer anteriorly, with amphicoelous articulations. The neural arches are large and slope posteriorly, reaching nearly the height of the centrum posteriorly.

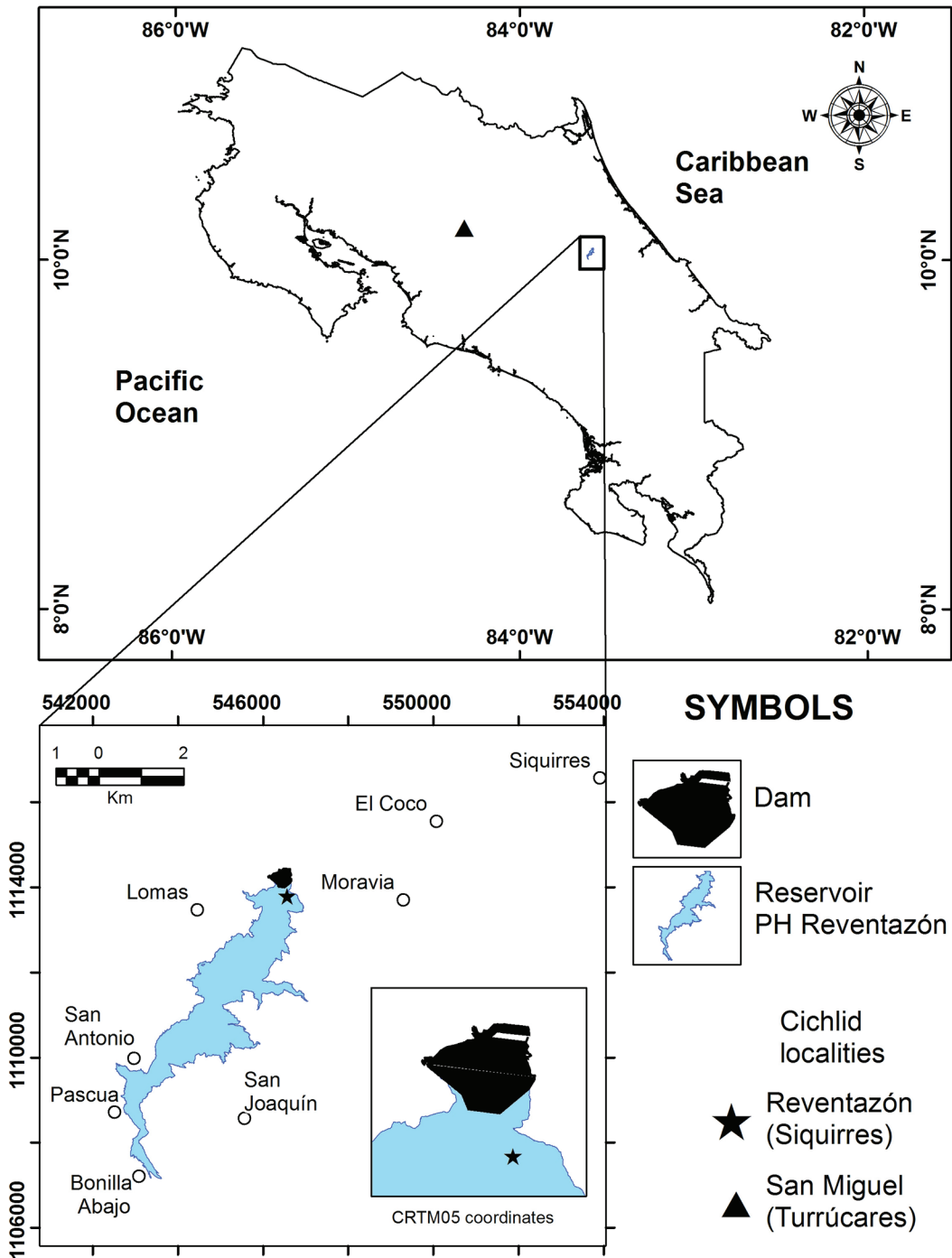


Fig. 1: Fossil cichlid localities in Costa Rica and detail of the locality at Río Reventazón.

