

# Identification of the Oligocene to early Miocene loricariid catfish †*Taubateia paraiba* as a member of the Rhinelepininae

Jonathan W. Armbruster<sup>1\*</sup>  and Nathan K. Lujan<sup>2,3</sup>

<sup>1</sup>Department of Biological Sciences, Auburn University Museum of Natural History, Auburn University, Alabama 36849, USA <[armbrjw@auburn.edu](mailto:armbrjw@auburn.edu)>

<sup>2</sup>American Museum of Natural History, 200 Central Park West, New York, New York 10024, USA <[nklujan@gmail.com](mailto:nklujan@gmail.com)>

<sup>3</sup>Royal Ontario Museum, 100 Queens Park, Toronto, Ontario, M5S 2C6 Canada

Correct identification of fossil taxa is immensely important for dating molecular phylogenies and understanding when and how quickly modern biodiversity evolved. Fossils that are available for a clade of interest and can be directly incorporated in the phylogenetic analysis are considered primary sources of time calibration, whereas calibrations inferred from other studies are secondary (Arroyave et al., 2013). Studies of taxonomic groups that lack fossils must either expand their analyses to include fossilized outgroup lineages, use secondary calibrations, or use more problematic primary calibrations, e.g., vicariant geologic events. The use of vicariant geologic events to calibrate phylogenies poses the risk of circular reasoning, because the goal of many such studies is to determine how geologic events have affected diversification. Near et al. (2012) argued that fossil calibrations external to clades of interest, but still within the broader Actinopterygian (ray-finned fishes) tree, could be used as means of calibrating a generalized molecular clock, but internal calibrations are still valuable for refining such inferences (Arroyave et al., 2013).

The Neotropics contain the greatest diversity of freshwater fishes in the world with over 6,200 named species and an estimated total of > 9,000 species (Albert et al., 2020). Most Neotropical species belong to the Ostariophysi, a group that consists of the Characiformes (tetras), Gymnotiformes (knife-fishes), and Siluriformes (catfishes). Within the Siluriformes, the largest family is the suckermouth armored catfish family Loricariidae, with just over 1,000 valid species (Fricke et al., 2021) representing approximately one-sixth of the Neotropical freshwater fish diversity. Loricariids exist from northern Argentina to Costa Rica. With their diversity and widespread distribution, understanding the timing of loricariid diversification is important for establishing the geological basis for diversification across Neotropical freshwater organisms.

Loricariids have a heavily ossified skeleton with many of the skull bones located at the surface and supporting integumentary teeth or odontodes (Schaefer, 1987; Armbruster, 2004). In addition, the sides of the body are covered by bony plates. Despite this heavily armored skeleton, there are very few loricariid fossils of note. Lundberg (1997) attributes a spine from the La Venta Formation of Colombia to *Acanthicus* Agassiz in Spix and Agassiz, 1829 and a partial neurocranium

to *Panaque* Eigenmann and Eigenmann, 1889, but these fossils are of too low quality to reliably assign to genera. Although *Panaque* is still present in the Río Magdalena drainage where the La Venta Formation is located, *Acanthicus* is not. Bogan and Agnolín (2020), however, described skull bones attributable to *Acanthicus* from the Ituzaingó Formation in the Parana River Basin (late Miocene, ~6–9 Ma), extending the distribution of the genus into the Paraná (extant collections of the genus are from the Amazon and Orinoco basins). *Acanthicus* is unique in having an extended compound pterotic bone that supports large odontodes (Armbruster, 2004; Chamon, 2016), leaving no doubt as to the genus of these fossils.

