Neotropical Ichthyology, 5(3):263-270, 2007

A fossil loricariid catfish (Siluriformes: Loricarioidea) from the Taubaté Basin, eastern Brazil

Maria Claudia Malabarba* and John G. Lundberg**

A new loricariid catfish is described from the Tremembé Formation (Late Oligocene to Early Miocene) sediments of the Taubaté Basin in eastern São Paulo State, Brazil. *Taubateia paraiba*, new genus and species, is based on a single specimen preserved as a ventral-side impression of an articulated partial neurocranium, dorsal elements of the pectoral girdle and anterior vertebrae. The fossil is identified as belonging to family Loricariidae based on obvious overall similarity and the presence of diagnostic derived characters such as: odontodes, dorsal margin of metapterygoid contacting lateral ethmoid, presence of mesethmoid disk (condyle), and compound pterotic-supracleithrum bone. Also, as in most loricariids, the ossified transcapular (Baudelot´s) ligament plus basiocciptal lateral process form a prominent transverse wall at the occiput. Other derived characters preserved in *Taubateia* are synapomorphies at different levels within Loricariidae, including a wide and low parasphenoid, form of pterotic-supracleithrum, shape and position of the mesethmoid disk, a triangular lateral ethmoid with expanded posterolateral corner and a rounded and low ridge articulating with the metapterygoid, and a pointed distal margin of transverse process of the Weberian compound centrum. The derived characters recognized in this fossil are a distinctive combination for diagnosing a new genus and species but not for its unambiguous placements in any of the currently recognized loricariid subfamilies.

É descrito um novo loricarídeo proveniente dos sedimentos lacustres da Formação Tremembé (Oligoceno-Mioceno), os sedimentos lacustres da bacia de Taubaté no leste do Estado de São Paulo, Brasil. *Taubateia paraiba* n. sp. é descrita com base em um único espécimen fossilizado como uma impressão ventral, representado por um neurocrânio, elementos dorsais da cintura peitoral e vértebras mais anteriores. A nova espécie é identificada como Loricariidae com base na óbvia semelhança geral e na presença de alguns caracteres derivados tais como: odontodes, metapterigóide contactando o etmóide lateral, um disco (côndilo) ventral no mesetmoide e o pterótico fusionado ao supracleitro. Ainda, como ocorre na maioria dos loricarídeos, o ligamento transcapular ossificado (Baudelot) e o processo lateral do basiocciptal formam uma parede transversal distinta no occipital. Outros caracteres derivados preservados em *Taubateia* são sinapomorfias em diferentes níveis dentro de Loricariidae: parasfenóide largo e baixo; forma do pterótico-supracleithrum; forma e posição do disco ventral do mesetmóide; etmóide lateral triangular com o canto póstero-lateral expandido e crista para contato com o metapterigóide baixa e arredondada; e a margem distal do processo transverso estreita. Os caracteres derivados reconhecidos no fóssil formam tal combinação que permite distingui-lo dos demais loricarídeos conhecidos e atribuí-lo a um novo gênero e espécie, mas não é suficiente para incluí-lo em uma das subfamílias.

Key words: Tremembé Formation, Fossil loricariid, Oligocene-Miocene, Neurocranium, *Taubateia paraiba*, Anterior vertebrae.

Introduction

The Taubaté rift basin in eastern São Paulo State, Brazil, is drained by the modern Paraíba do Sul River (Fig. 1). This structural basin and three others in eastern Brazil form the continental rift of southeastern Brazil (CRSB), which is associated with continental break-up and the continuous opening of the Atlantic Ocean. During the Eocene-Oligocene took place the main development phase of the CRSB with the formation of a continuous central hemigraben: São Paulo, Taubaté, Resende, and Volta Redonda. The sedimentation of this phase is represented by the Taubaté Group including the Resende (basal), Tremembé (middle) and São Paulo (top) formations (Riccomini *et al.*, 1987, 2004; Riccomini, 1989). The Tremembé Formation is a lacustrine sedimentary unit in the Taubaté basin dated as Late Oligocene to Early Miocene (~30-20 Myr) based on its fossil content (Lima *et al.*, 1985; Lundberg *et al.*, 1998; Soria & Alvarenga, 1989).

Remains of siluriforms are common in the Taubaté Basin and include articulated skeletons and detached elements be-

*Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, 90619-900 Porto Alegre, RS, Brazil. mariacm@pucrs.br

**Department of Ichthyology, The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA. lundberg@acnatsci.org

longing to the pimelodid *Steindachneridion*. These fossils occur in two levels of the Tremembé Formation: montmorilonite clays and dark greenish shales. Two fossil species of *Steindachneridion* were described from the Tremembé Formation: *S. iheringi* (Woodward, 1898) and *S. silvasantosi* Figueiredo & Carvalho (1999a).

Despite the recent diversity, fossil loricariid records are extremely rare. Malabarba (1988) reported isolated body plate and fin spines of a yet indeterminate loricariid catfish from the Tremembé Formation. More recently, loricariid remains have been identified in the Miocene sediments of the La Venta Group in Colombia (Lundberg, 1997) and Puerto Madryn Formation of the Argentinian Patagonia (Cione *et al*., 2005). In this paper we describe and illustrate a single loricariid specimen represented by an articulated ventral side impression of the neurocranium and most anterior vertebrae. Although the information is limited, the characters recognized are sufficient to diagnose the fossil as a new genus and species.

Material and Methods

The specimen described herein (DGM 17-P) comes from the sediments of Tremembé Formation, Taubaté Tertiary Basin, eastern São Paulo (Fig. 1). It is deposited in the collection of the Museu de Ciências da Terra of the Departamento Nacional de Produção Mineral (DNPM), Rio de Janeiro, Brazil. This specimen was listed among the examined materials in the redescription and reconstruction of *Steindachneridion iheringi* (Figueiredo & Carvalho, 1999b:871, 873).

