

## Systematics of *Lamontichthys* Miranda-Ribeiro (Siluriformes: Loricariidae), with the description of two new species

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The taxonomic revision of the genus *Lamontichthys* Miranda-Ribeiro, based on the examination of 164 specimens of different river drainages throughout the Amazon basin, revealed the presence of six species of which two are new. *Lamontichthys filamentosus* occurs in the upper and middle portions of the rio Amazonas basin; *L. llanero* in the río Orinoco basin; *L. maracaibero* in the lago Maracaibo basin; and *L. stibaros* in the upper río Amazonas basin. *Lamontichthys avacanoeiro*, new species, occurs in the upper rio Tocantins basin; and *L. parakana*, new species, in the lower rio Tocantins basin. The new species represent a considerable extension in the so far known distribution of the genus. A parsimony analysis, including 87 osteological and external morphological characters from *Lamontichthys* and related taxa (total of 16), resulted in three most parsimonious trees with 194 steps (CI = 0.73 and RI = 0.78). The hypothesis of monophyly of *Lamontichthys* is corroborated and supported by six derived characters. Within *Lamontichthys* two monophyletic assemblages are recognized, one includes *L. avacanoeiro* and *L. stibaros*, the other includes *L. maracaibero* and the clade formed by *L. filamentosus* and *L. llanero*. The relationships of *Lamontichthys parakana*, a species that was not included in the phylogenetic analysis is discussed. The monophyly and relationships of the monotypic genus *Pterosturisoma microps* are also discussed.

A revisão taxonômica do gênero *Lamontichthys*, realizada com base no exame de 164 exemplares de diversas drenagens da bacia amazônica, revelou a existência de seis espécies, das quais duas são novas. *Lamontichthys filamentosus* ocorre na bacia do alto e médio rio Amazonas; *L. llanero*, na bacia do rio Orinoco; *L. maracaibero*, na bacia do lago Maracaibo; e *L. stibaros*, na bacia do alto rio Amazonas. *Lamontichthys avacanoeiro*, espécie nova, ocorre na bacia do alto rio Tocantins e *L. parakana*, espécie nova, na bacia do baixo rio Tocantins. As novas espécies representam uma considerável ampliação da distribuição geográfica do gênero. Uma análise de parcimônia, incluindo 87 caracteres osteológicos e de morfologia externa de 16 táxons, incluindo *Lamontichthys* e grupos relacionados, resultou em três cladogramas mais parcimoniosos com 194 passos (CI = 0.73 and RI = 0.78). A hipótese de monofiletismo de *Lamontichthys* é corroborada e sustentada por seis sinapomorfias. Entre as espécies de *Lamontichthys*, dois grupos monofiléticos são reconhecidos, um incluindo *L. avacanoeiro* e *L. stibaros* e outro *L. maracaibero* e um clado formado por *L. filamentosus* e *L. llanero*. A relação de *Lamontichthys parakana* com as demais espécies do gênero é discutida, apesar da espécie não ter sido incluída na análise filogenética. O monofiletismo e as relações do gênero monotípico *Pterosturisoma microps* são também discutidos.

**Key words:** Loricariinae, Armored catfish, Taxonomy, Neotropical freshwater, Phylogeny.

### Introduction

Species of armored catfishes of the genus *Lamontichthys* Miranda-Ribeiro, comprise small to medium fishes, reaching approximately 20 cm in standard length, and occur in the northern and central regions of South America in the rio Solimões-Amazonas, rio Tocantins, and río Orinoco river basins and in the lago Maracaibo drainage. They inhabit the bottom of rapid flowing streams, but currently very little is known about the biology of the species of *Lamontichthys* in their natural habitats (Taphorn & Lilyestrom, 1984). As most other catfishes, they have the body completely covered with

dermal plates, a ventral sucker-like mouth and jaws provided with very small teeth that are used to scrape the substrate. In addition to having the dorsal and ventral most principal caudal-fin rays elongated, a common feature among loricariids, a few species of *Lamontichthys* possess the pectoral-fin spine and/or the dorsal-fin spine prolonged into a filament that may far exceed the body length, and large specimens sometimes possess a well developed hunch, dorsally on the head.

Among loricariids, *Lamontichthys* is currently included in the subfamily Loricariinae Bonaparte, whose members are traditionally recognized externally by the possession of a depressed caudal peduncle, the first unbranched principal

caudal-fin rays generally prolonged into a long filament, and by the absence of an adipose fin (Reis *et al.*, 2006; Covain & Fisch-Muller, 2007). The Loricariinae currently comprises 34 genera and approximately 200 species (de Pinna, 1998; Ferraris Jr., 2003, 2007) and the subfamily has been considered monophyletic based on various synapomorphies (Schaefer, 1987; Montoya-Burgos *et al.*, 1998). Armbruster (2004) recently discussed the hypotheses of relationships of the Loricariinae within the Loricariidae. Within the subfamily, *Lamontichthys* has been traditionally grouped together with the genera *Cteniloricaria* Isbrücker & Nijssen, *Harttiella* Boeseman, *Harttia* Steindachner, *Pterosturisoma* Isbrücker & Nijssen, *Sturisoma* and *Sturisomatichthys* Isbrücker & Nijssen (Boeseman, 1971; Isbrücker, 1978, 1980). A recent study focused on the systematics of the Loricariinae was carried out by Rapp Py-Daniel (1997).

The taxonomic history of *Lamontichthys* is relatively recent and the genus currently includes five nominal species, four of which are considered as valid (Ferraris Jr., 2003, 2007). The genus was first proposed by Miranda-Ribeiro (1939: 12) to include *Harttia filamentosa* LaMonte, from the rio Juruá, a tributary of the right margin of rio Solimões. Subsequently, Boeseman (1971: 6) considered *Lamontichthys* a junior synonym of *Parasturisoma* Miranda-Ribeiro. Isbrücker & Nijssen (1978b) examined the holotype of the type-species of *Parasturisoma* (*Loricaria brevirostris* Eigenmann & Eigenmann) and concluded that it is a member of the genus *Sturisoma* Swainson. The authors also diagnosed *Lamontichthys* based on the presence of seven branched pectoral-fin rays (*vs.* six in the remaining genera of the Loricariinae; Isbrücker & Nijssen, 1976), described *L. stibaros*, based on two specimens from Ecuador, and redescribed *Lamontichthys filamentosus* (LaMonte). *Harttia filamentissima* Eigenmann & Allen was provisionally considered by Isbrücker & Nijssen (1978b) as a junior synonym of *Lamontichthys filamentosus*. Although those authors observed variation in a few meristic and morphometric characters of *L. filamentosus*, the small number of specimens available for study at that time (only 15), precluded a more detailed evaluation of the meaning of such variation. More recently, Taphorn & Lilyestrom (1984) described two new species of *Lamontichthys*, *L. maracaibero* and *L. llanero*, from the lago Maracaibo drainage and the río Orinoco basin respectively, extending considerably the known distribution of the genus to the north and increasing to four the number of valid species in the genus.

No additional taxonomic studies of *Lamontichthys* were carried out subsequently to that of Taphorn & Lilyestrom (1984). Recently, examination of material deposited in various collections revealed that species of *Lamontichthys* are more widely distributed than previously recorded and in addition there are two additional undescribed species in the genus.

Current knowledge about the species level taxonomy and hypotheses of phylogenetic relationships of *Lamontichthys* derived from the studies mentioned above provide an appropriate framework for a more detailed study focusing on

the systematics of *Lamontichthys*.

The main objectives of the present study are to: 1) describe two new species of *Lamontichthys* and provide new diagnosis for all valid species; 2) update information about the geographic distribution of the recognized species; 3) evaluate the hypothesis of monophyly of *Lamontichthys*; 4) propose a hypothesis of phylogenetic relationships among the species of *Lamontichthys*.

## Material and Methods

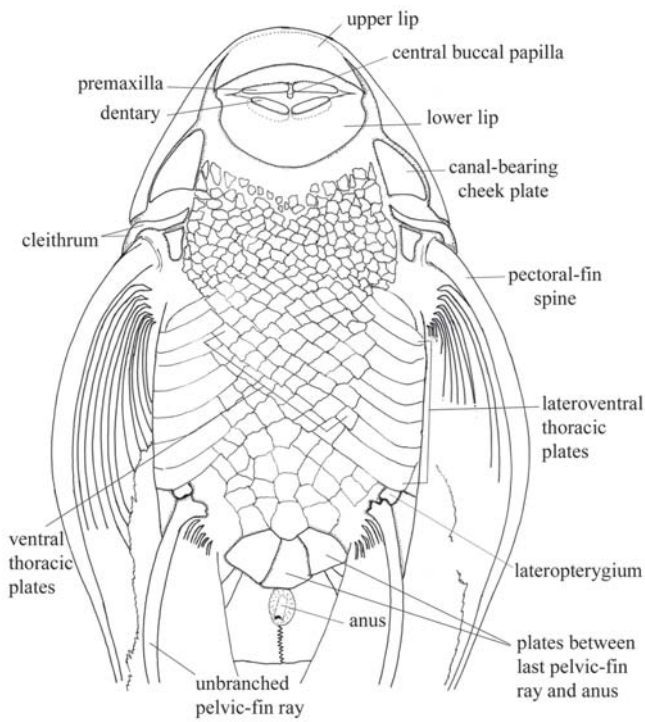
**Species accounts.** The taxonomic section of this study was based on the analysis of meristic and morphometric characters, color pattern, and external morphological features, of 164 specimens of *Lamontichthys*. Counts and measurements were made on the left side of specimens, except when the structure being measured or counted was recognizably abnormal or damaged, in which case corresponding data were taken from the right side.

Measurements were taken point to point with digital calipers. Counts were done with the help of a stereomicroscope. Counts and measurements follow Boeseman (1971, 1976), Isbrücker & Nijssen (1978a) and Taphorn & Lilyestrom (1984) with some modifications and with the inclusion of additional data as follows: dentary length: from the lateral to the medial tips of the dentary; caudal-peduncle depth: measured at the vertical through the anterior border of the last dorsal plate; length of branched dorsal-fin ray: measured from base to tip of first branched dorsal-fin ray; length of branched pectoral-fin ray: measured from base to tip of first branched pectoral-fin ray; caudal peduncle depth: measured at the anterior border of the penultimate postdorsal plate, which corresponds to the narrower point of the caudal peduncle.

Counts of body plates follow Schaefer (1997) and Reis & Pereira (2000) except as follows: lateroventral thoracic plates: number of plates between the last pectoral-fin ray and the unbranched pelvic-fin ray, and only those in contact with the lateral plates of the mid-ventral series; ventral thoracic plates: number of plates in the largest oblique row located between the contralateral series of lateroventral thoracic plates (Fig. 1).