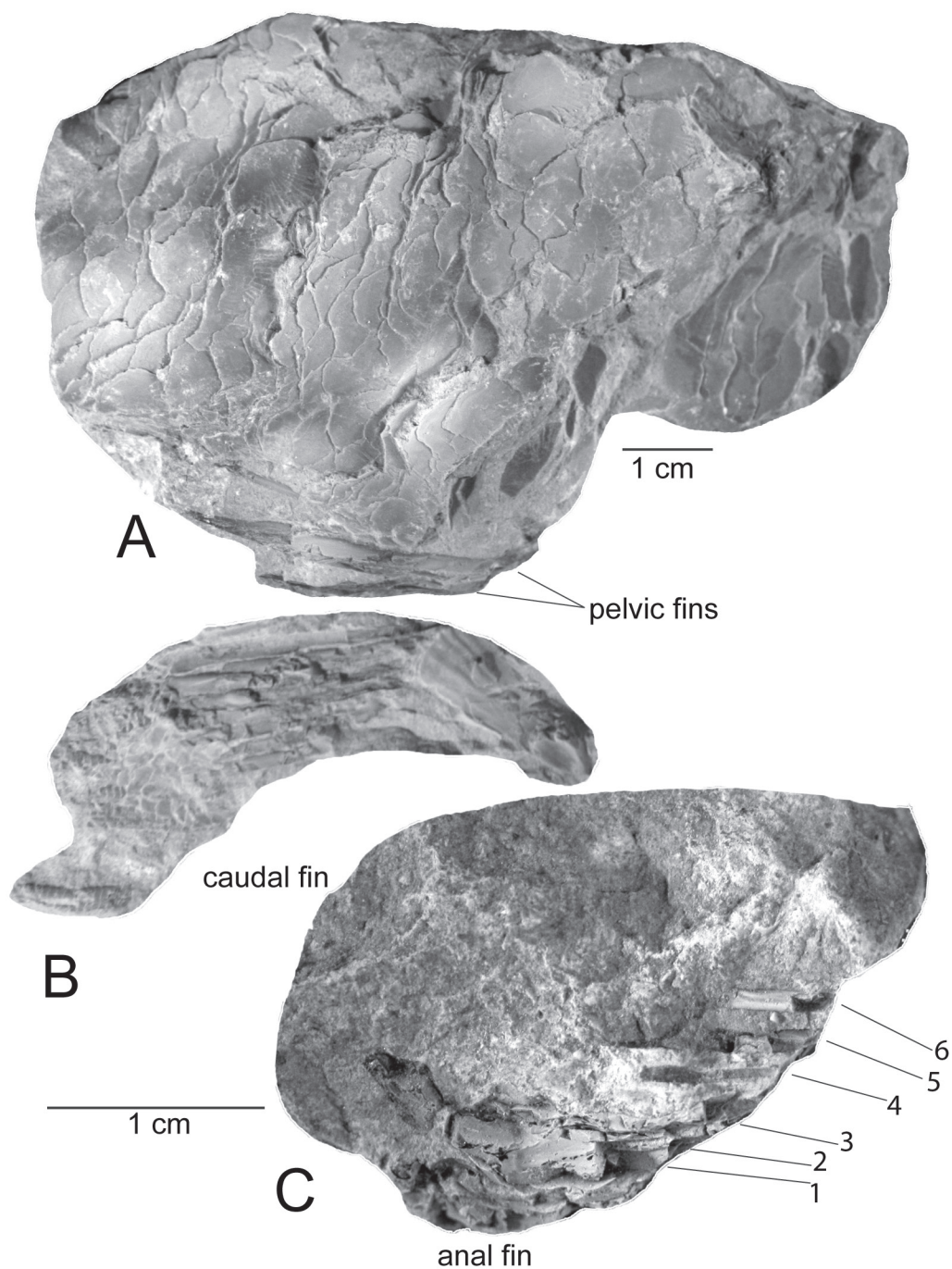


Fig. 2: Cichlid fossil from the Miocene of Costa Rica. A, Part of large fish, showing scales. B, Pelvic fin of large fish. C, Anal fin of large fish with spines numbered.

The second specimen has six vertebral centra partially preserved. These are each 9 mm long and 7 mm in diameter. They have long pits on the dorsal-lateral sides of each centrum. The neural arches outline a taller than long neural canal. The third specimen includes parts of six vertebrae in dorsal view. These are relatively short, measuring only 4 mm long and 6 mm diameter. We infer these to be from the posterior portion of the vertebral column based on the apparent anterior-to-posterior shortening of the centra.

The fourth specimen is composed of three-dimensionally preserved scales and the posterior portions of the pelvic and anal fins. The scales are ctenoid, with their width reduced toward the ventral side. The pelvic fin preserves one spine and five rays, with the largest closest to the midline and approximately 2 mm in diameter. The anal fin as preserved includes four rays, the anterior two of which are greatly enlarged spines, measuring up to 3 mm in diameter.