The general anatomical terminology used here follows Schaefer (1997) with the compound pterotic-posttemporal-supracleithrum bone being referred to simply as pterotic. Comparisons to modern fishes were made with cleared and stained (C&S) or dry skeletons (skel) as noted below.

Comparative material. *Acanthicus hystrix*, ANSP179537 (skel); *Ancistrus cirrhosus*, ANSP 78075 (skel); *Delturus brevis*, MCP 26927; *Harttia kronei* (C&S); *Hemiancistrus fuliginosus*, UFRGS 5404 (skel); *Hemipsilichthys gobio*, MNRJ 13654; *Hypostomus commersoni*, UFRGS 5482 (skel); *Hypostomus isbrueckeri*, UFRGS 5403 (skel); *Hypostomus regain*, UFRGS 5481 (skel); *Hypostomus* sp., ANSP 159092 (skel); *Ixinandria steinbachi* (C&S); *Kronichthys subteris*, MZUSP 58559; ANSP 78080 *Loricaria* sp., (skel); *Loricaria* sp., ANSP 187056 (skel); *Loricarichthys anus*, UFRGS 5500 (skel); *Neoplecostomus parati*, MCP 32149; Neoplecostominae nov. gen. nov. sp., MCP 27701; *Pareiorhapis cameroni*, MCP 17618; *Pareiorhina rudolphi*, MCP 18052; *Planiloricaria cryptodon*, ANSP 187054 (skel); *Pogonopoma wertheimeri*, MCP 15437 (C&S); *Pseudoloricaria* sp., ANSP 187058 (skel); *Pterygoplichthys* sp., ANSP 179358 (skel); *Pterygoplichthys* sp., ANSP 175540 (2 skel); *Reganella depressa*, ANSP 187055 (skel); *Rhinelepis* sp., MCP 19001 (C&S), UFRGS 5390 (skel); *Rineloricaria parva* (C&S); *Sturisoma* sp., ANSP 187057 (2 skel).

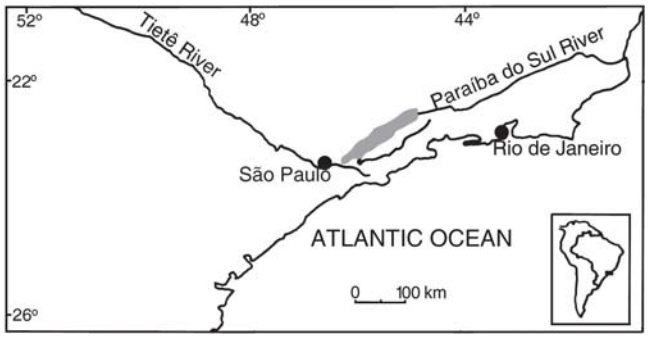

Fig. 1. Regional map indicating location of Taubaté Basin (in black) in the eastern of São Paulo State, Brazil.

Institutional abbreviations. ANSP, Academy of Natural Sciences, Philadelphia; DGM, Museu de Ciências da Terra, DNPM, Rio de Janeiro; MCP, Museu de Ciências e Tecnologia, Porto Alegre; UFRGS, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Results

Family Loricariidae
Taubateia, new genus
Figs. 2-5

Type species. *Taubateia paraiba*, new species.

Diagnosis. Mesethmoid with shallow median cleft, flanked by reduced and anteriorly rounded cornua (Fig. 4); mesethmoid ventral disk small, ball-shaped and subterminal (Fig. 4); mesethmoid shaft wide (Fig. 3a); anterior tip of prevomer forms spike-like sutural joint with mesethmoid (Fig. 3a); posterolateral corner of the lateral ethmoid greatly expanded (Figs. 2, 3a); ventral ridge on lateral ethmoid low and rounded (Figs. 2, 3a); parasphenoid wide and flat (Figs. 2, 3a); pterotic approximately square and widest at ventral margin(Figs. 2, 3a, 5); transverse process of Weberian complex centrum not contacting the ossified transcapular ligament and reaching the border of the pterotic (Fig. 5); ossified transcapular ligament forming a short transverse shelf medially reaching the basiocciptal lateral process (Fig. 5); aortic groove extending at least to the ninth vertebrae (Fig. 3a); absence of pleural ribs posterior to sixth vertebrae (Fig. 2).

Etymology. *Taubateia* from the name Taubate, in reference to the basin where the fossil comes from, with the suffix "*ia*" from the Latin and Greek, denoting pertaining to; gender feminine.

Taubateia paraiba, new species
Figs. 2-5

Holotype. DGM 17-P, a ventral impression of the anterior part of the fish including neurocranium and first vertebrae articulated, ventral skull length 54.5 mm.

Locality and geological age. Late Oligocene to Early Miocene shales from the Tremembé Formation, Taubaté Basin, cropping out near Tremembé county (22º 50' S, 45º 52' W), São Paulo State, Brazil.

Diagnosis. As for the genus.

Description. The description is necessarily limited to the ventral view of the head skeleton and anterior vertebrae.

Neurocranium. The neurocranium is roughly triangular in outline shape, narrow anteriorly and greatly expanded across the occipital region. The arrangement and shapes of cranial bones resemble those of other loricariids, and show typical loricariid features, such as: vertical projection in the anterior end of mesethmoid; the reduced mesethmoid cornua, triangular shaped and expanded lateral ethmoids, a compound pterotic posteriorly expanded.

