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

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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 (knifefishes), 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 Rhinelepinae.

Materials and methods

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

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*Corresponding author

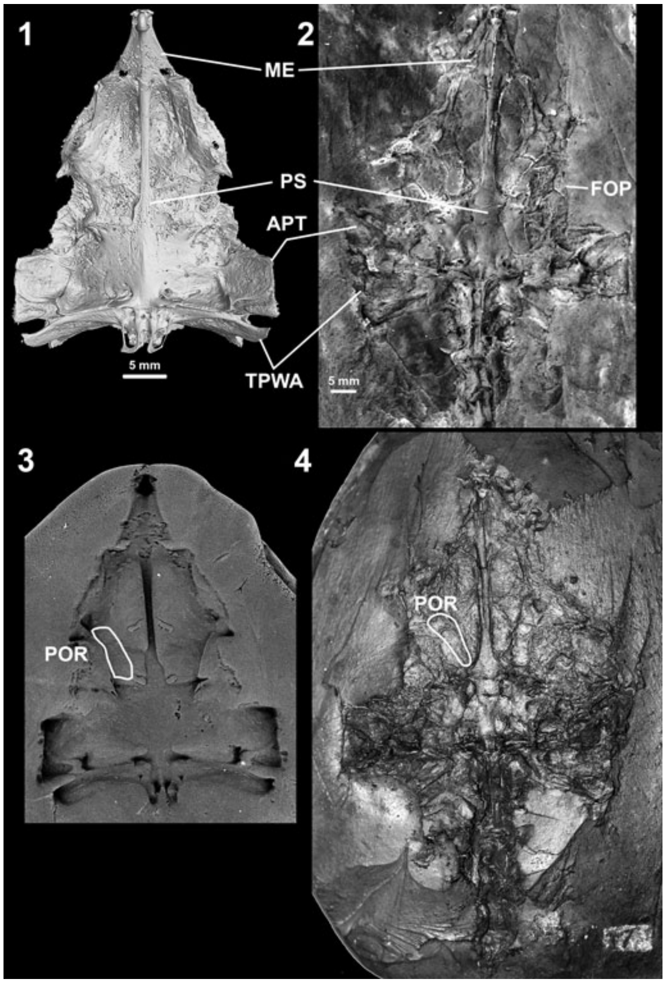

Figure 1. Neurocrania, ventral views: (**1**) *Rhinelepis aspera* Spix and Agassiz, 1829, AMNH 58332, CT scan; (**2**) †*Taubateia paraiba* Malabarba and Lundberg, 2007, DGM 17-P, from plastotype (latex positive of original specimen); (**3**) *Rhinelepis aspera*, cast of three-dimensional print of CT 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 Rhinelepinae 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 rhinelepines, 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 rhinelepines 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 Rhinelepinae (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 Rhinelepinae, 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 synapormorphies 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 rhinelepines, which is