According to Reis & Pereira (2000: 1030), counts of coalescing plates refer to the number of plates in the mid-ventral series in which the two keels are very close. In *Lamontichthys*, these two keels are not very evident, but through examination of cleared and stained specimens it was observed that the point in which the two keels meet is always coincident with the last plate of the mid-ventral series. In the specimens in alcohol, although the three series of lateral plates are not easily visualized, it is possible to distinguish the last plate of the mid-ventral series paired with the lateral plate of the median series. These two plates possess canals of the lateral sensory system. The last plate of the median series is triangular and situated on the base of the caudal-fin.

Roman numerals designate unbranched rays; uppercase roman numerals designate fin-spines. *Lamontichthys filamentosus* possesses the dorsal and pectoral-fin spines



**Fig. 1.** Ventral view of head and anterior portion of body of *Lamontichthys filamentosus* (INPA 17927, 79.4 mm SL). Odontods, plates on upper lip and papillae on lower lip not represented. Scale bar = 4 mm.

and *L. llanero* the dorsal-fin spine prolonged into long filaments that are often damaged. Therefore, in order to compare variation in dorsal and pectoral-fin lengths of all *Lamontichthys* species we chose to take this measurement from the base to the tip of the first branched fin ray.

The terms “tooth” and “odontods” follow Ørvig (1977), who considers tooth as dental units which are situated on the jaws and pharyngeal plates and odontods are dental units which occupy positions anywhere else in the dermal skeleton. Dentition terminology follows Schaefer (1987) and Müller & Weber (1992).

Meristic and morphometric characters were summarized using the program SYSTAT 10.0. Samples from proximate localities were first compared and grouped in one larger sample when no differences were detected. This was done successively until all samples were included in the analysis. Counts and measurements are presented in tables. Subunits of the head are given as proportions of head length (HL). Head length and measurements of body subunits are given as proportions of standard length (SL). In the “Material examined” section of each species account, lots are grouped by country and within each country, by state or department, followed by institutional abbreviation, catalog number, number of specimens in the lot, number of cleared and stained (cs) specimens when present, their range of standard lengths, and specific locality data. Institutional abbreviations follow Leviton *et al.* (1985) and Leviton & Gibbs (1988) except for

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Formal descriptions are provided only for the new species. Redescriptions of *Lamontichthys filamentosus*, *L. llanero*, *L. maracaibero*, and *L. stibaros* are not presented since their original descriptions or more recent redescriptions provide information to unambiguously diagnose each species (LaMonte, 1935; Isbrücker & Nijssen, 1978b; Taphorn & Lilyestrom, 1984). For these species we provide a synonymy list; diagnosis, geographical distribution, general remarks, and a list of examined material.

Osteological characters were not included in the species diagnoses due to the lack of cleared and stained specimens of all species for comparison.

**Phylogenetic procedures.** The phylogenetic study of *Lamontichthys* was based on the examination of 87 morphological characters, both osteological and from external morphology, in 16 taxa that include five species of *Lamontichthys* and representatives of nine genera of the Loricariinae proposed as more closely related to *Lamontichthys* (Boeseman, 1971; Isbrücker, 1978, 1980; Rapp Py-Daniel, 1997) plus one species of *Hypostomus* and one of *Neoplecostomus*. Rapp Py-Daniel’s (1997) unpublished study comprises the most recent and detailed cladistic analysis of the Loricariinae and provided the basis for selection of taxa and characters for the phylogenetic analysis carried out in the present study. For this reason and with the consent of the author, in the “Description of characters” section, Rapp Py-Daniel (1997), is credited for all characters or character states that were originally proposed in that study. Many characters were redefined after examination and reinterpretation of data available in the literature, and others were proposed for this just time in the present study. Specimens for osteological study were cleared and counterstained for cartilage and bone using a modification of the method outlined by Taylor & Van Dyke (1985). Cleared and stained specimens were dissected under a stereomicroscope using ophthalmologic instruments. Drawings were made by the first author with the aid of a camera lucida connected to a stereomicroscope. Unless noted in the figure legend, illustrations in lateral view are always oriented with the anterior side to the left, regardless of the side of the specimen used to prepare the illustration, and those in dorsal or ventral view with anterior side to top.

Osteological terminology follows Lundberg & Baskin (1969) and Schaefer (1987). Vertebral counts follow Schaefer (1997: 27), in considering each of the five vertebrae of the “Weberian apparatus” all fused in loricariids, and the vertebra that is incorporated in the hypural plate, as separate elements. Precaudal vertebrae refer to those anterior to the vertebra articulated with the first anal-fin pterygiophore, and caudal vertebrae are those posterior to the latter vertebra.

One of the new species diagnosed in this study, *Lamontichthys parakana*, was not included in the phylogenetic analysis due to the reduced number of specimens available which did not allow the preparation of cleared and stained material for the examination of osteological characters. For this species only the external

characters are presented in the text.

The monophyly of *Lamontichthys* and the phylogenetic relationships among its species were inferred using the cladistic methodology first proposed by Hennig (1950, 1966) and subsequently discussed by various authors. Detailed explanations about the principles of the cladistic method and its operational aspects are available in Nelson & Platnick (1981), Wiley (1981), Wiley *et al.* (1991), Swofford *et al.* (1996) and Amorim (2002). Parsimony analysis was employed to generate hypothesis of phylogenetic relationships and character state transformations using NONA (Goloboff, 1999) associated with Winclada ver. 1.00.08 (Nixon, 2002). The heuristic search was performed with 1000 replications (mult\*1000), keeping five trees in each replication (hold/5), and a multiple tree bisection-reconnection (TBR) + TBR search strategy. The cladograms were rooted on *Neoplecostomus ribeirensis*.

The most parsimonious hypotheses generated by the analysis were summarized in a strict consensus cladogram. No specific optimization method, *i.e.* accelerated transformation optimization (ACCTRAN), or delayed transformation optimization (DELTRAN) was used to optimize characters on the resulting cladograms (*i.e.* in the list of synapomorphies, ambiguous characters are listed separately from the unambiguous characters).

This study is focused on the evaluation of the monophyly of *Lamontichthys* and the phylogenetic relationships among its species. Characters pertaining to the question of phylogenetic relationships among other genera of the Loricariinae were included with the objective of providing a framework on which to study the relationships within *Lamontichthys*. Therefore, the scheme of relationships among outgroups that resulted from the present analysis should not be regarded as an attempt to propose a hypothesis of relationships among these taxa. In order to do that, we would have to survey a much larger number of characters and taxa. Discussion of character optimization, polarity and proposed synapomorphies are only provided for the portion of the cladogram pertinent to the question of monophyly of *Lamontichthys* and intrageneric relationships.

Multistate characters that showed a sequence of similarity among their states were treated as ordered (or “minimally connected” - Slowinski, 1993), and includes characters 3, 4, 8, 14, 15, 19, 28, 30, 40, 41, 48, 50, 51, 55, 59, 66, 69, 70, 75, 76, 79, 82, and 85. The initial point of this sequence is represented by state “0”. Multistate characters that did not show any apparent sequence of similarity were treated as unordered (or “maximally connected” - Slowinski, 1993) and includes characters 7, 10, 13, 16, 21, 23, 25, 34, 35, 39, 52, 53, 63, 65, 67, 71, 72, 77, 80, 83, and 84.

Species listed below followed by an asterisk (\*) provided the morphological basis for the phylogenetic analysis of *Lamontichthys* and are organized alphabetically by genus. The remaining species were examined as comparative material. Whenever a character is mentioned in the text for an outgroup genus without a species cited, it refers to the species listed below, and does not imply that the character is present in all

species of the genus.

Cleared and stained specimens are indicated by “cs” and those in alcohol are indicated by “alc”. Species name is followed by institutional catalog number, number of specimens in the lot, their range of standard lengths and specific locality data.

**Comparative taxa: Brazil:** *Acestridium discus*: MZUSP 88944, 1cs, 66.1, 7alc, 34.1-64.9, Amazonas, Rio Preto da Eva, rio Preto da Eva; *Farlowella nattereri*\*: MZUSP 57658, 1cs, 112.9, Amazonas, rio Madeira; *Harttia*: *H. carvalhoi*: MZUSP 48598, 1cs, 62.6, 5alc, 69.6-76.6, São Paulo, Pindamonhangaba, tributary of Ribeirão Grande; *H. kronei*: MZUSP 62390, 1cs, 59.9, São Paulo, Ribeira, Iporanga, rio Betari; *H. leiopleura*: MZUSP 42701, 2cs, 52.7-58.6, Minas Gerais, Nova Lima, rio das Velhas, tributary of rio Mutuca, paratypes; *H. loricariformis*\*: MZUSP 66187, 1cs, 67.7, Minas Gerais, Muriaé, rio Glória; *H. punctata*\*: MZUSP 40825, 1cs, 68.0, Tocantins, upper Tocantins, rio Bezerra; MNRJ 12726, 1cs, 59.8, 19 (of 120) alc, Goiás, upper Tocantins, córrego Bateias; *Harttia* sp.: MZUSP 100919, 1cs, 58.8, 2alc, São Paulo, Tietê, Perus, córrego Laranjeiras; *H. torrenticola*: MZUSP 37170, 1cs, 54.4, Minas Gerais, rio das Velhas, tributary of rio Paraopeba, paratype; *Hypostomus* sp.\*: MZUSP 100921, 1cs, 58.7, 1alc, no locality data; *Loricaria* sp.\*: MZUSP 23847, 1cs, 124.2, Pará, igarapé Açu, near São Domingos do Capim; *Neoplecostomus ribeirensis*\*: MZUSP 100920, 1cs, 45.3, 1alc, São Paulo, Ribeirão das Laranjeiras; *Pseudoloricaria punctata*\*: MZUSP 34542, 1cs, Roraima, rio Branco, Cachoeira do Bem-querer; *Pterosturisma microps*\*: MZUSP 79909, 1cs, 75.9, Amazonas, rio Solimões below rio Iça; *Rineloricaria* sp.\*: MZUSP 23748, 1cs, 91.5, 16alc, Pará, Oriximiná; *Sturisma* sp.\*: MZUSP 50112, 1cs, 115.2, Acre, rio Purus. **Colombia:** *Sturisomatichthys leightoni*\*: ANSP 84179, 1cs, 101.3, 2alc, rio Magdalena basin, Honda.

## Results

**Taxonomic account.** In the present study six species of *Lamontichthys* are recognized, two of which are new and recorded from the rio Tocantins basin. *Lamontichthys parakana*, new species is represented only by three specimens, and *L. avacanoeiro*, new species is recognized on the basis of 22 specimens.

### *Lamontichthys* P. de Miranda Ribeiro

*Lamontichthys* P. de Miranda Ribeiro, 1939: 12 [type-species: *Harttia filamentosa* LaMonte, 1935, by original designation and monotypy].