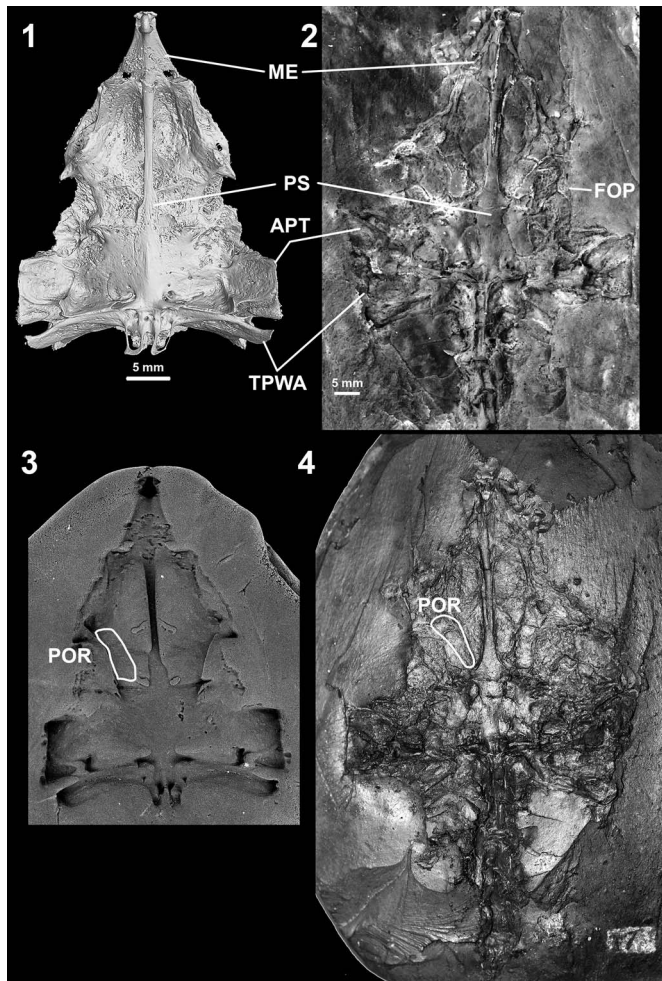
One of the earliest and most complete loricariid fossils is †*Taubateia paraiba*, which was described by Malabarba and Lundberg (2007) from southeastern Brazil based on a ventral impression of a neurocranium and some vertebrae. The fossil is from the lacustrine habitat of the Tremembé Formation of the Taubaté Group, which is dated to the Oligocene to early Miocene (~30–20 Ma). The locality (22°50'S, 45°52'W) is currently part of the Paraná River Basin. Based on an extensive database of measurements of loricariids by the authors, the 54.5 mm long skull equates to ~70 mm head length (snout to tip of supraoccipital), indicating a specimen that is ~175–210 mm long, which is fairly large for a loricariid. In the original description, Malabarba and Lundberg (2007) described the anatomy of the fossil in detail, but they were unable to resolve the identity of the fish beyond its placement within Loricariidae.

After examining a plastic peel of the original specimen (Fig. 1.2), photos of the fossil (Fig. 1.4), and comparison to loricariids examined by Armbruster (2004), some additional cleared and stained specimens, and a comprehensive library of cranial computed tomography (CT) scans of all loricariid genera (Supplementary File 1), we think that †*Taubateia* Malabarba and Lundberg, 2007 can now be confidently assigned to a subfamily. Based on skull morphology alone—particularly the frontal separated from the orbit by a plate (Armbruster 2004, character 94:1; Fig. 1.2, FOP)—the specimen must be a member of either the Hypostominae or Rhinelepininae.

## Materials and methods

*Repositories and institutional abbreviations.*—AMNH = American Museum of Natural History, New York; ANSP =

\*Corresponding author



**Figure 1.** Neurocrania, ventral views: (1) *Rhinelepis aspera* Spix and Agassiz, 1829, AMNH 58332, CT scan; (2) †*Taubateia paraiba* Malabarba and Lundberg, 2007, DGM 17-P, from plastotype (latex positive of original specimen); (3) *Rhinelepis aspera*, cast of three-dimensional print of CT scan made in Crayola Model Magic; (4) †*Taubateia paraiba*, DGM 17-P, photo of original specimen (provided by M.C. Malabarba). APT = anterior process of compound pterotic; FOP = frontal orbital plate; ME = mesethmoid; POR = prootic-orbitosphenoid ridge; PS = parasphenoid; TPWA = transverse process of Weberian apparatus.

Academy of Natural Sciences of Drexel University, Philadelphia; DGM = Coleção de Paleontologia do Museu de Ciências da Terra (MCT), Serviço Geológico do Brasil (CPRM), Ministério de Minas e Energia, Rio de Janeiro; MCP = Museu de Ciências e Tecnologia (MCT), Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre, Brazil; UF = Florida Museum of Natural History, University of Florida, Gainesville.