The fifth specimen includes only a 6 mm wide and 8 mm long patch of ctenoid scales similar to those present on other specimens. The sixth specimen includes parts of five centra and at least eight rows of the overlying scales. The vertebrae are amphicoelous and approximately 6 mm long and 5 mm in diameter. The scales become closer to the vertebrae posteriorly, nearly contacting the vertebrae along the posterior end of the fragment.

The seventh specimen is composed of larger ctenoid scales and neural arches. The arches are large, with a triangular dorsal spine and a large opening for the neural canal. The scales are approximately 12 mm high, with at least two ridges around the exterior of the scales, possibly indicating a more advanced age for this individual.

The eighth specimen is primarily composed of a curved wrap of ctenoid scales, and indeterminate bones on the opposite side of the rock fragment. The scales become smaller toward one of the lateral edges. The bones on the opposite side are too incomplete for a certain identification, but, given their placement and orientation, they are likely part of the vertebral column. The final specimen includes a small, 20 mm square patch of scales and several indeterminate fragments.

IDENTIFICATION

As Casciotta y Arratia (1993; also see Malabarba et al., 2006) stressed, the synapomorphic features of modern cichlids are generally not preserved on fossil material. This makes identifying fossil cichlids difficult and often tentative, as is the case here, especially because the Reventazón specimens lack complete cranial material. Thus, assignment of the specimens to the Cichlidae is based on overall morphological features characteristic of the family. Nevertheless, definitive assignment of the Reventazón specimens to the Cichlidae will require better material than is available to us, though nothing about the Reventazón specimens supports an identification other than Cichlidae.

Thus, the Reventazón specimens are assigned to the Cichlidae on the basis of the close resemblance of the cleithrum, vertebrae and fin rays to *Proterocara* (Malabarba et al., 2006) and the scales to those of the extant *Andinoacara rivulatus* (personal observation). The cleithrum is similar to both *Proterocara* and *Mahengechromis* from the Eocene of Argentina and Tanzania, respectively, but closer to *Proterocara* in form (Murray, 2001a; Malabarba et al., 2006). Also, the Costa Rican specimens show the pattern of robust pelvic fins with small, thinly rayed pectoral fins common to many South American cichlids (Kullander, 1986). The scales show a radiating pattern centered near the front of the scale, similar to those of extant *A. rivulatus*. The presence of more than three anal fin spines is also characteristic of the Cichlidae and excludes identification as a labroid (Carpenter, 2001). However, without a skull, a more precise identification than Cichlidae is impossible.

MIDDLE PLEISTOCENE COSTA RICAN CICHLIDS

In the Valle Central of Costa Rica, at San Miguel de Turrúcares (Fig. 1), lacustrine volcanoclastic deposits rich in diatomite and with fossil remains of fish are present. These are deposits of a freshwater lake almost contemporaneous

in age with the paleolake at Palmares. Alvarado (1986, 1994) described the lake deposits at San Miguel de Turrúcares in some detail. According to these authors, the lake was impounded by a lava flow or a debris avalanche deposit. At San Miguel de Turrúcares, the lake deposits appear to overlap volcanic debris avalanche deposits (Nuestro Amo Formation) and lava flows (lower Colima Formation) from the Middle Pleistocene, and breccias to ignimbrites presumably associated with the Middle Pleistocene Tiribí Formation (Lucas et al., 1997, fig. 3). This indicates that the age of the Turrúcares lake is likely between 0.53 and 0.32 Ma (Alvarado y Gans, 2012).

Alvarado (1989, 1994) mentioned the occurrence of a new cichlid species in the lake of San Miguel de Turrúcares, based on an unpublished manuscript title “*Cichlasoma turrucarensis*, nov. sp. from the Costa Rican Miocene” of the late Luis Diego Gómez (1944 - 2009), which was also mentioned by him in his published compilation (Gómez, 1977). Thus, Alvarado (1989, p. 281) mentioned the cichlids from San Miguel de Turrúcares as *Cichlasoma turrucarensis*. Alvarado (1994, p. 92, fig. 36A) also briefly mentioned this cichlid and illustrated two specimens, using the new but unpublished species name *Cyclasoma* [sic] *turrucarensis*. Given that the use of this name lacked a holotype designation or diagnosis, it is clearly a *nomen nudum* as used by Alvarado (1989, 1994). Gómez (unpublished) well justifies that these fossils are of a cichlid, but further work is needed to present complete documentation of this record (e.g., Fig. 3). In his publications, Alvarado pointed out that the cichlid fossils from Turrúcares are of Pleistocene age and not Miocene as was originally indicated by Gómez. The important point is that the San Miguel de Turrúcares diatomite is a freshwater deposit of Middle Pleistocene age. The cichlid record at San

Miguel de Turrúcares thus indicates the presence of cichlids living in freshwater in Costa Rica during the Pleistocene.