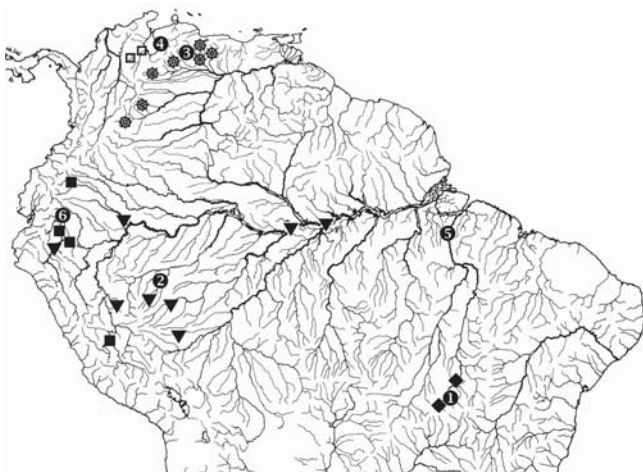
**Diagnosis.** Species of *Lamontichthys* can be distinguished from all other loricariids by the presence of seven branched rays in the pectoral-fin (*vs.* six). *Harttia leiopleura* Oyakawa and *Rineloricaria daraha* Rapp Py-Daniel & Fichberg also possess seven branched pectoral-fin rays. Species of *Lamontichthys* can be distinguished from *Harttia leiopleura* by the presence of dermal plates on the upper lip and lateroventral plates on the thoracic region (*vs.* absent; Oyakawa, 1993) and from *Rineloricaria daraha* by having button-like papillae on the ventral surface on the lower lip (*vs.* long digitiform papillae), the lack of a postorbital notch and

by having 14 caudal-fin rays (vs. 12; Rapp Py Daniel & Fichberg, 2008).

Five other characters observed only in skeletal preparations and detailed under “Character analysis and description” further distinguish *Lamontichthys* from other loriciariids: 1) the trapezoidal shape of the lower pharyngeal plate, with the medial and lateral borders almost parallel, the medial border larger than the posterior border and at least twice as large as the lateral border (character 13); 2) the triangular and relatively elongate posterior expansion of the first epibranchial (character 14); 3) the large coronoid process in the dentary (character 23); 4) the contact (or proximity) between the proximal portions of the first three anal-fin pterygiophores (character 69); 5) the presence of two broad apophysis on the second preural centrum (character 77).

**Common names.** The common names used for *Lamontichthys* usually refer to more than one species of the genus or even to other Loriciariinae. Brazil: “bode-cachoeira”, “bode-cachimbo” and “bode-casco-de-anta” (Silvano *et al.*, 2001; Cunha & Almeida, 2002); Colombia: “bomba” (Galvis *et al.*, 1997); Ecuador: “raspabalsa” (Ferraris Jr., 2003: 336); Finland: “siimaeva” (Varjo *et al.*, 2004); Germany: “filament-störwels” (Baensch & Riehl, 1997); Peru: “shitari” (Ortega & Vari, 1986); Venezuela: “tabla” or “paleta” (F. Provenzano, pers. comm.), and “paleta gibosa” (Taphorn & Lilyestrom, 1984b).

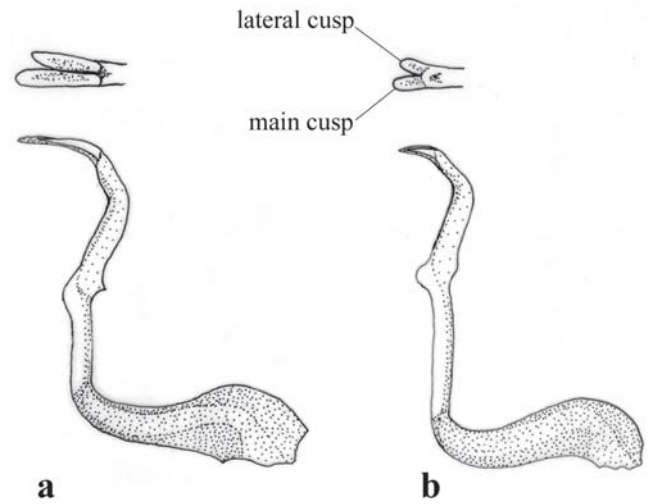
**Geographic distribution.** South American drainages including the upper and central portions of rio Solimões-Amazonas, the drainages of río Ucayali, río Marañon and río Napo, the upper regions of rio Purus and rio Juruá, rio Madeira and rio Tocantins basins. It also occurs in the middle and upper río Orinoco basin, and in the lago Maracaibo drainage (Fig. 2).



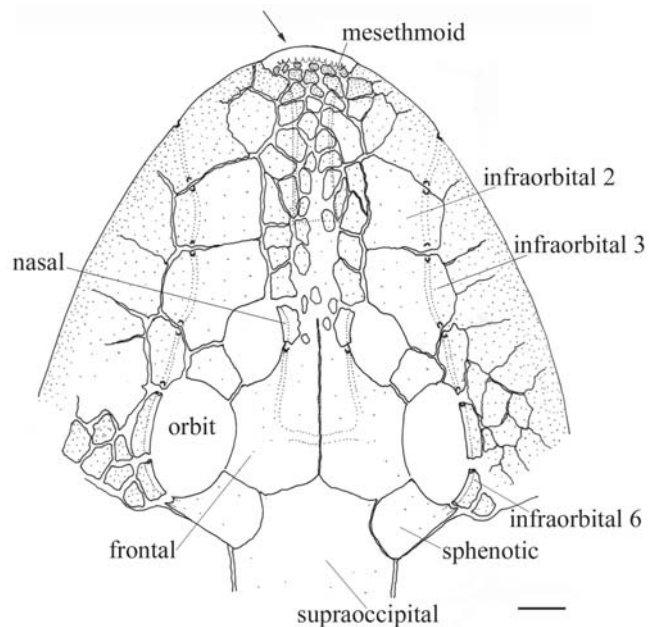
**Fig. 2.** Map of central and northern portions of South America showing geographic distribution of the species of *Lamontichthys* (numbers indicate type localities): 1. *L. avacanoeiro* (lozenge), 2. *L. filamentosus* (triangle), 3. *L. llanero* (rudder), 4. *L. maracaibero* (open squares), 5. *L. parakana* (number 5), and 6. *L. stibaros* (solid squares). Some symbols represent more than one locality or lot of specimens.

**Key to the species of *Lamontichthys***

- 1. Teeth with short cusps (Fig. 3b); anterior tip of snout covered with plates or with an inconspicuous area lacking plates; dentary 11.5-19.1% HL in specimens larger than 100 mm SL ..... 2
- 1'. Teeth with long cusps (Fig. 3a); anterior tip of snout not covered with plates (Fig. 4); dentary 18.4-23.4% HL in specimens larger than 100 mm SL ..... 4



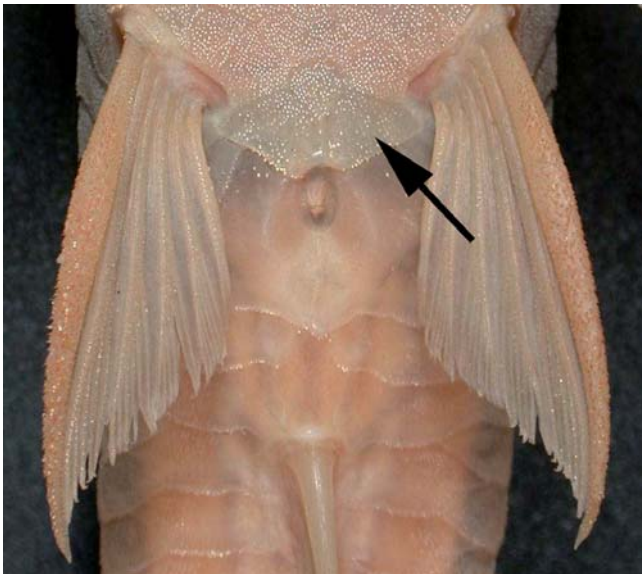
**Fig. 3.** Lateral view, distal portion to top, of left premaxillary tooth of *Lamontichthys avacanoeiro* (MZUSP 61974, 113.7 mm SL, paratype) (a), and *L. filamentosus* (LACM 41741-9, 119.4 mm SL) (b). Detail of cusps in anterior view, distal tip to left. Scale bar = 0.5 mm.



**Fig. 4.** Dorsal view of head of *Lamontichthys stibaros* (FMNH 84111, 62.4 mm SL). Location of mesethmoid represented by a dotted line on median portion of snout. Arrow points to portion of snout not covered with plates. Scale bar = 1 mm.

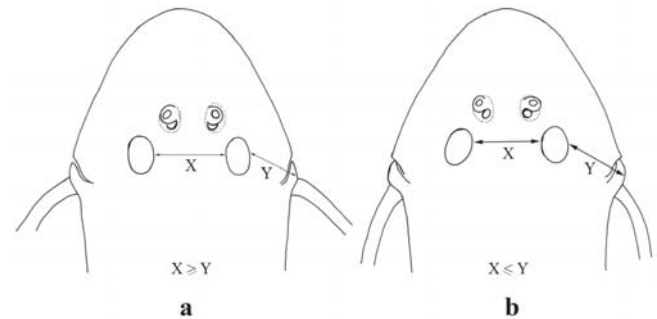
- 2. 19-21 lateral plates in the mid-ventral series; a single large triangular plate extending from base of last pelvic-fin ray to anterior margin of anus (Fig. 5); 5-6 lateroventral thoracic plates in specimens larger than 100 mm SL; dorsal-fin spine not prolonged into a long filament. (Iago Maracaibo drainage) ..... *L. maracaibero*
- 2'. 15-18 lateral plates in the mid-ventral series; more than one plate from base of last pelvic-fin ray to anterior margin of anus (Fig. 1); 6-10 lateroventral thoracic plates in specimens larger than 100 mm SL (Fig. 1); dorsal-fin spine prolonged into a long filament ..... 3

- 5. First branched dorsal-fin ray 26.1-36.8% SL and pectoral-fin spine 22.9-30.5% SL in specimens larger than 50 mm SL; dark pigments scattered along dorsal-fin spine. (tributaries of upper rio Amazonas) ..... *L. stibaros*
- 5'. First branched dorsal-fin ray 21.9-26.0% SL and pectoral-fin spine 19.7-22.4% SL in specimens larger than 50 mm SL; dark pigments arranged in transversal bands along dorsal-fin spine. (upper rio Tocantins basin) ..... *L. avacanoeiro*

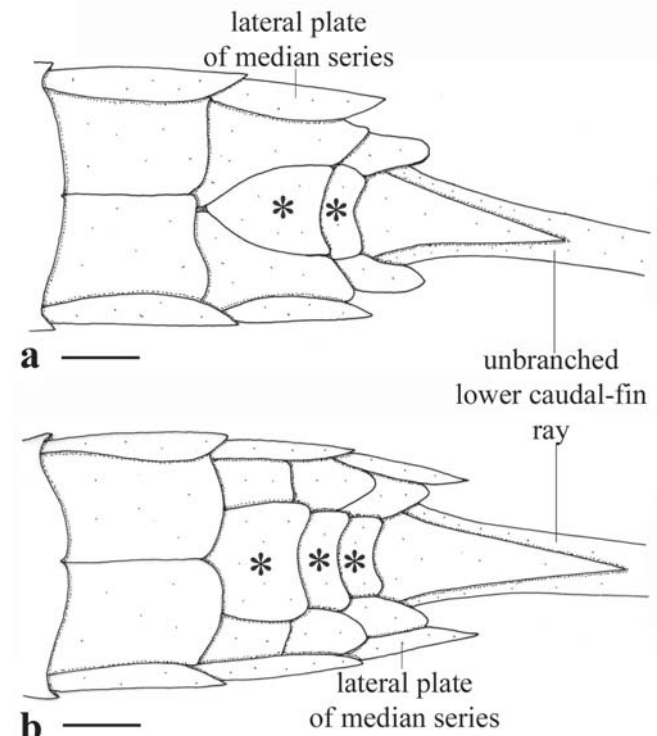


**Fig. 5.** Ventral view of pelvic region of *Lamontichthys maracaibero* (MCNG 3592, 154.9 mm SL). Arrow points to single plate from base of last pelvic fin-ray to margin of anus.