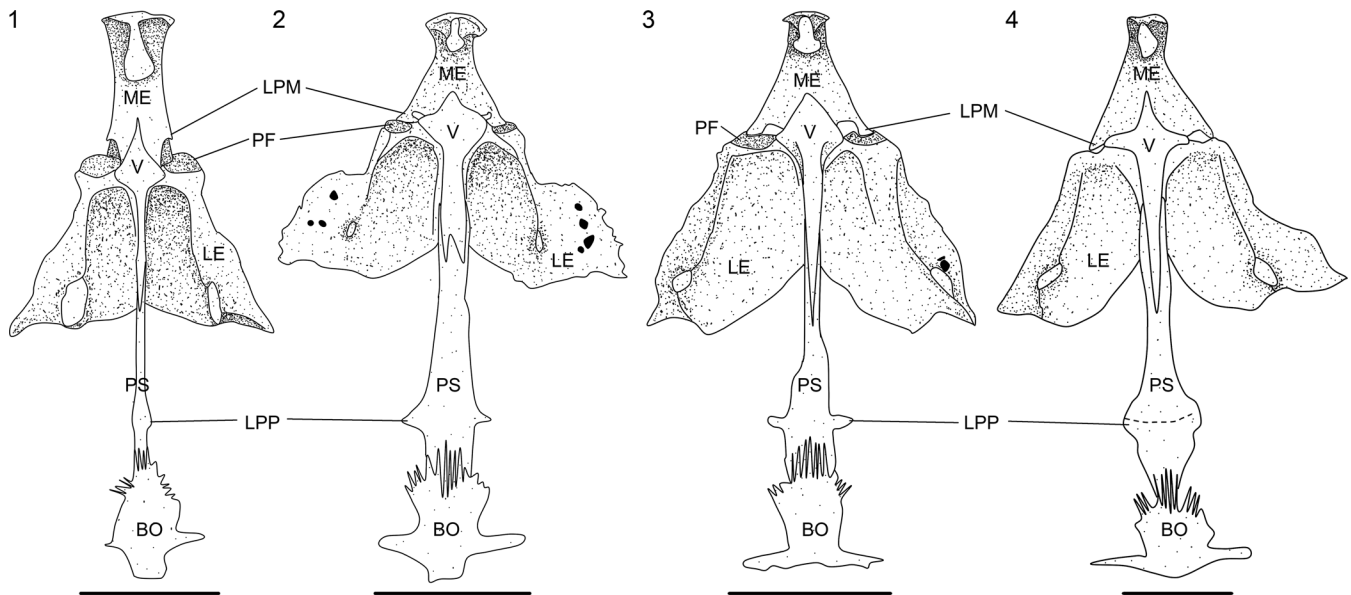
## Results and discussion

The species appears to be assignable to Rhinelepineae based on its low, wide parasphenoid—a synapomorphy of this subfamily (Armbruster, 1998, character 20:1; Armbruster, 2004, character 106:1; the parasphenoid of †*Taubateia* has a break just anterior of its contact with the basioccipital [Fig. 2.4, dashed line]). The parasphenoid typically has lateral projections anterior

of the basioccipital (Fig. 2, LPP; the processes are broader in †*Taubateia*); the width just posterior to these processes is approximately half or greater than the width of the main body of the basioccipital in rhinelepineae, but much less than half in hypostomines. In addition, the portion of the parasphenoid just anterior to the lateral processes is almost flush with the surrounding bones in rhinelepineae but is greatly raised in hypostomines. Some Hypoptopomatinae and Loricariinae have widened parasphenoids that do not form a tall ridge, but the anatomy is significantly different (Fig. 3.2, 3.4). Some loricariines also have flat skulls with wider, flatter parasphenoids (Fig. 3.4), but their skulls are generally narrow and lack the other synapomorphies between †*Taubateia* and *Rhinelepis* Agassiz in Spix and Agassiz, 1829.