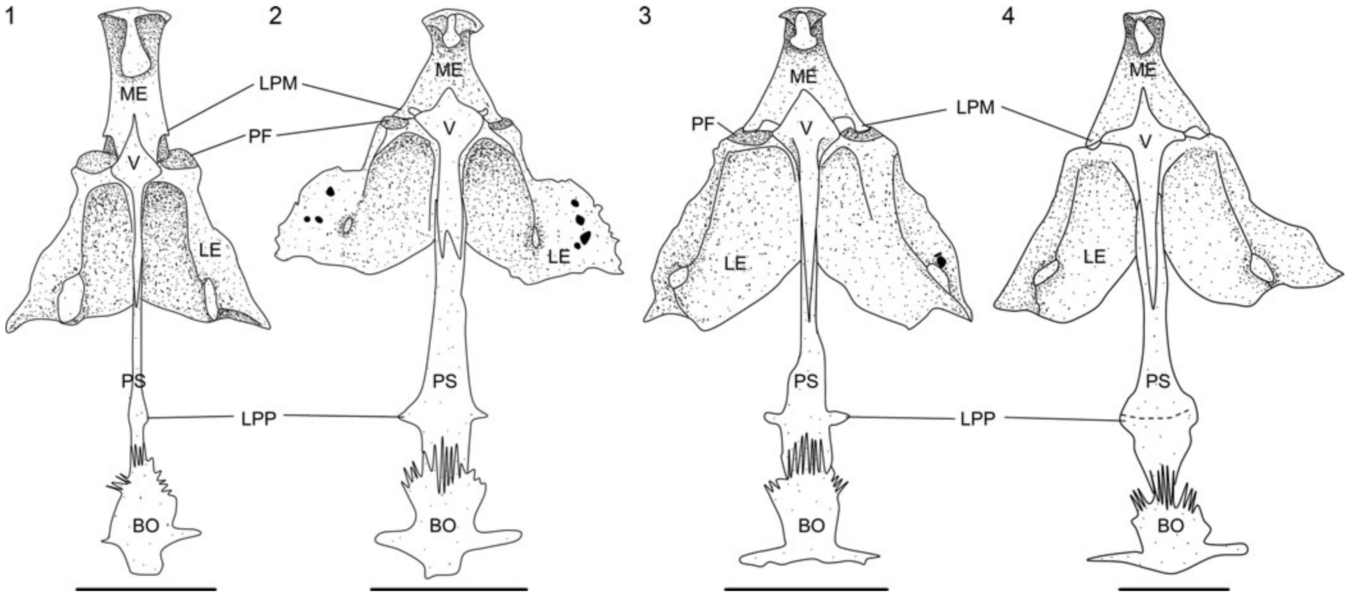

Figure 2. Ventral views of the medial bones and lateral ethomoids of the neurocrania of: (**1**) *Hypostomus luteus* (Godoy, 1980), MCP 12809; (**2**) *Pseudorinelepis genibarbus* (Valenciennes in Cuvier and Valenciennes, 1840), UF 162115; (**3**) *Rhinelepis aspera* Spix and Agassiz, 1829, AMNH 58332; (**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 rhinelepines, 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 Rhinelepinae, 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 Rhinelepinae has changed little in the last 20–30 Myr. This is likely true for other loricarioids 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 *Serrapinus* 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 Rhinelepinae 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 outgroup 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 Rhinelepinae based on the evidence provided. With the current assignment of †*Taubateia* to the Rhinelepinae 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.

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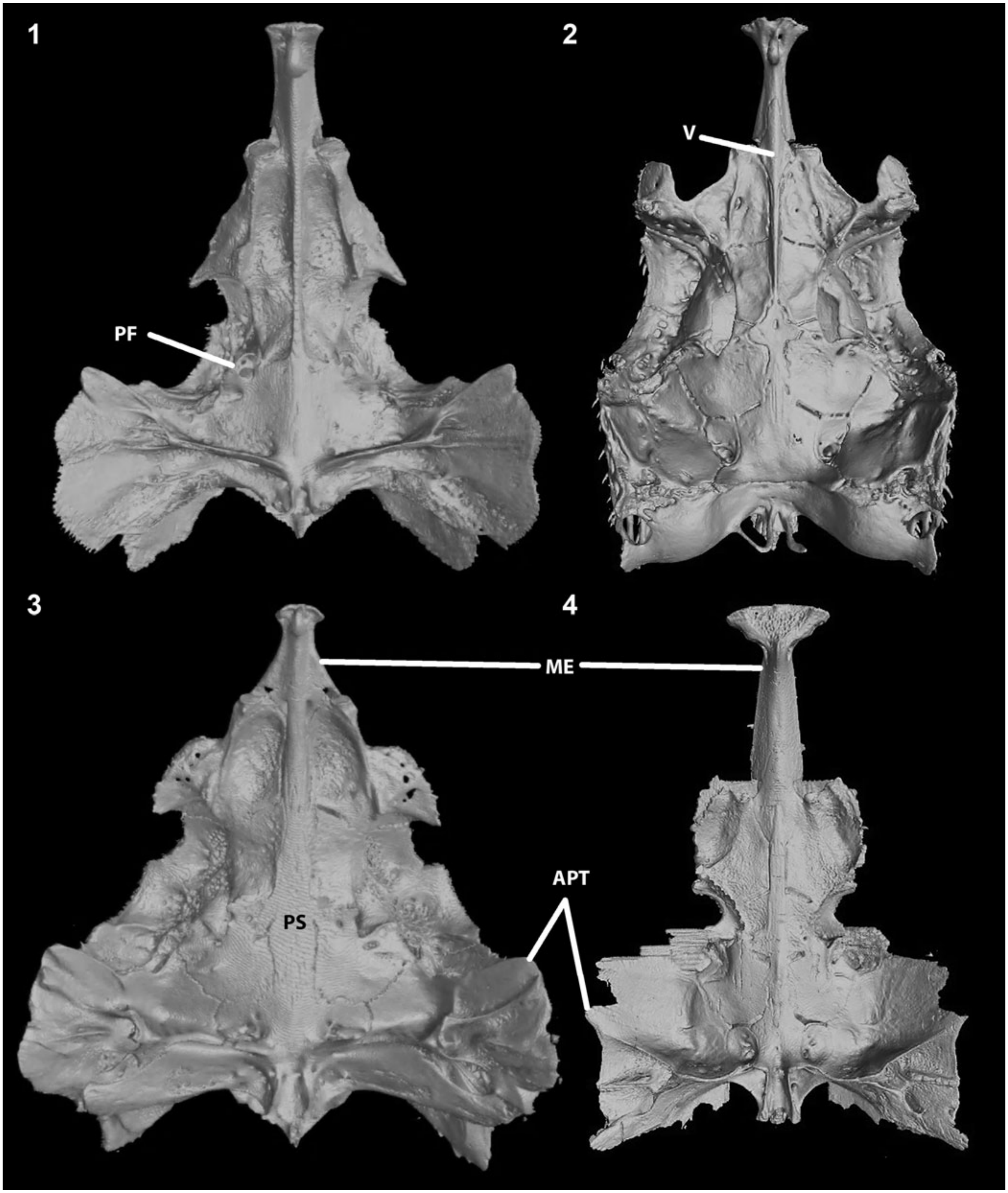

Figure 3. Comparative ventral-view cranial CT scans of representative loricariids (not to scale): (**1**) *Hypostomus luteus* (Godoy, 1980), MCP 12809; (**2**) *Otocinclus vittatus* Regan, 1904, ANSP 174732, (**3**) *Pseudorinelepis genibarbus* (Valenciennes in Cuvier and Valenciennes, 1840), UF 162115,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

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Data Availability Statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.p5hqbzkqt.

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