- 3. Pectoral-fin spine prolonged into a long filament in specimens larger than 60 mm SL; head width 97.4-111.1% HL; interorbital distance equal to distance from orbit to exposed margin of cleithrum (rarely shorter) (Fig. 6). (upper and middle rio Amazonas basin) ..... *L. filamentosus*
- 3'. Pectoral-fin spine not prolonged into a long filament; head width 82.6-96.9% HL; interorbital distance larger than (rarely equal to) distance from orbit to exposed margin of cleithrum (Fig. 6). (rio Orinoco basin) ..... *L. llanero*
- 4. Distal tip of last dorsal-fin ray extending short of vertical through anal-fin origin; orbital diameter 16.6-17.3% HL in specimens larger than 70 mm SL; two small plates on the ventral mid-line of the caudal peduncle (Fig. 7). (rio Tocantins basin) ..... *L. parakana*
- 4'. Distal tip of last dorsal-fin ray at the vertical through anal-fin origin; orbital diameter 13.6-16.8% HL in specimens larger than 70 mm SL; three small plates on the ventral mid-line of the caudal peduncle (Fig. 7) ..... 5



**Fig. 6.** Schematic drawing of dorsal view of head of *Lamontichthys llanero* (a) and *L. filamentosus* (b). The “x” indicates interorbital distance and “y” indicates distance from orbit to exposed border of cleithrum.



**Fig. 7.** Ventral view of distal tip of caudal peduncle of *Lamontichthys parakana* (INPA 3010, 112.7 mm SL, holotype) (a) and *L. avacanoeiro* (MZUSP 79750, 96.8 mm SL, paratype) (b). The asterisks indicate plates on the ventral mid-line of the caudal peduncle. Scale bar = 1 mm.

*Lamontichthys avacanoeiro*, new species

## Fig. 8

**Holotype.** MNRJ 32795, 150.5 mm SL, Brazil, Goiás, rio Tocantins, pools below U.H.E. Serra da Mesa, 1996, D. F. Moraes *et al.*

**Paratypes.** (22 specimens; 47.6-159.9 mm SL). **Brazil.** Goiás: MNRJ 18553, 1 cs, 7 alc, 76.0-145.6, same data of holotype; MZUSP 54090, 2, 47.6-58.4, rio Tocantinzinho and tributaries, Serra da Mesa, 48°21'66"S 13°53'33"W, 28 Out 1996, Expedition MZUSP/MNRJ; MZUSP 61974, 5, 1cs\*, 113.7-159.9, upper rio Tocantins, Minaçu, Serra da Mesa, 26 Out 1996, A. Akama & O. T. Oyakawa; MZUSP 79750, 5, 90.9-96.8, upper rio Tocantins, Uruaçu, rio Passa Três, above Ponte Nova, on road BR 153, 10 Jun 1998, D. F. Moraes.

**Non-types.** (4 specimens; 83.4-106.8 mm SL): **Brazil:** Goiás: MNRJ 23641, 1, 100.3, upper rio Tocantins, rio das Almas; MNRJ 23642, 1, 106.8, upper rio Tocantins, rio Bagagem, above ferry-boat to Garimpinho; MNRJ 23643, 2, 83.4-83.7, upper rio Tocantins,

Niquelândia, rio Traíras, above Indianópolis.

**Diagnosis.** *Lamontichthys avacanoeiro* differs from all congeners in the shorter first branched dorsal-fin ray (22.6-26.0%, vs. 26.4-40.5% SL) in specimens larger than 70 mm SL.

*Lamontichthys avacanoeiro* can be further distinguished from *L. filamentosus*, *L. llanero*, and *L. maracaibero* by the anterior tip of the snout with an oval shaped area without plates (vs. tip of snout totally covered with plates or, with only a very small area lacking plates), and by the teeth with long cusps (vs. short) (Fig. 3). *Lamontichthys avacanoeiro* can be further distinguished from *L. filamentosus* and *L. llanero* by the lower lip semi-oval shaped (vs. semicircular) (Fig. 9). *Lamontichthys avacanoeiro* also differs from *L. maracaibero* in having more than one plate between the base of the last pelvic-fin ray and the anterior margin of the anus

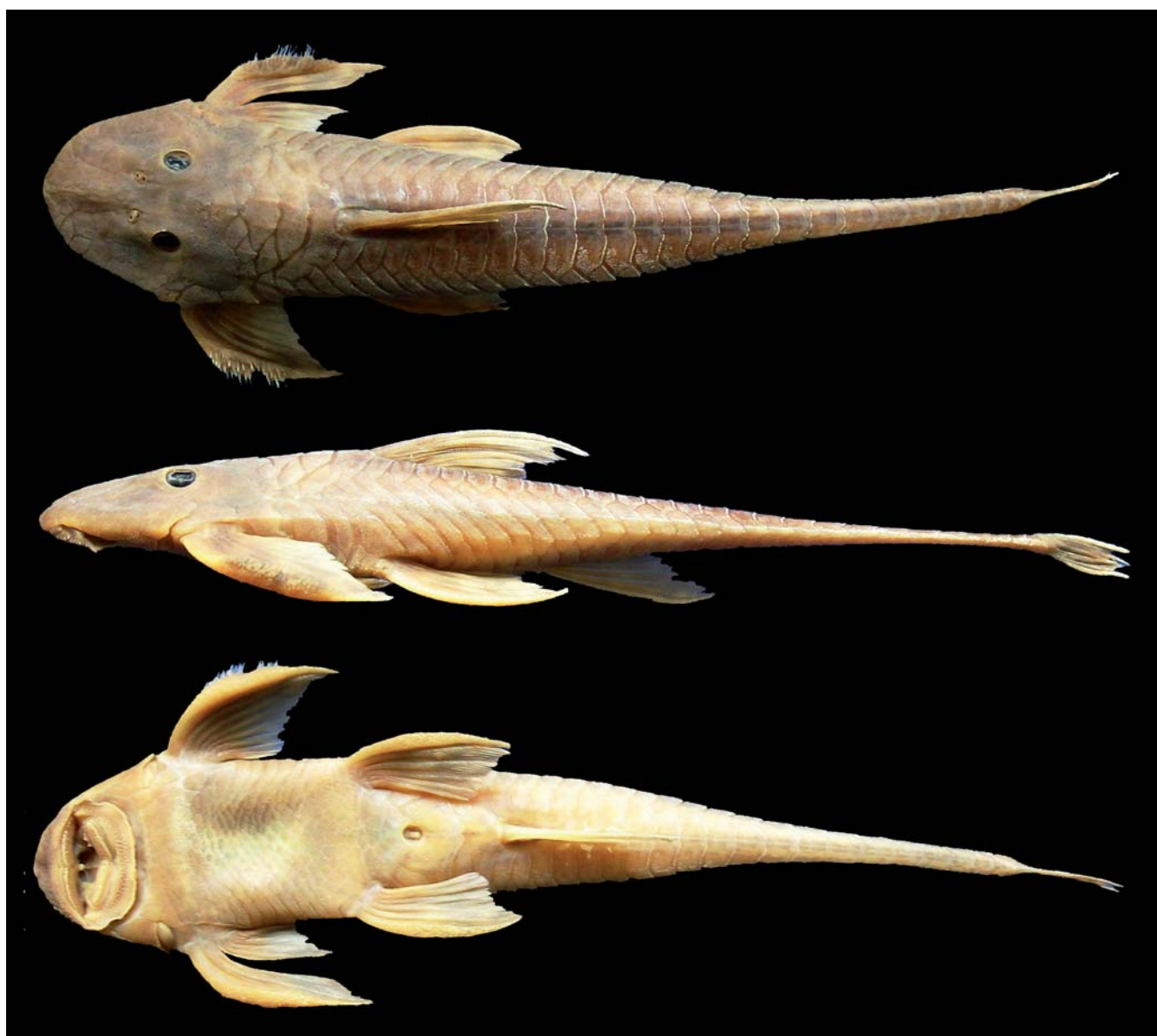


Fig. 8. *Lamontichthys avacanoeiro*, new species, MNRJ 32795, 150.5 mm SL, holotype. Dorsal, lateral and ventral views.

(vs. one plate) (Figs. 1 and 5) and in the greater abdominal length in specimens larger than 150 mm SL (17.6-17.7% [n = 2], vs. 14.1-16.3% SL [n = 5]). *Lamontichthys avacanoeiro* can be distinguished from *L. parakana* by the more posterior location of the anal-fin origin (at the vertical through the distal tip of the last dorsal-fin ray, vs. anterior to that point), by the shorter unbranched anal-fin ray (16.9-20.3%, vs. 21.4-24.8% SL), and by the smaller orbital diameter (13.6-16.2%, vs. 16.6-17.3% HL) in specimens larger than 70 mm SL.

*Lamontichthys avacanoeiro* also differs from specimens of *L. parakana* larger than 100 mm SL in the narrower head (91.3-100.9%, vs. 101.3-106.1% HL).

**Description.** Morphometric and meristic data presented in Table 1. Largest specimen 159.9 mm SL. Head and trunk totally covered with plates. Body depressed, deeper at vertical through dorsal-fin origin, gradually more depressed posteriorly to caudal-fin base and, anteriorly, to snout tip. Head ellipse shaped in dorsal view. Dorsal profile of head slightly convex. Dorsal profile of body straight from posterior tip of supraoccipital to dorsal-fin origin, posteroventrally slanted from latter point to vertical through tip of longest anal fin ray, straight from that point to caudal-fin base. Largest

body width at cleithrum, gradually narrower posteriorly to 20<sup>th</sup> to 21<sup>st</sup> lateral plate of median series, more abruptly posteriorly into caudal-fin base. Caudal peduncle long, narrow and very depressed. Ventral profile of body and head straight from snout tip to base of caudal fin. Pectoral-fin origin at vertical through posterior margin of orbit. Dorsal-fin origin immediately anterior to vertical through pelvic-fin origin. Anal-fin origin at or slightly posterior to vertical through distal tip of last dorsal-fin ray.