The mesethmoid is a triangular bone, anteriorly narrow and pointed, and expanded posteriorly. It is flattened with lateral expansions (crest of Py-Daniel, 1997) incorporated into the main body of the bone, as occurs in the depressed species. It presents the typical pair of greatly reduced and rounded anterolateral cornua, each with a shallow concavity in the center and a few grooves in the cornua base. The anterior edge of the mesethmoid is smooth with a small median cleft between the cornua. A moderately developed rounded disk (condyle) projects ventrally from the mesethmoid behind the cornua; there are no signs of concave facets on the disk but two depressions are present laterally. Based on the good preservation of this specimen, particularly the mesethmoid region, we may assume that these facets did not exist. The mesethmoid disk has a subterminal position, not contacting the anterior margin of the mesethmoid and would not be visible in a dorsal view. Posteriorly, the mesethmoid meets the prevomer in a V-shaped suture.

The prevomer has the shape of an elongated diamond with small lateral wings contacting the mesethmoid and the lateral ethmoid. The anterior end is moderately developed as a pointed spike that deeply interdigitates with the mesethmoid. Its posterior end is an elongate spine that extends between a pair of parasphenoid spikes.

The paired lateral ethmoids are large and triangular with the posterolateral corner expanded. The lateral ethmoid anterior border is straight and bears an anterolateral articular facet for the palatine. The lateral ethmoid expands posteriorly to form a distinct lateroposterior process at the anterior margin of the orbit. A low ridge, rounded in cross-section, extends longitudinally near the lateral ethmoid margin from the pa-

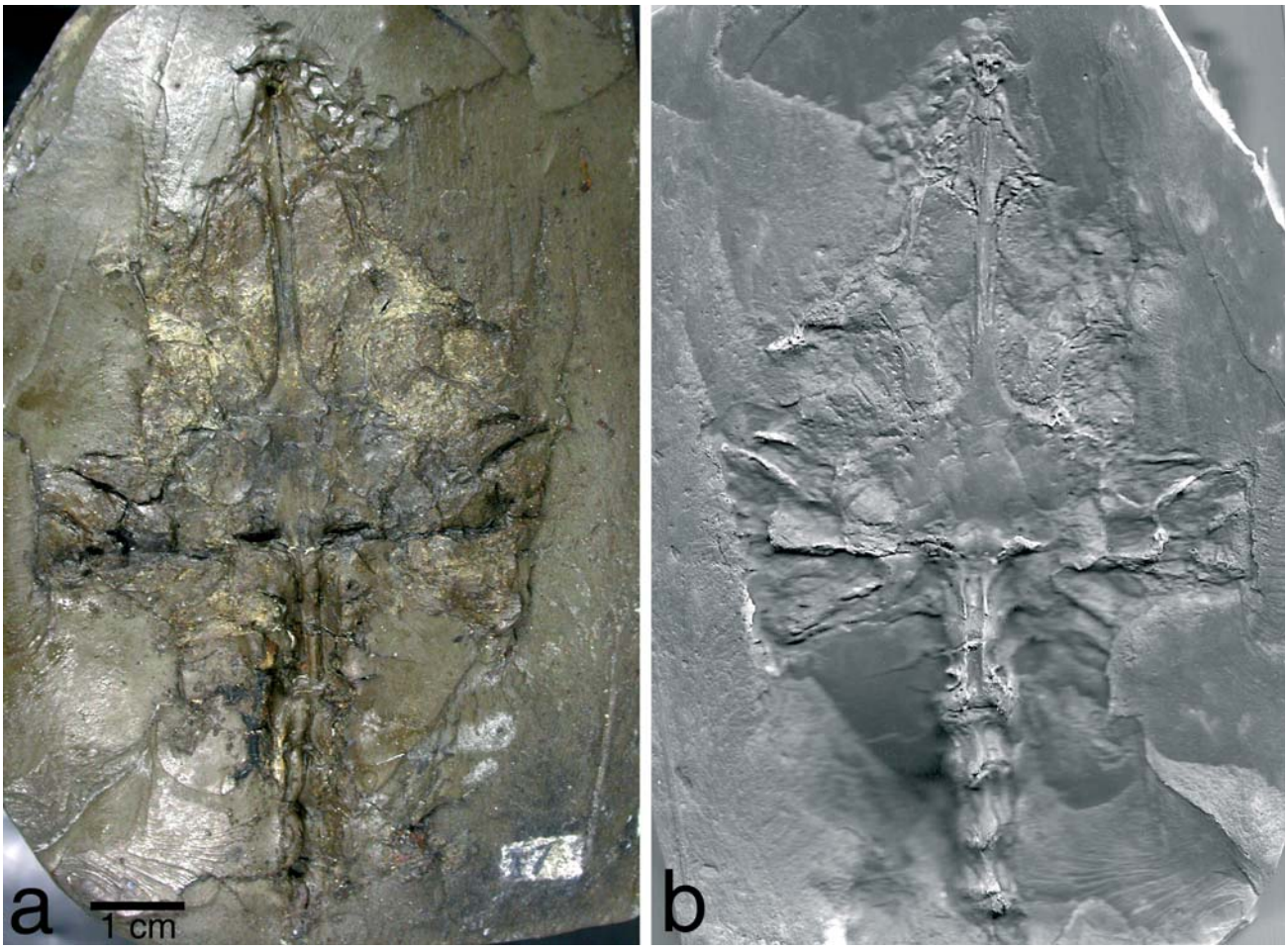

Fig. 2. *Taubateia paraiba*, DGM 17-P, holotype. Shale slab with fossil impression from the Tremembé Formation, Taubaté Basin (a) and the cast in latex (b).

latine articular facet to the posterior border to terminate at an ovoid condyle that would presumably articulate with dorsal surface of the metapterygoid. According to Py-Daniel (1997:38), regardless of the extent of contact between lateral ethmoid and metapterygoid, the posterior end of the lateral ethmoid is always involved via a condyle or suture. The state of preservation does not allow us to determine the structure of the nasal capsules.