Although we have not assessed the character fully across loricariids, the mesethmoid is very wide at its base (over twice as wide as the narrowest portion) in the Rhinelepineae (Figs. 1.1, 2.2, 2.3, 3.3) as well as in †*Taubateia* (Figs. 1.2, 1.4, 2.4). The mesethmoid generally has lateral flaps located on its dorsal surface (Fig. 2, LPM). Normally, the flap ends anterior to the palatine condyle of the lateral ethmoid. In Rhinelepineae, the processes continue posteriorly and contact the dorsal wall of the palatine roughly halfway or greater from the lateral midpoint of the condyle, leaving a small gap between the lateral process and the main body of the mesethmoid, producing a roughly triangular bone (Fig. 2.2–2.4; the palatine facet is unclear on †*Taubateia* but the lateral processes of the mesethmoid are extended). Most other loricariids have a much narrower mesethmoid (base less than twice the width of the narrowest portion) with a lateral process that does not extend to the palatine facet, resulting in a bone that is mainly rectangular posterior to the flared anterior portion; Figs. 2.1, 3.1, 3.2, 3.4). We did find a similar state in *Rineloricaria rupestris* (Schultz, 1944); however, the process was sutured to the lateral ethmoid in *Rineloricaria rupestris* (versus just contacting) and the mesethmoid was much more elongate in *Rineloricaria rupestris*, with the greatest width only about twice the width of the narrowest. †*Taubateia* is also much larger than any known *Rineloricaria* sp. and overall cranial shape is a poor fit.

Although we have not examined this character across Loricariidae, there is an unusual feature of the fossil impression of †*Taubateia*: evidence of a two-part flat ridge across the prootic and orbitosphenoid bones and located within the orbit (outlined in Fig. 1.3, 1.4). This structure is visible on the CT scan of *Rhinelepis*, but to get a better view of it, we made a resin, three-dimensional print of the *Rhinelepis* neurocranium and pressed it into a substance called Model Magic (Crayola, Easton, Pennsylvania, USA). Model Magic is a lightweight, foam-like material that can hold impressions and hardens to keep its form. The imprint of the *Rhinelepis* skull is very similar to that of †*Taubateia* (Fig. 1.3, 1.4) in dimensions and depth of the impression of structures and the synapomorphies mentioned. We have not observed this ridge in any other loricariid. Also, the strong concavities on either side of the vomer that are present in most loricariids (Fig. 3.1, 3.3), but are much shallower in both *Rhinelepis* and †*Taubateia*, are noteworthy (Fig. 1.1, 1.2). The neurocrania of *Rhinelepis* and †*Taubateia* are comparatively flatter than in other rhinelepineae, which is



**Figure 2.** Ventral views of the medial bones and lateral ethmoids of the neurocrania of: (1) *Hypostomus luteus* (Godoy, 1980), MCP 12809; (2) *Pseudorinelepis genibarbus* (Valenciennes in Cuvier and Valenciennes, 1840), UF 162115; (3) *Rhinelepis aspera* Spix and Agassiz, 1829, AMNH 58332; (4) †*Taubateia paraiba* Malabarba and Lundberg, 2007, DGM 17-P; dashed line indicates a break in the parasphenoid. BO = basioccipital; LE = lateral ethmoid; LPM = lateral process of mesethmoid; LPP = lateral process of parasphenoid; ME = mesethmoid; PF = palatine facet; PS = parasphenoid; V = vomer. Scale bars = 1 cm.

likely one feature that allowed for the excellent preservation of †*Taubateia*.

*Rhinelepis* was described by Armbruster (2004) as lacking an anterior process of the compound pterotic; however, an extremely short anterior process is present in the CT scan (Fig. 1.1). In addition, the anterior edge of the compound pterotic lies nearly at a right angle to the long axis of the body. †*Taubateia* has a normal anterior process of the compound pterotic causing the anterior margin of the bone to be at an ~45° angle to the long axis of the body (Fig. 1.2). In addition, the transverse process of the Weberian apparatus is well-separated from the compound pterotic in *Rhinelepis* and only slightly separated from the compound pterotic in †*Taubateia*, and the anterior end of the mesethmoid is wider in *Rhinelepis* than in †*Taubateia*. Unique to †*Taubateia* is the shape of the posterior end of the parasphenoid, which tapers to the basioccipital posterior to broad lateral processes (Fig. 2.4). In other rhinelepinæ, the posterior end of the parasphenoid is approximately parallel with the sagittal plane posterior to the narrow, more pointed lateral processes (Fig. 2.2, 2.3). Based on these differences, we choose to continue recognizing †*Taubateia* as a distinct and valid genus in Rhinelepinæ, which is nonetheless more closely related to *Rhinelepis* than to *Pogonopoma* Regan, 1904 or *Pseudorinelepis* Bleeker, 1862.