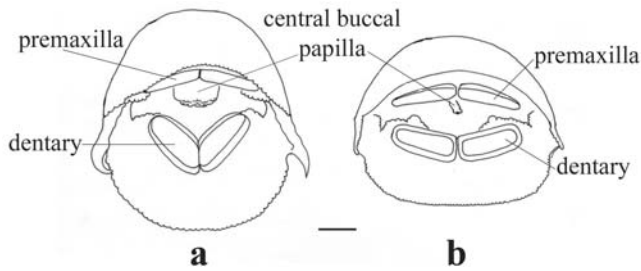
Eyes located dorsally, anterior to vertical through pectoral-fin origin. Interorbital distance shorter or equal to distance from orbit to exposed borders of cleithrum. Mouth ventral, upper and lower lips semi-oval shaped. Lower lip extending short of vertical through anterior margin of orbit and covered with small papillae on ventral surface and along its border. Dorsal surface of lower lip smooth. Upper lip narrower than lower lip, its ventral surface (internal) with small papillae and dorsal surface (external) with small, round plates covered with odontods. Maxillary barbel inconspicuous, united by membrane to lateral border of lower lip.

Teeth setiform, long, hook-shaped and bicuspid. Tooth cusps long, flattened and unequal, with round tips, darker than rest of tooth. Median cusp slightly longer and broader

**Table 1.** Morphometric and meristic data for *Lamontichthys avacanoeiro* and *L. filamentosus*. SD = standard deviation. Range of *L. avacanoeiro* includes paratypes.

Variable	<i>L. avacanoeiro</i>					<i>L. filamentosus</i>				
	Holotype	N	Range	Mean	SD	N	Range	Mean	SD	
Standard length (mm)	150.5	24	47.6-159.9	108.1		64	38.8-172.5	134.9		
Percents of standard length										
Head length	20.9	24	19.8-25.3	22.3	1.5	64	16.0-20.2	17.6	0.9	
Predorsal length	29.9	24	28.4-33.0	30.5	1.2	64	26.0-30.8	27.7	0.9	
Postanal length	49.9	24	47.7-52.7	50.0	1.3	64	51.3-57.3	55.1	1.0	
Abdominal length	16.9	24	15.2-17.7	16.7	0.7	64	13.6-16.8	15.4	0.6	
Thoracic length	16.9	24	13.7-16.9	15.2	0.9	64	13.6-16.7	15.2	0.7	
Dorsal-fin length	-	21	20.5-26.0	24.1	1.3	57	27.8-39.9	36.0	2.3	
Pectoral-fin length	19.3	24	18.2-22.0	20.1	0.8	62	20.5-26.1	23.4	1.3	
Pelvic-fin length	17.7	24	17.7-20.6	19.2	0.8	64	18.9-23.0	20.7	1.0	
Anal-fin length	17.3	22	16.9-20.3	19.1	1.0	56	19.9-26.9	23.3	1.4	
Body depth at dorsal-fin origin	11.8	23	9.3-12.5	10.6	1.1	64	10.2-13.9	12.5	0.8	
Caudal peduncle depth	1.5	24	1.3-1.8	1.5	0.1	64	1.4-1.9	1.6	0.1	
Body width at dorsal-fin origin	16.6	24	13.5-16.9	15.4	0.9	64	13.8-16.9	15.6	0.7	
Body width at anal-fin origin	12.9	23	10.2-13.1	12.0	0.8	64	11.2-14.4	13.1	0.6	
Body width at caudal-fin origin	2.7	23	2.4-2.9	2.7	0.2	64	2.5-3.3	2.9	0.2	
Percents of head length										
Head width	97.7	23	85.6-100.9	92.8	3.9	64	96.7-111.1	105.2	3.7	
Interorbital distance	27.3	24	25.4-29.4	27.1	1.2	64	28.4-35.2	32.1	1.6	
Orbital diameter	13.8	24	13.6-16.2	14.6	0.8	64	10.9-18.4	16.4	1.2	
Snout length	62.2	24	60.6-64.8	62.7	1.1	64	55.4-63.3	59.8	1.4	
Dentary length	20.8	24	18.4-23.4	20.8	1.5	64	11.5-20.2	14.1	1.4	
Lower lip width	14.8	22	13.0-21.2	16.0	2.3	64	7.6-16.7	12.2	1.9	
Meristic data										
Lateral plates of median series	32	23	31-34	32.6	0.8	64	32-34	32.8	0.5	
Lateral plates of mid-ventral series	19	24	14-20	17.7	1.5	63	14-18	14.8	0.8	
Ventrolateral thoracic plates	7	24	6-9	7.0	0.8	63	5-8	6.9	0.7	
Premaxillary teeth	96	21	60-100	82.8	10.7	61	33-78	62.5	8.4	
Dentary teeth	83	21	50-87	73.4	9.4	60	30-70	55.1	7.8	
Dorsal-fin rays	II,7	22	II,7	II,7	0.0	62	II,6-7	I,7	0.1	
Pectoral-fin rays	I,7	22	I,7	I,7	0.0	64	I,7	I,7	0.0	
Pelvic-fin rays	i,5	22	i,5	i,5	0.0	64	i,5	i,5	0.0	
Anal-fin rays	i,5	22	i,5	i,5	0.0	64	i,5	i,5	0.0	
Caudal-fin rays	i,12,i	22	i,12,i	i,12,i	0.0	61	i,12,i	i,12,i	0.0	





**Fig. 9.** Ventral view of oral region of *Sturisoma* sp. (MZUSP 50112, 115.2 mm SL) (a) and *Lamontichthys avacanoeiro* (MNRJ 18553, 98.1 mm SL, paratype) (b). Scale bar = 2 mm.

than lateral cusp. Number of jaw teeth increasing with growth. Number of premaxillary teeth approximately 8% greater than number of dentary teeth. Emergent teeth placed in two irregularly arranged rows; teeth gradually smaller laterally. Replacement teeth oriented at 90 degrees relative to emergent teeth and covered with skin. Anteroventral tip of snout without plates, forming distinct naked portion, approximately oval shaped, covered with stiff connective tissue. Anterior border of head covered with small and flexible plates between snout tip and anterolateral margin of upper lip. Lateral border of head covered with large dorsal plates anteroventrally curved.

Three horizontal keels along trunk, on lateral plates, converging from plate 5 to 15 or 16, continuing as a single keel posteriorly. Lower keel more evident, upper keel less evident. Last lateral plate of median series small and triangular, with one diminutive plate on each side of its base, located between two other plates of similar shape (one upper and other lower), above caudal-fin base. Lateral plates of median series, 31 to 34. Lateroventral thoracic plates 6 to 9 in specimens larger than 50 mm SL. Ventral thoracic plates, small, lozenge shaped, irregularly arranged in oblique rows; longest row with 8 to 10 plates delimited by ventrolateral thoracic plates. Region of abdomen anterior to anus covered with small, lozenge-shaped plates followed by three large polygonal plates, and the anal plate larger and bordering anterior margin of anus.

Pectoral- and dorsal-fin spines, unbranched pelvic- and anal-fin rays not projecting as long filaments. Unbranched caudal-fin rays projecting as long filaments. Branched caudal-fin rays gradually longer toward dorsal and ventral unbranched rays. Dorsal most branched caudal-fin ray longer than ventral most ray. Unbranched pelvic-fin ray reaching to vertical through second ventral plate, located posterior to base of last anal-fin ray, unbranched anal-fin ray reaching to vertical through seventh ventral plate, located posterior to the base of last anal-fin ray. Dorsal-fin rays II,7; pectoral-fin rays I,7; pelvic-fin rays i,5; anal-fin rays i,5; caudal-fin rays i,12,i.

**Color in alcohol.** Ground coloration of head and body of adults and juveniles varying between brown and yellow. Ventral region of head and body lighter, uniformly yellow. Dorsal region of upper lip dark brown. Straight unpigmented median stripe from base of last anal-fin ray to base of

unbranched lower caudal-fin ray. Fins and dorsal region of body and head with dark brown and yellow spots. One dark brown, longitudinal band extending from base of dorsal fin to base of caudal fin.

**Etymology.** The species name, *avacanoeiro*, is in reference to the Avá-canoeiros, inhabitants from the upper rio Tocantins basin. Avá-canoeiros, an American group that historically inhabited the area of the upper rio Tocantins, drainage from which the examined specimens of the species in this study originated.

**Geographic distribution.** Upper rio Tocantins basin (Fig. 2).

**Comments.** The occurrence of *Lamontichthys* in the upper rio Tocantins was first reported by Rapp Py-Daniel (pers. comm.), based on specimens collected in the region of Serra da Mesa, State of Goiás, Brazil. Specimens from lots MNRJ 23641 - 23643 are in poor condition, therefore they were not designated as paratypes.

#### *Lamontichthys filamentosus* (LaMonte, 1935)

##### Fig. 10

*Harttia filamentosa* LaMonte, 1935: 5-6, fig. 4 [original description; type locality: Brazil, Amazonas, rio Juruá drainage, vicinity of mouth of rio Embira, tributary of the rio Tarauacá, 7°30'S 70°15'W]; Conci & Michelangeli, 1974: 226 [listed].

*Lamontichthys filamentosa*: Miranda-Ribeiro, 1939: 12 [original description of genus; designation of type-species]; Gosline, 1945: 108 [listed]; Barzanti & Oldani, 1976: 130-137 [incorrect identification; based on four specimens of probably, *Loricaria* sp., Loricariinae; Argentina, rio Paraná basin - specimens not examined].

*Harttia filamentissima* Eigenmann & Allen, 1942: 211, 445, pl. VIII figs. 1 and 2 [original description; type locality: Peru, Loreto, rio Huallaga; Fowler, 1945: 109 [listed; Peru]; Gosline, 1945: 108 [listed]; Tovar Serpa, 1967: 222 [listed; Peru]; Ovchynnyk, 1968: 258 [Chicherota, near the mouth of the rio Bobonaza, tributary of the upper rio Pastaza, specimen not examined].