The parasphenoid lies flat on the ventral midline between the prevomer anteriorly to basioccipital posteriorly. Anteriorly the parasphenoid forms a wide and slightly raised ridge separating the lateral ethmoids; posteriorly its margin is gently curved laterally below the orbitosphenoid, and expanded, forming small lateral wings in contact with the prootics. The posterior margin of the parasphenoid strongly interdigitates with the basioccipital across the ventral midline.

The basioccipital is laterally sutured with the prootic and exoccipital. Its lateral process contacting with the mesial end of the ossified transcapular (Baudelot's) ligament of the posttemporal-supracleitrum that continues laterally forming a wall sutured to the exoccipital and pterotic. In a developmental study of the skeleton of the loricariid *Ancistrus* cf. *triradiatus,* Geerinckx *et al*. (2007) show that the ossification of the transcapular ligament arises from two sources: medially from the basioccipital (our "basioccipital lateral process") and laterally from the pterotic-supracleithrum (our ossified transcapular ligament).

The orbitosphenoid is nearly retangular in form with concave lateral margins. It is sutured to the lateral ethmoid anteriorly, and with the prootic posteriorly. Despite the large expansion of the lateral ethmoid posterior border, the orbitosphenoid does not follow this enlargement, and the anterior (with the lateral ethmoid) and the posterior (with prootic) sutures remain with similar lengths.

The exoccipitals are a small pair of bones limited anteriorly by the prootic and mesially by the basioccipital. Posteriorly, the exoccipital remains limited by the basioccipital lateral process and transcapular ligament. The exoccipital is

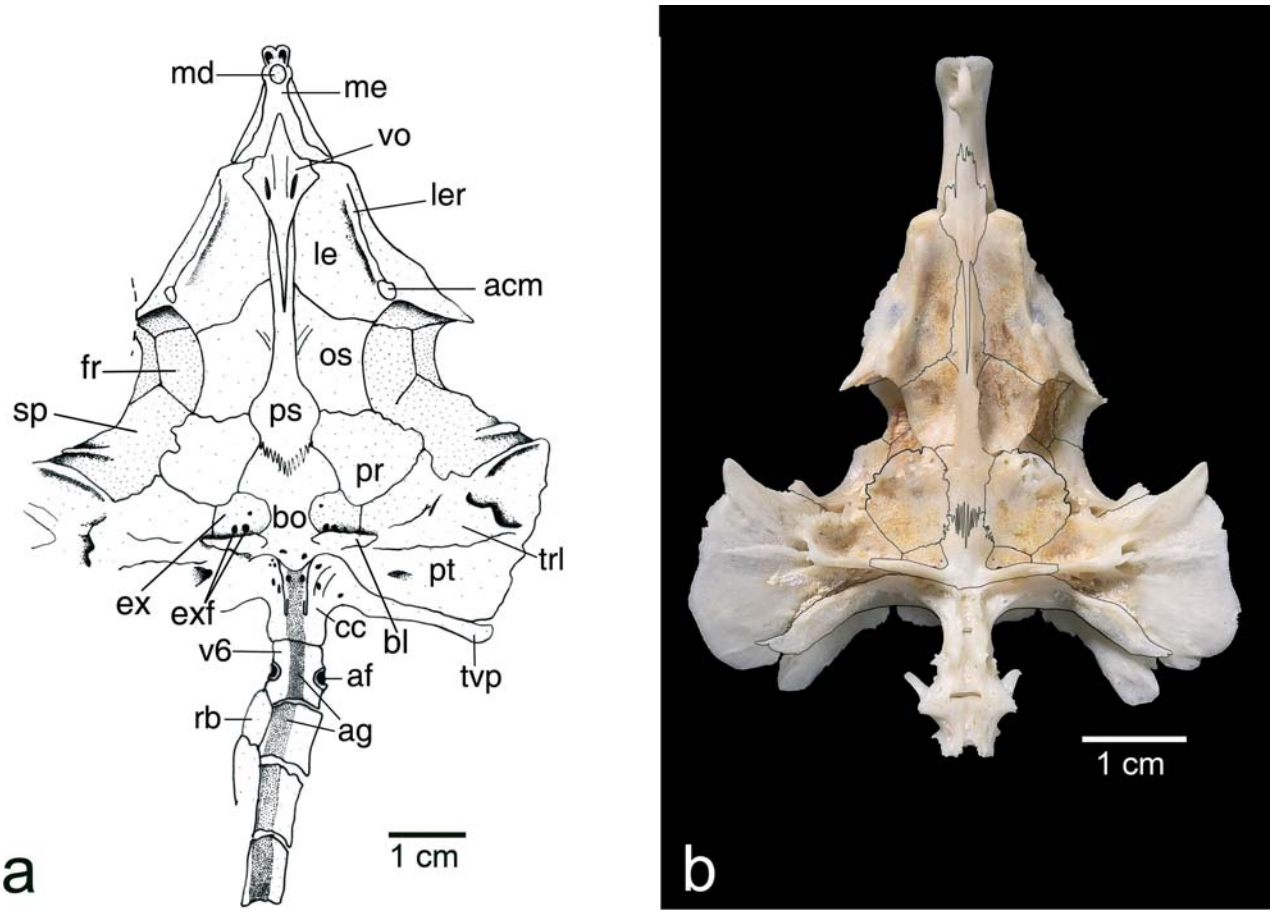

Fig. 3. Comparison between an interpretative drawing of *Taubateia paraiba* (a) and a *Hypostomus* sp. neurocranium (b), both in ventral view. **Abbreviations**: acm, articular condyle for metapterygoid; af, articular facet for rib on v6; ag, aortic groove; bl, basioccipital lateral process; bo, basioccipital; cc, Weberian complex centrum; ex, exoccipital; exf, exoccipital foramina; fr, frontal; le, lateral ethmoid; ler, lateral ethmoid ridge for metapterygoid; me, mesethmoid; md, mesethmoid disk; os, orbitosphenoid; pr, prootic; ps, parasphenoid; pt, pterotic-supracleithrum; rb, rib; sp, sphenotic?; trl, transcapular ligament; tvp, transverse process of the Weberian compound centrum; v6, sixth vertebrae.

pierced by the two foramina for the glossopharyngeal and vagus nerves, near its posterior border.