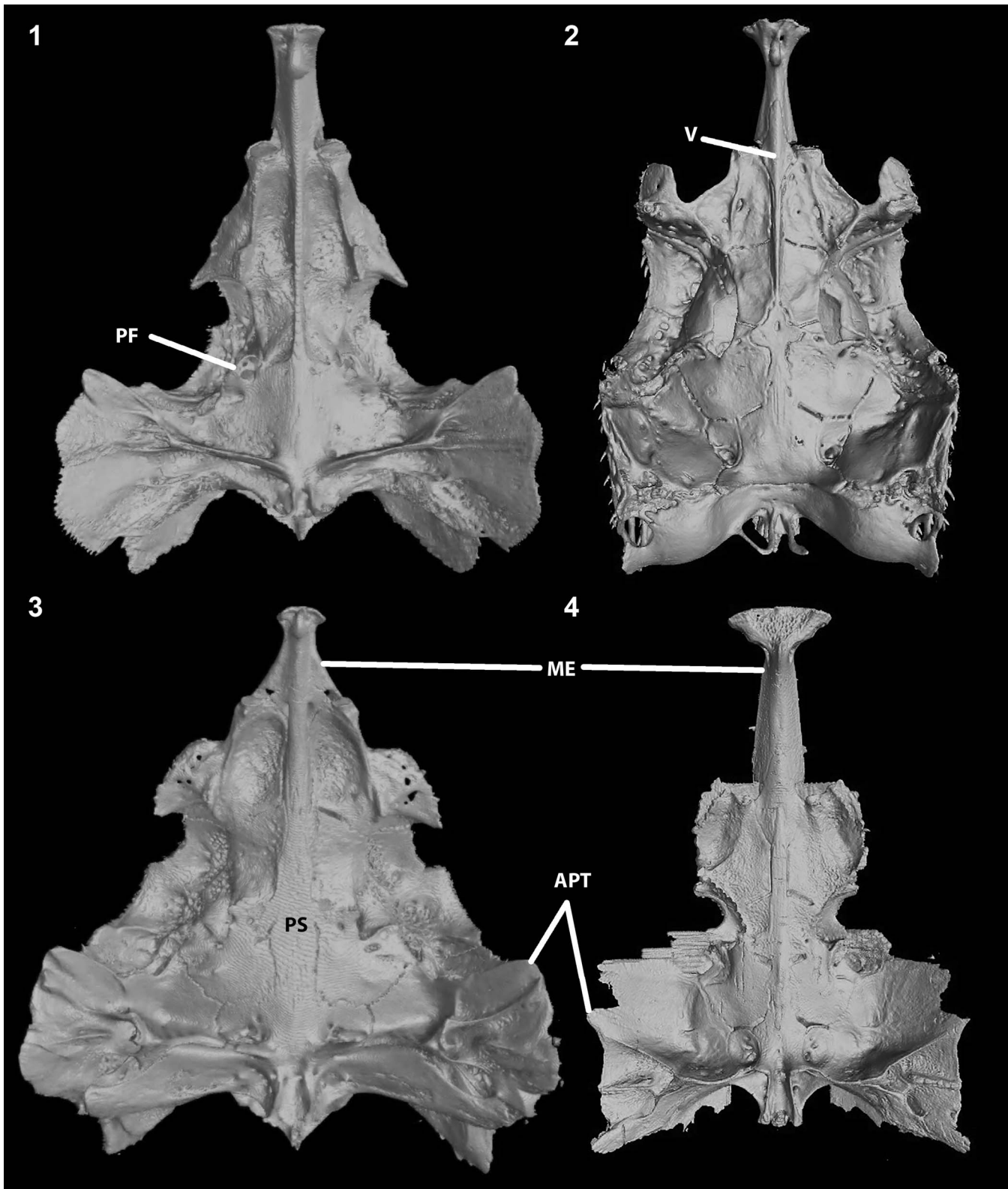
The morphological similarity of †*Taubateia* to *Rhinelepis* suggests that the two are sister taxa or perhaps chronospecies and that Rhinelepinæ has changed little in the last 20–30 Myr. This is likely true for other loricariids as well. †*Corydoras revelatus* Cockerell, 1925 (Callichthyidae) is a fossil species from the late Paleocene Mais Gordo Formation of Argentina (~58.5 Ma) that differs little from living *Corydoras* spp. (Lundberg et al. 1998, 2007; Reis, 1998). Characiform fish fossils found with †*Taubateia* in the Tremembé Formation are also considered congeners with living taxa, including †*Brycon avus* Woodward,