*Lamontichthys filamentosus*: Ovchynnyk, 1968: 258 [Eastern Ecuador]; Isbrücker & Nijssen, 1976: 121-122 [7 branched pectoral-fin rays as diagnostic for *Lamontichthys*; *Harttia filamentissima* presumed to be a synonym of *L. filamentosus*]; Isbrücker & Nijssen, 1978b: 57-80, fig. 1-4, 7, 10a,c, 14, table Ia, IIa-h, IIIa [redescription; *Harttia filamentissima* as synonym of *L. filamentosus*; photographs of types of both species; specimens not examined]; Isbrücker, 1978: 88 [listed]; Isbrücker, 1980: 91 [listed]; Ortega & Vari 1986: 17 [literature compilation; Peru]; Burgess, 1989: 426-427, 440 [description]; Barriga, 1991: 66 [eastern drainages of Ecuador]; Lauzanne *et al.*, 1991: 70, 73, table I and IV [Bolivia, upper rio Madeira basin,

rio Chapare; specimens not examined]; Eschmeyer, 1998: 578 [listed]; Chernoff *et al.*, 1999a, 1999b: 59 [Bolivia, upper río Orthon basin]; Sarmiento *et al.*, 1999: 92 [Bolivia, Pando, río Tahuamanu]; Machado-Allison *et al.*, 1999: 50 [Bolivia, Pando, upper and middle río Tahuamanu, specimens not examined]; Begossi *et al.*, 1999: 79, table I [Brazil, Acre, upper río Juruá; common name]; Silvano *et al.*, 2001: 158-159 [Brazil, Acre, upper río Juruá; common name; photograph]; Isbrücker, 2001: 27, 29 [listed]; Ferraris Jr., 2003: 336 [listed]; Buckup *et al.* 2007:88 [listed]; Ferraris Jr., 2007: 263 [listed].

*Parasturisoma filamentosa*: Boeseman, 1971: 9 [listed].

*Parasturisoma filamentissima*: Boeseman, 1971: 9 [listed].

**Diagnosis.** Specimens of *Lamontichthys filamentosus* larger than 60 mm SL are distinguished from all congeners by having the pectoral-fin spine extending into a very long filament that may exceed four times the length of the first branched pectoral-fin ray (*vs.* not extending into a long filament in the remaining species of *Lamontichthys*) (Fig. 10). The pectoral-fin filament is very fragile, breaks off easily, and it is frequently damaged in preserved specimens.

*Lamontichthys filamentosus* is further distinguished from all other *Lamontichthys* species, except *L. llanero*, by having the dorsal-fin spine prolonged into a long filament that may reach the posterior margin of the caudal fin (*vs.* dorsal-fin spine not extending into a long filament) and by the lower lip



**Fig. 10.** *Lamontichthys filamentosus*, MZUSP 85803, 158.6 mm SL. Dorsal, lateral and ventral views.

with a semicircular shape (Fig. 9a) (*vs.* semi-oval, Fig. 9b). *Lamontichthys filamentosus* is further distinguished from *L. llanero* by having a broader head (97.4–111.1%, *vs.* 82.6–96.9% HL).

*Lamontichthys filamentosus* is distinguished from *L. maracaibero*, *L. stibaros*, and *L. parakana* by having fewer lateral plates on the mid-ventral series (14 to 18, *vs.* 18 to 20). The presence of more than one plate between the base of the innermost pelvic-fin ray and the anterior margin of the anus further distinguishes *Lamontichthys filamentosus* from *L. maracaibero*, which has only one plate (Figs. 1 and 5).

*Lamontichthys filamentosus* is further distinguished from *L. stibaros*, *L. avacanoeiro*, and *L. parakana* by having the anterior portion of the snout almost totally covered with plates (*vs.* anterior portion of the snout with a large nude area lacking plates) and by the teeth with short cusps (*vs.* long) (Fig. 3). The longer first branched dorsal-fin ray further distinguishes *Lamontichthys filamentosus* from *L. avacanoeiro* (27.8–39.9%, *vs.* 20.5–26.0% SL). Morphometric and meristic data are presented in Table 1.

**Geographic distribution.** Upper and middle rio Amazonas basin (Fig. 2). *Lamontichthys filamentosus* occurs in sympatry with *L. stibaros* in the drainages of río Ucayali and río Marañón (upper rio Amazonas basin).

**Comments.** Specimens smaller than 80 mm SL differ from adults in having various poorly defined transversal bands on the back, between the base of the last dorsal-fin ray and the base of the caudal fin.

Fins of specimens from the upper rio Madeira (FMNH 107021, 1, 119.6 mm SL), upper rio Juruá (MZUSP 50379 and 50497, 3, 158.3–172.5 mm SL) and one specimen from upper rio Purus basin (MCP 28834, 154.9 mm SL) have gray and light brown small spots, forming short transversal bands more evident on the pectoral-fin spine and unbranched pelvic-fin ray. In addition, the specimens from the upper rio Madeira basin (FMNH 107021) and upper rio Purus basin (MCP 28834) also have the head relatively larger than the other specimens of similar size (18.2–19.3%, *vs.* 16.5–18.0% SL,  $n = 13$ , 119.4–172.5 mm SL). Isbrücker & Nijssen (1978b) previously reported on the variation of color pattern in specimens of *L. filamentosus* from the río Chapare, upper rio Madeira basin in Bolivia, and suggested that those specimens could represent a distinct subspecies or species. Although some differences were observed in specimens from the upper rio Juruá, rio Purus and rio Madeira basins, the reduced ( $n = 6$ ) number of specimens from these localities do not allow to infer if these differences are significant, and we therefore chose to conservatively assign them to *L. filamentosus*.

Although the holotype of *Harttia filamentissima* Eigenmann & Allen (1942: 211) was not examined, information from the literature and photographs (available at [www.calacademy.org](http://www.calacademy.org)) allowed us to confirm the synonymy of this species with *L. filamentosus*, previously proposed by Isbrücker & Nijssen (1978b).

**Material examined** (63 specimens; 38.8–172.5 mm SL): **Bolivia:** FMNH 107021, 1, 119.6, upper rio Madeira, Pando, 1.5 km above mouth of río Muyumanu. **Brazil:** Acre: MZUSP 50379, 1, 172.5, upper rio Juruá, Colocação São João; MZUSP 50497, 2, 158.3–158.7, upper rio Juruá, mouth of rio Tejo; MCP 28834, 2, 154.9–168.8, upper rio Purus, Bujari, igarapé Antimari, BR 364, 58 km SE of Sena Madureira. Amazonas: MZUSP 57463, 1, 62.3, rio Amazonas, below rio Madeira; MZUSP 75367, 1, 38.8, rio Amazonas, below rio Negro; INPA 17927, 2, 75.8–79.4; MZUSP 57460, 1, 65.9, rio Solimões, below rio Purus. **Ecuador:** FMNH 104334, 1, 155.7, Napo, río Napo. **Peru:** Amazonas: LACM 41724–9, 10, 120.2–150.8, Marañón, río Santiago; LACM 41705–9, 11, 130.7–153.3; LACM 41729–29, 13, 128.2–154.1, Marañón, río Santiago in La Poza; LACM 41741–9, 13, 82.5–169.0, 1cs\*, 119.4, LACM 42001–7, 1, 162.8, LACM 41740–13, 1, 167.4, confluence of río Marañón with río Nieva; LACM 42005–6, 1, 155.8, Marañón, near Caterpiza; LACM 39884–7, 1, 139.2, Marañón, Galilea, río Santiago.

### *Lamontichthys llanero* Taphorn & Lilyestrom, 1984

#### Fig. 11

*Lamontichthys llanero* Taphorn & Lilyestrom, 1984a: 96–98, fig. 2, table 1 [original description; type locality: “Venezuela, Portuguesa, río Guanare Viejo cerca de La Hoyada”]; Provenzano *et al.*, 1998: 11, 21, 23 [type listed]; Eschmeyer, 1998: 923 [listed]; Armbruster, 2004 [phylogenetic relationships]; Armbruster, 1998: 665, table 1 [analysis of the digestive tract]; Mojica, 1999: 562 [listed]; Isbrücker, 2001: 29 [listed]; Ferraris Jr., 2003: 336 [listed]; Ferraris Jr., 2007: 264 [listed]

**Diagnosis.** *Lamontichthys llanero* is distinguished from all other congeners, except *L. filamentosus*, by having the lower lip semicircular in shape (*vs.* semi-oval, Fig. 9). *Lamontichthys llanero* differs from *L. filamentosus* in the narrower head (82.6–96.9%, *vs.* 97.4–111.1% HL). *Lamontichthys llanero* has the interorbital distance larger ( $n = 36$ ) and only rarely equal ( $n = 2$ ) to the distance from the orbit to the exposed border of the cleithrum. All other species of *Lamontichthys* possess the interorbital distance shorter or equal to the distance from the orbit to the exposed border of the cleithrum (Fig. 6).

The presence of two plates between the base of the last pelvic-fin ray and the anterior border of the anus (*vs.* one) (Figs. 1 and 5), and 7 to 10 lateroventral thoracic plates in specimens larger than 50 mm SL (*vs.* 5 to 6) further distinguishes *L. llanero* from *L. maracaibero*. Specimens of *Lamontichthys llanero* larger than 70 mm SL further differs from *L. stibaros*, *L. avacanoeiro*, and *L. parakana*; in having the snout entirely covered with plates or with only a round inconspicuous area lacking plates at its anterior tip (*vs.* with a large oval area lacking plates), and teeth with short cusps (*vs.* long) (Fig. 3). *Lamontichthys llanero* further differs from *L. avacanoeiro* in the longer first branched dorsal-fin ray, in specimens larger than 50 mm SL (30.9–40.5%, *vs.* 21.9–26.0% SL). Morphometric and meristic data are presented in Table 2.



**Fig. 11.** *Lamontichthys llanero*, MZUSP 85799, 106.4 mm SL. Dorsal, lateral and ventral views.

**Geographic distribution.** Río Orinoco basin (Fig. 2).

**Comments.** *Lamontichthys llanero* has been collected near the margins of rivers varying from less than 10 m until 1 km of width, in areas with muddy waters, and sand or mud in the bottom (F. Provenzano, pers. comm.).

**Material examined** (37 specimens; 32.4-162.5 mm SL): **Colombia:** Meta: ANSP 131621, 1, 118.3, río Guayariba; ANSP 131617, 1, 106.2, confluence of río Guayariba with río Metica; ANSP 131619, 1, 96.3, río Metica; ANSP 131623, 1, 84.0, río Negro; **Venezuela:** Apure: INHS 28391, 1, 45.2, Caño. Barinas: INHS 29957, 5 (of 9), 91.1-132.4, 1cs\*, 105.2, tributary of río Masparro; INHS 29900, 3, 88.0-116.7, río Masparro. Cojedes: INHS 28989, 2, 32.4-86.1, río San Carlos; INHS 32029, 1, 87.9, río San Carlos; INHS 60236, 1, 36.3, río Pao. Guarico: MBUCV-V 31534 7, 86.3-152.2, río Orituco;

ANSP 131624, 2, 64.2-75.7, 18 km SSE Calabozo; ZMA 120469, 1, 146.8, río Guarico basin. Portuguesa: INHS 28649, 1, 162.5, Mata Larga, río Portuguesa; INHS 35687, 3 (of 4), 117.5-144.0, río Portuguesa, 3 km NE El Barriero; INHS 31993, 1, 80.1, río Guanare; INHS 69262, 3 (of 4), 81.2-124.9, Caño Los Manires; INHS 34097, 1, 70.3, río Tucupido; INHS 54657, 1, 110.7, río Portuguesa; INHS 56125, 1, 110.1, río Guanare; INHS 56151, 3 (of 4), 97.3-150.2, río Portuguesa.