PALEOBIOGEOGRAPHY

Hypotheses of the origins of Central American and Greater Antilles cichlids fall into two broad categories. First are those suggesting a marine dispersal event from South America to Central America, and then from Central America to Cuba and Hispaniola (Myers, 1966; Álvarez de Villar, 1978; Briggs, 1984; Martin and Bermingham, 1998; Murray, 2001b; Chakrabarty, 2006a; Hulsey et al., 2011). The second hypothesis suggests an immigration from South America via the Antilles and the Aves ridge (termed GAARlandia: Iturralde-Vinent and MacPhee, 1999) and then into Central America (Říčan et al., 2013).

The specimens documented here provide the first records of fossil cichlids in Central America. The cichlid fossil record of Central America and the Greater Antilles as now known thus is confined to the Miocene of Hispaniola and the Miocene and Pleistocene of Costa Rica. The occurrence of a Miocene cichlid in shallow marine sediments in Costa Rica is a record in what was the marine gap between the core of Central America and South America. This supports a likely marine dispersal of cichlids from South America to Central America, as suggested in the first hypothesis. It also fits the idea that cichlids are of Paleogene origin and crossed shallow marine waters to achieve their current distribution (Murray, 2001b). Martin and Bermingham (1998) concluded that molecular data identify a cichlid presence in Central America since the Miocene, and the Miocene cichlid fossils from Reventazón support that conclusion. The freshwater Middle



Fig. 3: A cichlid fossil from the lake deposits at San Miguel de Turrúcares in the collection of the Museo Nacional de Costa Rica (catalogued as CFM-279, photograph courtesy of A.L. Valerio).

Pleistocene cichlid fossils from San Miguel de Turrúcares indicate that by that time, cichlids inhabited freshwater habitats in Costa Rica, as they now do across much of Central America.

ACKNOWLEDGMENTS

Sr. Alvaro Bustamante donated and provided information on the fossils. Ana Lucía Valerio provided a PDF of the unpublished manuscript of Luis Diego Gómez, and photographs of cichlids from the San Miguel de Turrúcares paleo-

lake deposits. Allison Murray provided a helpful review of an earlier draft of this paper.

REFERENCES

- Alvarado, G. E. (1986). Hallazgos de megamamíferos fósiles en Costa Rica. *Revista Geológica América Central*, 4, 1-46.
- Alvarado, G. (1989). Historia de la paleontología de los vertebrados en Costa Rica. In A. Ruiz and L. Camacho (eds.), *Historia*

- de la ciencia y la tecnología. El avance de una disciplina* (pp. 273-289). Cartago: Editorial Tecnológica de Costa Rica.
- Alvarado, G. E. (1994). *Historia natural antigua: los intercambios biológicos interamericanos*. San José: Editorial Tecnológica de Costa Rica.
- Alvarado, G. E. and Gans, P. B. (2012). Síntesis geocronológica del magmatismo, metamorfismo y metalogenia de Costa Rica, América Central. *Revista Geológica América Central*, 46, 7-122.
- Álvarez-del-Villar, J. (1978). Relación entre la geomorfología mesoamericana y la distribución actual de los peces. In I. Ferrusquía-Villafranca (ed.), *Conexiones terrestres entre Norte y Sudamérica* (Vol. 101, pp. 182-192): Universidad Nacional Autónoma de México, Boletín del Instituto Geológico.
- Bardack, D. (1961). New Tertiary teleosts from Argentina. *American Museum Novitates*, 2041, 1-27.
- Bowin, C. (1975). The geology of Hispaniola. In A. E. M. Nairim and F. G. Stehli (eds.), *The ocean basins and margins* (pp. 501-552). New York: Plenum.
- Briggs, J. C. (1984). Freshwaters fishes and biogeography of Central America and the Antilles. *Systematic Zoology Journal*, 33, 428-435.
- Carpenter, K. E. (2001). Suborder Laboroidei Cichlidae. In K. E. Carpenter and V. H. Niem (eds.), *FAO species identification guide for fishery purposes the living marine resources of the western central pacific* (pp. 3333-3336). Rome: FAO.
- Casciotta, J. and Arratia, G. (1993). Tertiary cichlid fishes from Argentina and reassessment of phylogeny of New World cichlids. *Kaupia*, 2, 195-240.
- Cassel, D. T. and Sen-Gupta, B. K. (1989a). Foraminiferal stratigraphy and paleoenvironments of Tertiary Uscari Formation, Limon Basin of Costa Rica. *Journal of Foraminiferal Research*, 19, 52-71.
- Cassel, D. T. and Sen-Gupta, B. K. (1989b). Pliocene foraminifera and environments, Limon Basin of Costa Rica. *Journal of Paleontology*, 63(2), 146-157.
- Chakrabarty, P. (2006a). Systematics and historical biogeography of Greater Antillean Cichlidae. *Molecular Phylogenetics and Evolution*, 39, 619-627.
- Chakrabarty, P. (2006b). Taxonomic status of the Hispaniolan Cichlidae. *Occasional Papers Museum of Zoology, University of Michigan*, 737, 1-17.
- Cockerell, T. D. A. (1923). A fossil cichlid fish from the Republic of Haiti. *Proceedings of the United States National Museum*, 63, 1-3.
- Cooke, C. W., Gardner, J. and Woodring, W. P. (1943). Correlation of the Cenozoic formations of the Atlantic and Gulf coastal plain and the Caribbean region. *Geological Society of American Bulletin*, 54, 1713-1723.
- Espinoza, G. J. (2012). *Estudio de estanqueidad del embalse del Proyecto Hidroeléctrico Reventazón, Instituto Costarricense de Electricidad* (Tesis de licenciatura inédita), Universidad de Costa Rica, San José.
- Gómez, L. D. (n.d.). *Cichlasoma turrucarensis, nov sp. from the Costa Rican Miocene*. San José: Museo Nacional de Costa Rica. Unpublished manuscript.
- Gómez, L. D. (1977). *Bibliografía geológica y paleontológica de Centroamérica y el Caribe*. San José: Museo Nacional de Costa Rica.