1898, †*Lignobrycon ligniticus* (Woodward, 1898), and †*Cyphocharax mosesi* Travassos and Santos, 1955, whereas †*Megacheirodon unicus* (Travassos and Santos, 1955) is considered sister to the extant taxa *Serrapinnus* Malabarba, 1998b and *Spintherobolus* Eigenmann, 1911 of the Cheirodontinae (Malabarba, 1998a, c). The extant pimelodid catfish genus *Steindachneridion* Eigenmann and Eigenmann, 1919 also has two extinct species in the Taubaté Basin (Bogan and Agnolín, 2019).

Using a molecular clock, Roxo et al. (2019) found that Rhinelepinæ was one of the earliest branching lineages of the Loricariidae (~47 Ma), and they suggested that many of the loricariid genera were already present by the late Oligocene or early Miocene. Roxo et al. (2019) used two calibration points: the calculated age of Siluriformes from other studies (Lundberg, 1993; Sullivan et al., 2006; Lundberg et al., 2007) and the out-group fossil †*Corydoras revelatus*. Although †*Taubateia* should be more thoroughly compared across loricariids, particularly species still found in the same region today, the genus is best recognized as a member of the Rhinelepinæ based on the evidence provided. With the current assignment of †*Taubateia* to the Rhinelepinæ as well as the recent identification of *Acanthicus* by Bogan and Agnolín (2020), there are now two internal Loricariidae calibration points available for future molecular dating analyses.

## Acknowledgments

The authors would like to thank C. Malabarba and J. Lundberg for discussions on †*Taubateia* and for use of an image of the specimen; R. Wilhite for printing the neurocranium of *Rhinelepis*; and D. Catania, K. Conway, R. Covain, O. Crimmen, E. Holm, K. Murphy, H. Ortega, M. de Pinna, R. Reis, R. Robbins, F. Roxo, M. Sabaj, K. Swagel, and D. Werneke for loans of specimens. NKL was supported by a Gerstner



**Figure 3.** Comparative ventral-view cranial CT scans of representative loricariids (not to scale): (1) *Hypostomus luteus* (Godoy, 1980), MCP 12809; (2) *Otocinclus vittatus* Regan, 1904, ANSP 174732, (3) *Pseudorinelepis genibarbus* (Valenciennes in Cuvier and Valenciennes, 1840), UF 162115, (4) *Planiloricaria cryptodon* (Isbrücker, 1971), ANSP 191512. APT = anterior process of compound pterotic; ME = mesethmoid; PF = prootic foramina; PS = parasphenoid; V = vomer.

Fellowship from the Richard Gilder Graduate School at the American Museum of Natural History, New York.