***Lamontichthys maracaibero* Taphorn & Lilyestrom, 1984**  
**Fig. 12**

*Lamontichthys maracaibero* Taphorn & Lilyestrom, 1984a: 94-95, 98, fig.1, table 1 [original description; type locality: "Venezuela, Zulia, Distrito Miranda, río Motatán in el

**Table 2.** Morphometric and meristic data for *Lamontichthys llanero* and *L. maracaibero*. SD = standard deviation.

Variable	<i>L. llanero</i>				<i>L. maracaibero</i>			
	N	Range	Mean	SD	N	Range	Mean	SD
Standard length (mm)	37	32.4-162.5	104.1		9	63.4-210.2	150.0	
Percents of standard length								
Head length	37	17.4-23.2	19.0	1.4	9	16.7-21.4	18.0	1.6
Predorsal length	37	26.5-31.9	28.1	1.2	9	25.5-29.6	27.5	1.3
Postanal length	37	47.0-57.1	54.9	2.0	9	53.5-57.1	55.2	1.2
Abdominal length	36	13.7-15.8	14.6	0.5	9	13.7-16.3	15.0	0.9
Thoracic length	37	13.6-16.5	14.8	0.8	9	13.2-15.6	14.0	0.8
Dorsal-fin length	26	25.3-40.5	34.0	3.0	9	25.7-31.4	29.7	1.9
Pectoral-fin length	37	20.2-25.4	22.2	1.3	9	20.0-21.7	21.0	0.6
Pelvic-fin length	37	17.7-22.8	20.2	1.1	9	18.2-19.9	19.1	0.5
Anal-fin length	35	17.9-25.2	21.8	1.6	9	19.6-22.0	21.1	0.8
Body depth at dorsal-fin origin	37	9.6-13.6	11.5	1.0	9	11.4-15.1	13.6	1.5
Caudal peduncle depth	37	1.3-1.8	1.5	0.1	8	1.5-1.7	1.6	0.1
Body width at dorsal-fin origin	37	11.4-15.5	14.3	0.8	9	14.4-16.9	15.8	0.9
Body width at anal-fin origin	37	8.5-12.9	11.5	0.9	9	11.5-14.5	13.2	1.1
Body width at caudal-fin origin	37	2.3-3.1	2.8	0.2	9	2.3-2.8	2.5	0.2
Percents of head length								
Head width	37	82.6-96.9	92.4	3.1	9	90-112.7	103.4	7.2
Interorbital distance	37	29.4-35.0	31.9	1.4	9	29.7-33.4	31.2	1.3
Orbital diameter	37	15.0-19.4	17.5	1.1	9	12.8-16.4	14.9	1.2
Snout length	37	54.8-61.8	59.3	1.4	9	57.7-64.2	61.5	2.0
Dentary length	37	11.7-15.6	13.6	0.8	9	13.0-19.1	16.9	1.8
Lower lip width	37	9.0-16.6	12.5	1.7	9	11.1-14.0	12.4	1.0
Meristic data								
Lateral plates of median series	36	32-33	32.7	0.5	9	32-34	33.0	0.5
Lateral plates of mid-ventral series	36	15-17	15.9	0.6	9	18-20	18.9	0.8
Ventrolateral thoracic plates	36	5-10	8.2	1.1	9	5-6	5.3	0.5
Premaxillary teeth	34	33-75	58.2	9.8	9	58-100	84.8	15.5
Dentary teeth	32	27-60	47.3	7.4	9	57-91	75.3	11.4
Dorsal-fin rays	37	II,7	II,7	0.0	9	II,7-8	II,7	0.3
Pectoral-fin rays	37	I,7	I,7	0.0	9	I,7	I,7	0.0
Pelvic-fin rays	37	i,5	i,5	0.0	9	i,5	i,5	0.0
Anal-fin rays	37	i,5	i,5	0.0	9	i,5	i,5	0.0
Caudal-fin rays	36	i,12,i	i,12,i	0.0	9	i,12,i	i,12,i	0.0

Puente Tres de Febrero”; paratypes from río Motatán and río Ariguísá]; Taphorn & Lilyestrom, 1984b: 17, 29 [key and common name; lago Maracaibo, Venezuela]; Galvis *et al.*, 1997: 88 [description, habits, common names, illustrations, río Catatumbo system in Colombia and Venezuela]; Provenzano *et al.*, 1998: 11-12, 21, 23 [type listed]; Eschmeyer, 1998: 1014 [listed]; Mojica, 1999: 562 [listed]; Isbrücker, 2001: 29 [listed]; Ferraris Jr., 2003: 336 [listed]; Ferraris Jr., 2007: 264 [listed].

**Diagnosis.** *Lamontichthys maracaibero* differs from all congeners in the presence of a single plate (*vs.* two plates) between the pelvic-fin base and the anterior margin of the anus (Figs. 1 and 5).

Specimens of *L. maracaibero* larger than 150 mm SL possess a deeper body at the predorsal region (14.0-15.1%, *n* = 6, *vs.* 11.5-13.5%, *n* = 26) relative to the other species of *Lamontichthys* (except for *L. parakana* for which specimens larger than 150 mm SL were not available for comparison), forming a hump between the head and the dorsal-fin origin. *Lamontichthys maracaibero* is further distinguished from *L. filamentosus* and *L. llanero* by the semi-oval shape of the lower lip (*vs.* semicircular) (Fig. 9); and from *L. llanero* by the reduced number of lateroventral thoracic plates in specimens smaller

than 50 mm SL (5 to 6 plates, *vs.* 7 to 10), and from *L. stibaros*, *L. avacanoeiro*, and *L. parakana* by having the snout totally covered with plates at its anterior tip (*vs.* presence of an area lacking plates) and by the teeth with short cusps (*vs.* long) (Fig. 3). The specimens of *Lamontichthys maracaibero* larger than 100 mm SL also differs from *L. stibaros*, *L. avacanoeiro*, and *L. parakana* in the relatively shorter head (16.7-17.8%, *vs.* 19.8-23.0% SL) and shorter dentary (14.8-19.1%, *vs.* 18.4-23.4% HL). Morphometric and meristic data are presented in Table 2.

**Geographic distribution.** Lago Maracaibo basin (Fig. 2).

**Material examined** (9 specimens; 63.4-210.2 mm SL): **Colombia:** ICNMHN 2166, 5, 149.1-210.2, Catatumbo, Santander, río Catatumbo, córrego La Gabarra. **Venezuela:** Trujillo: lago Maracaibo drainage: MCNG 3592, 1, 154.9, holotype; MCNG 3593, 1 (of 4), 63.4, 1 cs\*, 83.8, paratypes, Betijoque, río Motatán, bridge “Tres de Febrero”. Zulia: INHS 35473, 1, 131.3, río Santa Rosa.

### *Lamontichthys parakana*, new species

#### Fig. 13

**Holotype.** INPA 3010, 112.7 mm SL, Brazil, Pará, lower rio Tocantins basin, rio Tocantins, below dam of Tucuruí, 31 Ago 1984,



**Fig. 12.** *Lamontichthys maracaibero*, INHS 35473, 131.3 mm SL. Dorsal, lateral and ventral views.

Ichthyology team of INPA.

**Paratype.** INPA 31251, 2, 72.2-119.0 mm SL, same data as holotype.

**Diagnosis.** *Lamontichthys parakana* differs from all other species of the genus in the more anterior position of the anal-fin (anal-fin origin situated anterior to the vertical through the distal tip of the last dorsal-fin ray, vs. anal-fin originating posteriorly).

*Lamontichthys parakana* further differs from the other species of *Lamontichthys*, except *L. avacanoeiro* and *L. stibaros*, in the lack of plates on the anterior tip of the snout (vs. snout entirely covered with plates or with an inconspicuous naked area), in the teeth with long cusps (vs. short) (Fig. 3), and in the longer dentary in specimens larger than 50 mm SL (20.1-22.6%, vs. 11.5-19.1% HL).

The semi-oval shaped lower lip further distinguishes *Lamontichthys parakana* from *L. filamentosus* and *L. llanero* that have the lower lip semicircular shaped (Fig. 9).

Among the species of *Lamontichthys*, *L. parakana* is more similar to *L. avacanoeiro* and *L. stibaros*, from which it may be distinguished by the broader head (101.3-106.1%, vs. 78.9-101.4% HL) and the greater orbital diameter (16.6-17.3%, vs. 13.7-15.5% HL), in specimens larger than 100 mm SL.

*Lamontichthys parakana* also differs from *L. avacanoeiro* in the longer length of the first branched dorsal-fin ray (26.4-31.0%, vs. 20.5-26.7% SL).

**Description.** Morphometric and meristic data presented in Table 3. Largest specimen 119.0 mm SL (n = 3). Head and trunk totally covered with plates. Body depressed, deeper at

vertical through dorsal-fin origin, gradually more depressed posteriorly, to caudal-fin base and anteriorly, to snout tip. Head ellipse shaped in dorsal view, with slight prominence at anterior tip. Dorsal profile of head slightly convex. Dorsal profile of body slightly convex from posterior tip of supraoccipital to dorsal-fin origin, posteroventrally slanted from latter point to vertical through tip of last anal fin ray, straight to caudal-fin base. Largest body width at cleithrum, gradually narrower to 18<sup>th</sup> to 19<sup>th</sup> lateral plate of median series more abruptly so posteriorly, into base of caudal-fin. Caudal peduncle long, narrow and very depressed. Ventral profile of head and body straight from snout tip into base of caudal-fin. Pectoral-fin origin at vertical through posterior border of orbit. Dorsal-fin origin immediately anterior of vertical through pelvic-fin origin. Base of last anal-fin ray at vertical through distal tip of last dorsal-fin ray.

Eyes located dorsally, anterior to vertical through pectoral-fin origin. Interorbital distance shorter or equal to distance from orbit to exposed borders of cleithrum. Mouth ventral.

Upper and lower lip semi-oval shaped. Lower lip extending short of vertical through anteriormost margin of orbit, covered with small papillae on ventral surface and along its border. Dorsal surface of lower lip smooth. Upper lip narrower, with small papillae on ventral surface (internal) and with small round plates covered with odontods on dorsal surface (external). Maxillary barbel inconspicuous, united by membrane to lateral border of lower lip.