- Graham, A. (1990). Late Tertiary microfossil flora from the Republic of Haiti. *American Journal of Botany*, 77, 911-926.
- Hulseley, C. D., Keck, B. P. and Hollingsworth, P. R. Jr. (2011). Species tree estimation and the historical biogeography of heroine cichlids. *Molecular Phylogenetics and Evolution*, 58, 124-131.
- Iturralde-Vinent, M. A. and Macphee, R. D. (1999). Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1-95.
- Kullander, S. O. (1986). *Cichlid fishes of the Amazon River drainage of Peru*. Stockholm: Swedish Museum of Natural History.
- Lucas, S. G., Alvarado, G. E. and Vega, E. (1997). The Pleistocene mammals of Costa Rica. *Journal of Vertebrate Paleontology*, 17, 413-427.
- Malabarba, M. C., Zuleta, O. and Del Papa, C. (2006). *Proterocara argentina*, a new fossil cichlid from the Lumbra Formation, Eocene of Argentina. *Journal of Vertebrate Paleontology*, 26, 267-275.
- Martin, A. P. and Bermingham, E. (1998). Systematics and evolution of lower Central American cichlids inferred from analysis of Cytochrome b gene sequences. *Molecular Phylogenetics and Evolution*, 9, 192-203.
- Miller, R. R. (1966). Geographical distribution of Central American freshwater fishes. *Copeia*, 773-802.
- Murray, A. M. (2001a). The oldest fossil cichlids (Teleostei: Perciformes): Indication of a 45 million-year-old species flock. *Proceedings of the Royal Society of London*, B 258, 679-684.
- Murray, A. M. (2001b). The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). *Biological Journal of the Linnean Society*, 74, 517-532.
- Myers, G. S. (1966). Derivation of the freshwater fish fauna of Central America. *Copeia*, 4, 766-773.
- Pizarro, D. (1993). Los pozos profundos perforados en Costa Rica: aspectos litológicos y bioestratigráficos. *Revista Geológica América Central*, 15, 81-85.
- Řičan, O., Piálek, L., Zardoya, R., Doadrio, I. and Zrzavý. (2013). Biogeography of the Mesoamerica Cichlidae (Teleostei: Heroini): Colonization through the Gaarlandia land bridge and early diversification. *Journal of Biogeography*, 40, 579-593.
- Schaeffer, B. (1947). Cretaceous and Tertiary actinopterygian fishes from Brazil. *Bulletin of the American Museum of Natural History*, 89, 1-39.
- Taylor, G. D. (1975). The Geology of the Limón area of Costa Rica part. 1-2. *Bulletin of American Paleontology*, 9(39), 179-460.
- Woodward, A. S. (1898). Considerações sobre alguns peixes Terciários dos schistos de Taubaté, Estado de São Paulo, Brasil. *Revista do Museo Paulista*, 3, 63-70.
- Woodward, A. S. (1939). Tertiary fishes from Maranhao, Brazil. *Annals and Magazine of Natural History*, 11(3), 450-453.