## Data Availability Statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p5hqbzqkq>.

## References

- Albert, J.S., Tagliacollo, V.A., and Dagosta, F., 2020, Diversification of Neotropical freshwater fishes: Annual Review of Ecology, Evolution, and Systematics, v. 51, p. 27–53, <https://doi.org/10.1146/annurev-ecolsys-011620-031032>.
- Armbruster, J.W., 1998, Phylogenetic relationships of the suckermouth armored catfishes of the *Rhinelepis* group (Loricariidae: Hypostominae): Copeia, v. 1998, p. 620–636.
- Armbruster, J.W., 2004, Phylogenetic relationships of the suckermouth armored catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae: Zoological Journal of the Linnean Society, v. 141, p. 1–80, <https://doi.org/10.1111/j.1096-3642.2004.00109.x>.
- Arroyave, J., Denton, J.S., and Stiassny, M.L., 2013, Are characiform fishes Gondwanan in origin? Insights from a time-scaled molecular phylogeny of the Citharinoidei (Ostariophysi: Characiformes): PLoS One, v. 8, p. e77269, <https://doi.org/10.1371/journal.pone.0077269>.
- Bleeker, P., 1862, Atlas Ichthyologique des Indes Orientales Néerlandaises, Volume 2, Siluroïdes, Chacoïdes et Heterobranchoides: Amsterdam, Muller, 112 p.
- Bogan, S., and Agnolín, F.L., 2019, Phractocephaline catfishes from the late Miocene of Argentina, with the description of a new taxon: Journal of Vertebrate Paleontology, v. 39, p. e1676254, <https://doi.org/10.1080/02724634.2019.1676254>.
- Bogan, S., and Agnolín, F.L., 2020, First fossil of the giant armored catfish *Acanthicus* (Siluriformes, Loricariidae) from the late Miocene of Entre Ríos Province, Argentina: Zootaxa, v. 4808, p. 571–581, <https://doi.org/10.11646/zootaxa.4808.3.11>.
- Chamon, C.C., 2016, Redescription of *Acanthicus hystrix* Agassiz, 1829 (Siluriformes: Loricariidae), with comments on the systematics and distribution of the genus: Zootaxa, v. 4088, p. 395–408, <https://doi.org/10.11646/zootaxa.4088.3.5>.
- Cockerell, T.D.A., 1925, A fossil fish of the family Callichthyidae: Science, v. 62, p. 397–398.
- Cuvier, G., and Valenciennes, A., 1840, Histoire Naturelle des Poissons, Tome Quinzième: Paris, Pitois, 540 p.
- Eigenmann, C.H., 1911, New characins in the collection of the Carnegie Museum: Annals of the Carnegie Museum, v. 8, p. 164–180.
- Eigenmann, C.H., and Eigenmann, R.S., 1889, Preliminary notes on South American Nematognathi: Proceedings of the California Academy of Science (ser. 2), v. 1, p. 119–172.
- Eigenmann, C.H., and Eigenmann, R.S., 1919, *Steindachneridion*: Science (n. ser.) v. 50(1301), p. 525–526.
- Fricke, R., Eschmeyer, W. N., and Fong, J. D., 2021, Genera/species by family/subfamily in Eschmeyer's catalog of fishes: <http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp> (accessed March 2021).
- Godoy, M.P., 1980, Poluição, peixes e pesca, reconhecimento preliminar com descrição de duas espécies novas de peixes: Rios Uruguai, Pelotas e Apuaê, aproveitamentos de Itá e de Machadinho: Rio de Janeiro, Centrais Elétricas do Sul do Brasil, S.A., Eletrobrás, Centrais Elétricas Brasileiras, S.A., 45 p.
- Isbrücker, I.J.H., 1971, Scientific results of the Peru-Bolivia-expedition Dr. KH Liiling 1966: *Pseudohemiodon (Planiloricaria) cryptodon*, a new species and subgenus from Peru (Pisces, Siluriformes, Loricariidae): Bonner Zoologische Beiträge, v. 21, p. 274–283.
- Lundberg, J.G., 1993, African-South American freshwater fish clades and continental drift: Problems with a paradigm, in Goldblatt, P., ed., Biological Relationships Between Africa and South America: New Haven, Connecticut, Yale University Press, p. 156–199.
- Lundberg, J.G., 1997, Fishes of the La Venta fauna: Additional taxa, biotic and paleoenvironmental implications, in Kay, R.F., Madden, R.H., Cifelli, R.L., and Flynn, J.J., eds., Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia: Washington, DC, Smithsonian Institution Press, p. 67–91.
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L., and Wesselingh, F., 1998, The stage for Neotropical fish diversification: A history of tropical South American rivers, in Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, X.M.S., and Lucena, C.A.S., eds., Phylogeny and Classification of Neotropical Fishes: Porto Alegre, Brazil, PUCRS University Press (EDIPUCRS; Pontifícia Universidade Católica do Rio Grande do Sul), p. 13–48.