The prootic forms the ventrolateral floor of the neurocranium posterior to the orbitosphenoid. It is a large bone sutured posteriorly to the basioccipital, exoccipital and pterotic. A circular notch is present in the anterolateral border of the prootic representing the trigeminofacial foramen. Almost in the center of the bone there is a smaller foramen presumably for the hyomandibular branch of the facial nerve.

Generally in loricariids the sphenotic is a paired bone mostly developed and visible on the dorsal side of neurocranium. However, in DGM 17-P a portion of this bone is preserved in a ventral view, displaying its anterior suture to the frontal and the spine projected from its lateral border. Some odontode marks can be observed along the sutures and lateral border of the sphenotic. Even a few odontodes are preserved scattered in the sediment.

The paired pterotics are broad compound bones (pterotic + supracleithrum) forming most of the posterolateral part of the skull. Each pterotic is greatly expanded and squarish in shape with the lateral margin nearly straight. The ventral surface of the pterotic bears a strong ridge for pectoral girdle articulation. Posteriorly it is closely associated but not fused with the transverse processes of complex vertebrae. The ventral aspect of *Taubateia* shows the transverse process of the Weberian compound centrum surrounding the swimbladder.

Weberian apparatus and anterior axial skeleton. The Weberian complex centrum is almost square and relatively short, not much longer than the seventh centrum. It is fused to the basioccipital anteriorly and sutured to the sixth vertebrae centrum posteriorly. The transverse process and the complex centrum form nearly a 70º angle, being slightly ventrally directed. The distal tip of the transverse process of the Weberian complex centrum is in contact with the pterotic with about the same width than the shaft. It is distally rounded (not pointed) and cancellous.

In addition to the vertebrae incorporated into the Weberian apparatus, vertebral centra six through nine are preserved. The sixth centrum has a large pair of ventrolaterally placed facets for articulation with the first pair of ribs. The aortic groove runs open and delimited by laminar bone from the complex centrum to at least the vertebra centrum 9.

Etymology. The specific name *paraiba* (a noun in apposition) refers to the modern river Paraíba do Sul, which crosses the geological basin where the fossil was collected; gender feminine.

.

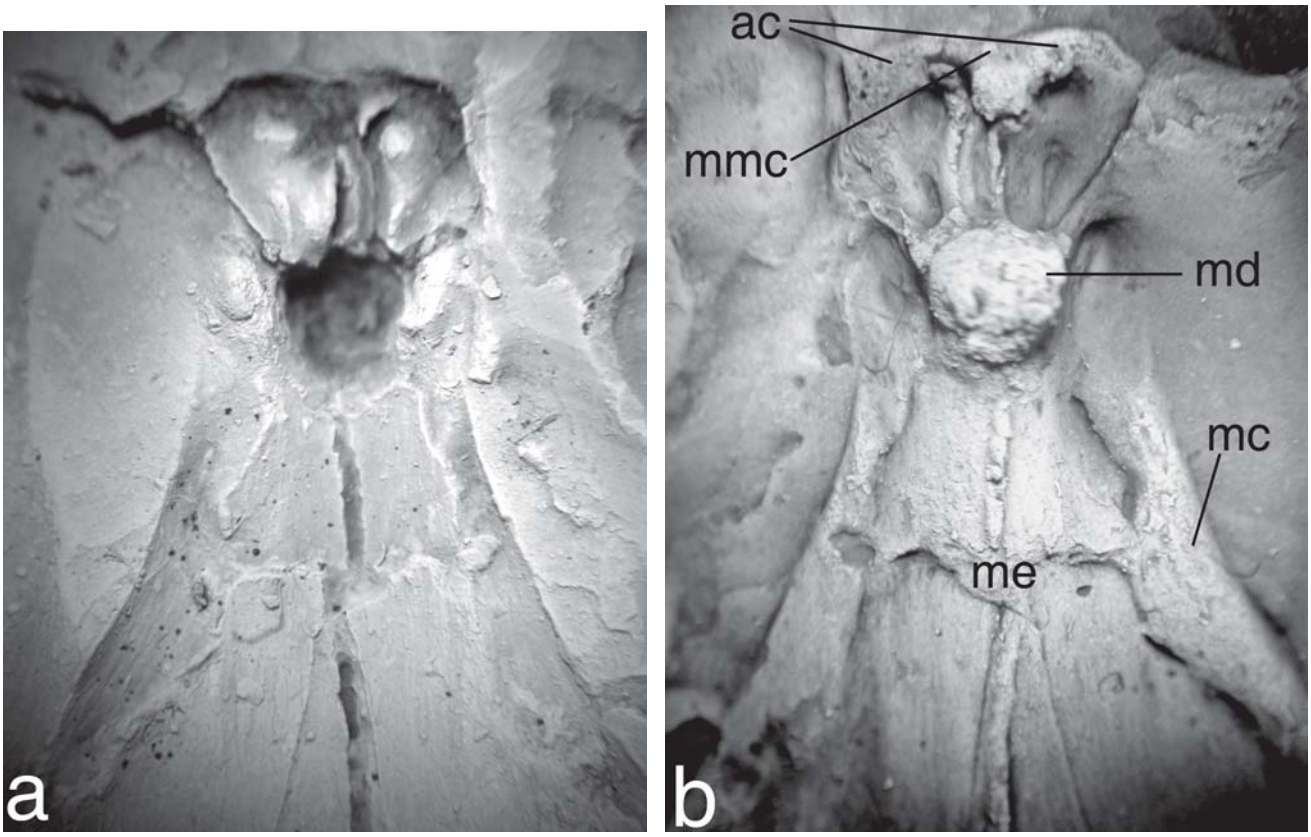

Fig. 4. *Taubateia paraiba*, most anterior part of the neurocranium showing mesethmoid features: a, original fossil impression sprinkled with ammonium chloride; b, cast in latex sprinkled with ammonium chloride. **Abbreviations**: ac, mesethmoid anterior cornua; mc, mesethmoid crest; md, mesethmoid disk; me, mesethmoid; mmc, mesethmoid median cleft.

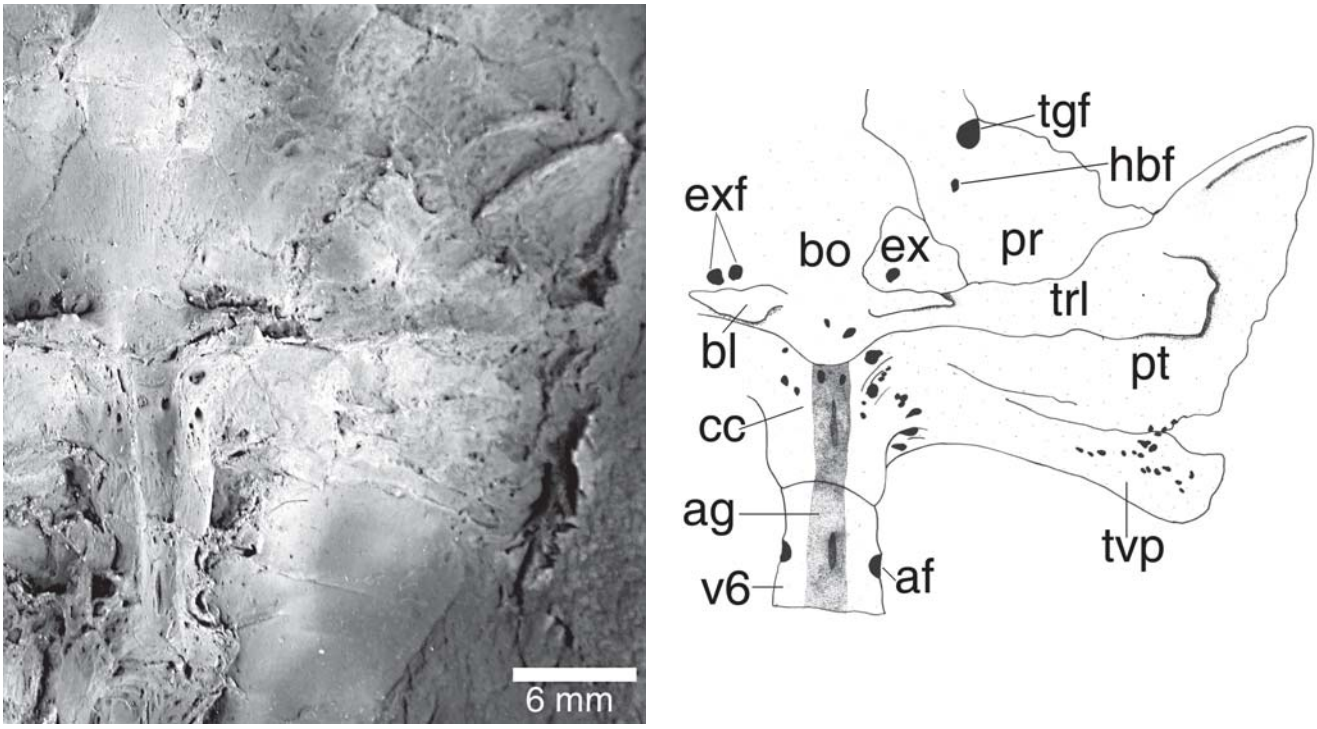

Fig. 5. *Taubateia paraiba*, posterior region of the neurocranium and first vertebrae articulated: a, fossil sprinkled with ammonium chloride; b, interpretative drawing. **Abbreviations**: af, articular facet for rib on v6; ag, aortic groove; bl, basioccipital lateral process; bo, basioccipital; cc, Weberian complex centrum; ex, exoccipital; exf, exoccipital foramina; hbf, hyomandibular branch of facial nerve foramen; pr, prootic; pt, pterotic-supracleithrum; tgf, trigeminofacial foramen; v6, sixth vertebrae.

Discussion

The fossil specimen described herein is the sole representative of its taxon and preserves only a ventral side impression of the neurocranium and anterior vertebrae. Consequently, the observable features for this species are limited to a small fraction of those documented in broader comparative and phylogenetic studies of Loricariidae (e.g. Schaefer, 1987, 1991, 2003; Py-Daniel, 1997; Armbruster, 2004). Nevertheless, some of the preserved characters are derived states and recognized as synapomorphies for monophyletic subgroups within Loricariidae.

Despite of the limited information, *Taubateia* can be phylogenetically placed in family Loricariidae based on the presence of three synapomorphies: dorsal margin of the metapterygoid contacting the lateral ethmoid (Schaefer, 1987; Armbruster, 2004: character 97), which can be inferred from the presence of the lateral ethmoid ridge and condyle; a mesethmoid disk (Armbruster, 2004: character 100); pterotic fused with supracleithrum and expanded posteriorly (Schaeffer, 1987). In addition, *Taubateia* shows an ossified transcapular (Baudelot´s) ligament forming a distinct wall along the occiput, as occurs in most loricariids (Neoplecostominae, Hypoptopomatinae, Loricariinae and Hypostominae; Armbruster, 2004: character 93).