- Lundberg, J.G., Sullivan, J.P., Rodiles-Hernández, R., and Hendrickson, D.A., 2007, Discovery of African roots for the Mesoamerican Chiapas catfish, *Lacantunia enigmatica*, requires an ancient intercontinental passage: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 156, p. 39–53, [https://doi.org/10.1635/0097-3157\(2007\)156\[39:DOARFT\]2.0.CO;2](https://doi.org/10.1635/0097-3157(2007)156[39:DOARFT]2.0.CO;2).
- Malabarba, M.C.S.L., 1998a, *Megacheirodon*, a new fossil genus of characiform fish (Ostariophysi: Characidae) from Tremembe Formation, Tertiary of São Paulo, Brazil: Ichthyological Exploration of Freshwaters, v. 8, p. 193–200.
- Malabarba, L.R., 1998b, Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae), in Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, X.M.S., and Lucena, C.A.S., eds., Phylogeny and Classification of Neotropical Fishes: Porto Alegre, Brazil, PUCRS University Press (EDIPUCRS; Pontifícia Universidade Católica do Rio Grande do Sul), p. 193–233.
- Malabarba, M.C.S.L., 1998c, Phylogeny of fossil Characiformes and paleobiogeography of the Tremembé Formation, São Paulo, Brazil, in Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, X.M.S., and Lucena, C.A.S., eds., Phylogeny and Classification of Neotropical Fishes: Porto Alegre, Brazil, PUCRS University Press (EDIPUCRS; Pontifícia Universidade Católica do Rio Grande do Sul), p. 69–84.
- Malabarba, M.C., and Lundberg, J.G., 2007, A fossil loricariid catfish (Siluriformes: Loricarioidea) from the Taubaté Basin, eastern Brazil: Neotropical Ichthyology, v. 5, p. 263–270, <https://doi.org/10.1590/S1679-62252007000300005>.
- Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C., Friedman, M., and Smith, W.L., 2012, Resolution of ray-finned fish phylogeny and timing of diversification: Proceedings of the National Academy of Sciences, v. 109, p. 13698–13703, <https://doi.org/10.1073/pnas.1206625109>.
- Regan, C.T., 1904, A monograph of the fishes of the family Loricariidae: The Transactions of the Zoological Society of London, v. 17, p. 191–350.
- Reis, R.E., 1998, Anatomy and phylogenetic analysis of the neotropical callichthyid catfishes (Ostariophysi, Siluriformes): Zoological Journal of the Linnean Society, v. 124, p. 105–168.
- Roxo, F.F., Ochoa, L.E., Sabaj, M.H., Lujan, N.K., Covain, R., Silva, G.S., Melo, B.F., Albert, J.S., Chang, J., Foresti, F., and Alfaro, M.E., 2019, Phylogenomic reappraisal of the Neotropical catfish family Loricariidae (Teleostei: Siluriformes) using ultraconserved elements: Molecular Phylogenetics and Evolution, v. 135, p. 148–165, <https://doi.org/10.1016/j.ympev.2019.02.017>.
- Schaefer, S.A., 1987, Osteology of *Hypostomus plecostomus* (Linnaeus), with a phylogenetic analysis of the loricariid subfamilies (Pisces, Siluroidei): Contributions in Science, Natural History Museum of Los Angeles County, v. 394, p. 1–31.
- Schultz, L.P., 1944, The catfishes of Venezuela, with descriptions of thirty-eight new forms: Proceedings of the United States National Museum, v. 94, p. 173–338.
- Spix, J.B.V., and Agassiz, L., 1829, Selecta Genera et Species Piscium quos in Itinere per Brasiliam Annos 1817–1820 Jussu et Auspici Maximiliani Josephi I: Bavariae Regis Augustissimi Peracto Collegit et Pingendos Curavit, Typis C: Munich, Wolf, 138 p.
- Sullivan, J.P., Lundberg, J.G., and Hardman, M., 2006, A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using rag1 and rag2 nuclear gene sequences: Molecular Phylogenetics and Evolution, v. 41, p. 636–662, <https://doi.org/10.1016/j.ympev.2006.05.044>.
- Travassos, H., and Santos, R.D.S., 1955, Caracídeos fósseis da Bacia do Paraíba: Anais da Academia Brasileira de Ciências, v. 27, p. 297–322.
- Woodward, A.S., 1898, Considerações sobre alguns peixes Terciários dos schistos de Taubaté, Estado de São Paulo, Brasil: Revista do Museu Paulista, São Paulo, v. 3, p. 63–70.

Accepted: 22 October 2021