Some derived characters associated with loricariid subfamilies or genera are preserved in *T. paraiba*. Thus, we recognize characters of the Loricariinae: a wide and low parasphenoid, the shape of pterotic, and the size and position of the mesethmoid disk. Although, none of the foregoing are among the unambiguous changes listed for Loricariinae by Armbruster (2004) *Taubateia* shares the following derived character with subgroups within Loricariinae: a trapezoidal pterotic widest ventrally (108:1) is shared with the Loricariini (*Loricariichthys, Loricaria, Crossoloricaria, Rineloricaria, Ixinandria* in Armbruster's analysis); a wide and only slightly raised parasphenoid (character 106, state 1) is shared with *Loricarichthys*, *Loricaria* and *Crossoloricaria* (clade 28); and a longitudinal, low ridge on lateral ethmoid shared with *Harttia* and *Lamontichthys*.

Of the 29 synapomorphies listed by Py-Daniel (1997) for Loricariini, two are preserved in *T. paraiba*: parapophyses of the fourth vertebrae (transverse process of Weberian complex centrum) reaching the border of the pterotic; and contact of the lateral ethmoid with the suspensorium via broad suture (this is assumed from the presence of a lateral ethmoid ridge). Among these loricariin synapomorphies is the basioccipital not sutured to ossified transcapular (Baudelot's) ligament; with the exoccipital between the two bones (character 18, state 1). In *Taubateia*, the basioccipital is in contact with the ligament and the exoccipital lies at the corner formed by them (character 18, state 0) as occurs in *Hemiodontichthys* (a reversion) in this tribe.

However, derived characters of *T. paraiba* shared with

subfamilies other than Loricariinae, create a conflicting pattern precluding a clear assignment of the fossil to a subfamily. Among these are a triangular lateral ethmoid with a longitudinal ridge and a posterior condyle (or facet) for contacting the metapterygoid. The triangular lateral ethmoid with greatly expanded posteroventral corner of *Taubateia* is synapomorphic for some hypoptopomatines (Armbruster, 2004: character 95, state 1). The presence of the ridge is widespread in loricariids, but it is rounded and low (character 97, state 1) in Hypostominae, some loricariines (*Harttia* sp, *Lamontichthys*), most hypoptopomatines (Armbruster, 2004: clade 16), and is also present in *Lithogenes*. On other hand, an additional posterior condyle for articulating with metapterygoid is synapomorphic for Hypostominae plus Ancistrinae (Schaefer, 1987). Still, *Taubateia* shares a wide and flat parasphenoid with Rhinelepini (in special with *Pseudorinelepis*) and the absence of ribs posterior to the sixth vertebra (Armbruster, 1998).

In the redescription of *Lithogenes villosus*, Schaefer (2003) lists 11 synapomorphies supporting the clade *Lithogenes* + Loricariidae. Two of these are visible in *Taubateia*: the presence of a mesethmoid condyle (character 1) and metapterygoid contacting the lateral ethmoid (character 12). The other nine synapomorphies were not preserved and can not be verified in the fossil. *Lithogenes* is diagnosed by nine synapomorphies, none of which are preserved in *Taubateia*. The Loricariidae clade, represented in the Schaefer's paper by *Loricariichthys, Hemipsilichthys, Neoplecostomus, Parotocinclus, Ancistrus and Kronichthys*, is supported by 8 synapomorphies. The character 2, mesethmoid condyle shape, is the only one verifiable in the fossil. Shaefer (2003) defined two states for this character: state 0, spherical as in *Lithogenes*; and state 1, laterally compressed, discoid as in the Loricariidae clade. In *Taubateia* the mesethmoid condyle is not discoid; it is round, ball-like, but in a very different way from *Lithogenes* spherical condyle. Whereas in *Lithogenes villosus* the condyle is wide, slightly anteriorly projected, with two anterior processes (in Schaefer, 2003: fig. 5), in *Taubateia* it is small, straight ventrally projected with no processes.

In order to obtain additional information about its phylogenetic relationships, *Taubateia* was included in the taxon/character matrix of Schaefer (2003) and an exhaustive search using PAUP 3.1 (Swofford, 1993) was performed. This search resulted in 15 most parsimonious trees with length=65, CI=0.754, and RI=0.714. The addition of *Taubateia* resulted in more numerous trees which are shorter than those obtained by Schaefer (2003, five equally parsimoniuous trees with 66 steps. In the 15 parsimonious trees, three different positions are suggested for *Taubateia*: as sister group to loricariids (including *Lithogenes*); as sister group to nonlithogenine loricariids; and as sister-group to *Lithogenes* and that pair forming the sister group to nonlithogenine loricariids. Other tree topologies vary only in terms of the relative position of the six nonlithogenine loricariid representatives, as occurred in the Schaefer's (2003) analysis. In all trees *Taubateia* plus *Lithogenes* plus Loricariids form a monophyletic group. The strict consensus of the 15 equally parsimonious trees shows a polytomy with *Taubateia*, *Lithogenes* and loricariids.

Summarizing all above information, *Taubateia* shows few derived characters which can be considered derived at different levels within loricarioids: mesethmoid slightly cleft with very reduced and rounded lateral cornua; presence of a mesethmoid condyle; mesethmoid condyle, small, spherical and subterminal; mesethmoid shaft wide; posterolateral corner of the lateral ethmoid expanded; lateral ethmoid with rounded ridge for contacting the metapterigoid; parasphnoid on orbitosphenoid wide and flat; transcapular (Baudelot's) ligament forming a wall; relatively short Weberian complex centrum; parapophyses of 4th vertebrae with approximately same length as the pterotic; aortic-groove extending to vertebrae 9; pleural ribs posterior to sixth vertebrae absent; pterotic trapezoidal and expanded posteriorly. At this time the position of *Taubateia* is uncertain within Loricariidae, the character combination of the fossil does not fit in any of the subfamily diagnoses and this is only partly a result of non-preservation. For this reason, it would be premature to assign the fossil taxon to any subfamily.

Acknowledgements

The authors thank to D. A. Campos and Rita C. Cassab at DNPM-RJ for the loan of fossil specimens for study; and to Kyle Luckenbill for preparing the photo of the modern *Hypostomus* skull. Thanks also to E. Pereira, P. Lehmann and M. Rodriguez for providing comparative material and information. The U.S. National Science Foundation supported this work through research grant DEB 0089612 to JGL, partial support of publication costs was provided by the All Catfish Species Inventory (NSF DEB 0315963).

Literature Cited

Armbruster, J. W. 1998. Phylogenetic relationships of the suckermouth armored catfishes of Rhinelepis group (Loricariidae: Hypostominae). Copeia, 1998: 620-636.

Armbruster, J. W. 2004. Phylogenetic relationships of the suckermouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. Zoological Journal of the Linnean Society, 141: 1-80.

Cione, A. L., M. M. Azpelicueta, J. R. Casciotta & M. T. Dozo. 2005. Tropical freshwater teleosts from Miocene beds of eastern Patagonia, southern Argentina. Geobios, 38:29-42.

Figueiredo, F. J. & B. C. Carvalho 1999a. *Steindachneridion silvasantosi* n.sp. (Teleostei, Siluriformes, Pimelodidae) from the Tertiary of Taubaté Basin, State of São Paulo, Brazil. Anais da Academia Brasileira de Ciências, 71: 683-695.

Figueiredo, F. J. & B. C. Carvalho 1999b. Redescription of *Steindachneridion iheringi* (Woodward, 1898) (Teleostei, Siluriformes, Pimelodidae) from the Tertiary of Taubaté Basin, São Paulo State, Brazil. Anais da Academia Brasileira de Ciências, 7: 869-884.

Geerinckx, T., M. Brunain & D. Adriaens. 2007. Development of the Osteocranium in the Suckermouth Armored Catfish

Ancistrus cf. *triradiatus* (Loricariidae, Siluriformes). Jounal of Morphology, 268: 254-274.

Lima, M., M. Salard-Cheboldaeff & K. Suguio. 1985. Etude palynologique da la formation Tremembé, Tertiaire tu Bassin de Taubaté (État de São Paulo), d'aprés lês echantillons du sondage n-42 du CNP. Coletânea de trabalhos Paleontológicos, MME, Ser. Zool., 27: 379-393.

Lundberg, J. 1982. The comparative anatomy of the toothless blindcat, *Trogloglanis pattersoni* Eigenmann, with a phylogenetic analysis of the ictalurid catfishes. Miscelaneous publications of the Museum of Zoology, 163, 85p.

Lundberg, J. 1997. Fishes of the La Venta fauna: additional taxa, biotic and paleoenviromental implications. Pp. 67–91.In: R. F. Kay, R. L. Madden, R. H. Cifelli & J. J. Flynn (Eds.). Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta. Smithsonian Institution Press, 608p.

Lundberg, J., L. Marshall, J. Guerrero, B. Horton, M. C. S. L. Malabarba & F. Wesselingh. 1998. The Stage For Neotropical Fish Diversification: A History of Tropical South American Rivers. Pp. 13-48. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. Lucena (Eds.). Phylogeny and Classification of Neotropical Fishes. Porto Alegre: Edipucrs, 603p.

Malabarba, M. C. S. L. 1988. Loricariid dermal plate and pectoral fin spines (Osteichthyes, Siluriformes). Comunicações do Museu de Ciências da PUCRS, Sér. Zool., 5: 1-5.

Rapp Py-Daniel, L. H. 1997. Phylogeny of the Neotropical Armored Catfishes of the subfamily Loricariinae (Siluriformes; Loricariidae). University of Arizona, Unpublished Thesis. 280p.

Riccomini, C. 1989. O rift continental do Sudeste do Brasil. Unpublished Ph. D. Dissertation. Universidade de São Paulo, São Paulo. 256p.

Riccomini, C, C. J. Appi, E. L. Freitas & M. Arai. 1987. Tectônica e sedimentação no sistema de rifts continentais da Serra do Mar (Bacia de Volta Redonda, Resende, Taubaté e São Paulo). Simpósio de Geologia RJ-ES, 1, Rio de Janeiro, Anais, p. 253-298.

Riccomini, C, L. G. Sant'Anna & A. L. Ferrari. 2004. Evolução geológica do rift Continental do Sudeste do Brasil. Pp. 383-405. In: V. Montesso-Neto (Org.). Geologia do continente sul-americano: evolução da obra de Fernando Flavio Marques de Almeida. São Paulo: Beca, 647p.

Soria, M. & H. Alvarenga. 1989. Nuevos restos de mamíferos de la cuenca de Taubate, Estado de São Paulo, Brasil. Anais da Academia brasileira de Ciências, 27(3): 297-322.

Schaefer, S. 1987. Osteology of *Hypostomus plecostomus* (Linnaeus) with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). Contributions in Science, 394, 31p.

Schaefer, S. 1991. Phylogenetic analysis of the loricariid subfamily Hypoptomatinae (Pisces: Siluroidei: Loricariidae), with comments on generic diagnoses and geographic distribution. Zoological Journal of Linnean Society, 102: 1-41.

Schaefer, S. 1997. The Neotropical cascudinhos: Systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). Proceedings of the Academy of Natural Sciences of Philadelphia, 148: 1-120.

Schaefer, S. 2003. Relationships of *Lithogenes villosus* Eigenmann, 1909 (Siluriformes, Loricariidae): Evidence from High-Resolution computed microtomography. American Museum Novitates, 3401: 1-55.

Swofford, D. A. 1993. PAUP: phylogenetic analysis using parsimony Version 3.1. Champaign, Sinauer Associates.

Woodward, A. S. 1898. Considerações sobre alguns peixes Terciários dos schistos de Taubaté, Estado de S. Paulo, Brazil. Revista do Museu Paulista, 3:63-70.

Submitted April 2007
Accepted July 2007