Teeth setiform, long, hook-shaped and bicuspid. Tooth cusps long, flattened and unequal, with round tips, darker than rest of tooth. Median cusp slightly longer and broader than lateral cusp. Number of jaw teeth increasing with growth. Number of premaxillary teeth approximately 16% greater than number of dentary teeth. Emergent teeth placed in two irregularly arranged rows; teeth gradually smaller laterally. Replacement teeth oriented at 90 degrees relative to emergent teeth and covered with skin.

Anteroventral tip of snout without plates, with distinguishable naked portion, approximately oval shaped,



**Fig. 13.** *Lamontichthys parakana*, INPA 3010, 112.7 mm SL, holotype. Dorsal, lateral and ventral views.

**Table 3.** Morphometric and meristic data for *Lamontichthys parakana* (n = 3) and *L. stibaros*. SD = standard deviation. Range of *L. parakana* includes holotype and paratypes.

Variable	<i>L. parakana</i>				<i>L. stibaros</i>			
	Holotype	Range	Mean	SD	N	Range	Mean	SD
Standard length (mm)	112.7	72.2-119.0	101.3		25	27.2-172.8	73.7	
Percents of standard length								
Head length	20.6	20.6-22.4	21.3	1.0	25	18.4-28.5	22.5	2.2
Predorsal length	29.1	29.1-31.1	30.1	1.0	25	23.3-33.7	30.4	2.2
Postanal length	51.6	51.6-60.6	55.3	4.7	25	41.3-62.3	50.9	3.8
Abdominal length	16.8	15.9-17.1	16.6	0.6	25	4.9-17.0	15.0	2.2
Thoracic length	14.7	14.7-16.1	15.4	0.7	25	13.3-17.1	15.4	0.9
Dorsal-fin length	29.9	26.4-31.0	29.1	2.4	24	24.0-36.8	29.4	3.1
Pectoral-fin length	22.4	21.0-22.8	22.0	1.0	25	20.7-25.1	23.0	1.1
Pelvic-fin length	21.5	18.8-22.2	20.8	1.8	25	17.5-22.9	20.1	1.3
Anal-fin length	22.8	21.4-24.8	23.0	1.7	25	17.5-22.9	20.3	1.4
Body depth at dorsal-fin origin	11.6	10.8-12.7	11.7	0.9	25	1.8-12.1	10.2	2.0
Caudal peduncle depth	1.5	1.5-1.8	1.7	0.1	25	1.5-9.8	2.1	1.6
Body width at dorsal-fin origin	15.2	14.1-16.5	15.3	1.2	25	10.2-16.4	14.4	1.3
Body width at anal-fin origin	12.5	11.6-13.2	12.4	0.8	25	7.8-26.2	17.5	5.6
Body width at caudal-fin origin	2.6	2.6-3.1	2.8	0.3	25	2.3-3.1	2.7	0.2
Percents of head length								
Head width	101.3	95.2-106.1	100.9	5.5	25	73.5-102.2	88.6	6.5
Interorbital distance	26.4	26.4-30.1	27.6	2.1	25	26.4-30.9	28.3	1.2
Orbital diameter	16.6	16.6-17.3	16.9	0.4	25	13.8-27.8	16.6	2.7
Snout length	61.6	59.3-62.5	61.1	1.6	25	52.8-65.8	59.4	2.8
Dentary length	21.7	20.1-22.6	21.5	1.2	25	14.7-24.3	19.9	2.3
Lower lip width	14.0	14.0-18.0	16.0	2.0	25	11.2-18.9	14.5	2.0
Meristic data								
Lateral plates of median series	32	32-33	32.3	0.6	25	33-35	34.0	0.5
Lateral plates of midventral series	18	18	18	0.0	25	19-20	19.5	0.5
Ventrolateral thoracic plates	6-7	6-7	6.3	0.6	25	0-8	6.3	1.5
Premaxillary teeth	76-88	55-76	64.3	10.7	24	36-109	60.9	16.6
Dentary teeth	64-67	49-67	55.3	10.1	25	34-94	58.6	14.8
Dorsal-fin rays	II,7	II,7	II,7	0.0	25	II,7	II,7	0.0
Pectoral-fin rays	I,7	I,7	I,7	0.0	25	I,7	I,7	0.0
Pelvic-fin rays	i,5	i,5	i,5	0.0	25	i,5	i,5	0.0
Anal-fin rays	i,5	i,5	i,5	0.0	25	i,5	i,5	0.0
Caudal-fin rays	i,12,i	i,12,i	i,12,i	0.0	24	i,12,i	i,12,i	0.0

covered with stiff connective tissue. Anterior border of head with small, flexible plates between snout tip and anterolateral margin of upper lip. Lateral border of head covered with larger dorsal plates anteroventrally curved.

Three inconspicuous horizontal keels along body, from plates 6 to 14 or 16. Last plate of median lateral series diminutive and triangular, located on caudal-fin base, between two slightly larger plates of similar shape (one upper and one lower, upper plate slightly larger than lower plate). Lateral plates of median series, 32-33. Small ventral thoracic plates lozenge shaped, arranged in irregular, oblique rows. Longest row with 7 to 8 plates delimited by lateroventral thoracic plates. Region of abdomen anterior to anus covered with small, lozenge shaped plates, followed by one larger plate that form anterior border of anus.

Pectoral- and dorsal-fin spines, unbranched pelvic- and anal-fin rays not projecting into long filaments. Unbranched caudal-fin rays of both specimens damaged, except lower unbranched caudal- fin ray from one specimen which projects as long filament. Branched caudal-fin rays gradually longer toward upper and lower unbranched rays. Dorsal most branched caudal-fin ray slightly longer than ventral most ray. Unbranched pelvic-fin ray reaching vertical through anterior

border of first ventral plate posterior to base of anal fin. Unbranched anal-fin ray reaching eighth ventral plate posterior to base of anal fin.

Dorsal-fin rays II,7; pectoral-fin rays I,7; pelvic-fin rays i,5; anal-fin rays i,5; caudal-fin rays i,12,i.

**Color in alcohol.** Coloration of paratype faded, uniform yellow. Color pattern based only on holotype. Ground coloration of head and body brown or yellow. Ventral region of head and body lighter, uniform yellow. Dorsal region of upper lip dark brown. Straight unpigmented median stripe from last anal-fin ray to base of unbranched lower caudal-fin ray. Dorsal region of body with three longitudinal, dark brown bands extending from base of dorsal fin to base of caudal fin. Two of these bands extending ventrally to cover lateral plates. Third band extending along dorsal midline of body, from dorsal-fin base to caudal-fin base. Bands gradually narrower posteriorly. A transversal, dark brown band between bases of pectoral-fins, with anterior margin at posterior tip of supraoccipital. Dorsal portion of head dark brown with slightly lighter areas. All fin rays with dark brown pigmentation. Anterior half of dorsal-fin dark brown, remaining of fin hyaline. Paired fins and anal-fin dark brown. Caudal-fin base and three upper most and



lower most branched rays dark brown.

**Etymology.** The species name, parakana, is in reference to the Parakanã, inhabitants of the margins of the lower rio Tocantins, in the State of Pará. Parakanã, an American group that historically inhabited the area of the lower rio Tocantins, drainage from which the examined specimens of the species in this study originated.

**Geographic distribution.** Known from the type locality at lower rio Tocantins, below Tucuruí Dam (Fig. 2).

### *Lamontichthys stibaros* Isbrücker & Nijssen, 1978

#### Fig. 14

*Lamontichthys stibaros* Isbrücker & Nijssen, 1978b: 66-69, figs. 8 and 9, 10d, 14, table Ic, li-j, IIIb [original description; type locality: Ecuador, "Prov. Pastaza, rio Amazon system, rio Bobonaza in Chicherota, 02°25'S 76°38'W, altitude aprox. 260-280 m, upper rio Pastaza"]; Isbrücker, 1980: 92 [listed]; Ortega & Vari, 1986: 17 [literature compilation; Peru]; Burgess, 1989: 426-427 [listed; description]; Barriga, 1991: 66 [literature compilation; Oriental Ecuador]; Ferraris & Vari, 1992: 27 [type listed]; Eschmeyer, 1998: 1611 [listed]; Isbrücker, 2001: 29 [listed]; Ferraris Jr., 2003: 336 [listed]; Ferraris Jr., 2007: 264 [listed]; Sullivan *et al.*, 2006: [Siluriform higher-level relationships; molecular data, specimen not examined].

**Diagnosis.** *Lamontichthys stibaros* differs from all other species of the genus, with the exception of *L. avacanoeiro* and *L. parakana*, in the lack of plates on the anterior tip of the snout (*vs.* anterior portion of snout totally covered with plates or with an inconspicuous naked area), in the teeth with long cusps (*vs.* short) (Fig. 3), and in the lower lip semi-oval shaped (*vs.* semicircular) (Fig. 3).

*Lamontichthys stibaros* differs from *L. avacanoeiro* and *L. parakana* in the longer first branched dorsal-fin ray (29.7-36.8%, *vs.* 22.6-31.0% SL), in specimens larger than 70 mm SL. It further differs from *L. avacanoeiro* in the longer first branched pectoral-fin ray (21.7-25.1%, *vs.* 19.2-22.0% SL) and from *L. parakana* in the narrower head (89.1-101.4%, *vs.* 101.3-106.1% HL).

The presence of 19 to 20 lateral plates along the mid-ventral series (*vs.* 14 to 18) and the longer dentary (18.6-23.2%, *vs.* 11.5-17.3% HL) in specimens larger than 70 mm SL also distinguishes *L. stibaros* from *L. filamentosus* and *L. llanero*. *Lamontichthys stibaros* differs from *L. maracaibero* in having more than one plate between the base of the last pelvic-fin ray and the anterior border of the anus (*vs.* one plate) (Figs. 1 and 5) and in the uniform color pattern of the fins (*vs.* with brown and gray spots). Morphometric and meristic data are presented in Table 3.

**Geographic distribution.** Upper rio Amazonas basin (Fig. 2). *Lamontichthys stibaros* occurs in sympatry with *L.*

*filamentosus* in the drainages of río Santiago, río Marañón and río Ucayali, in Peru.

**Material examined** (25 specimens; 27.2-172.8 mm SL): **Peru:** Amazonas: LACM 39897-1, 3, 42.2-89.5, río Santiago; LACM 39884-3, 2, 100.2-120.1, Marañón, río Santiago; LACM 39647-1, 1, 172.6, Marañón, río Cenepa, close to río Tujushiku. Ayacucho: ROM 47093, 2, 122.6-150.1, near to confluence between río Mantaro and Tambo Apurimac. Ucayali: FMNH 84137, 7, 27.2-58.2, río San Alejandro; FMNH 84131, 2, 43.8-47.3; FMNH 84112, 3, 63.3-86.6, río San Alejandro; FMNH 84111, 6, 49.3-100.1, 1 cs\*, 62.4, río San Alejandro.

### Description of characters and phylogenetic analysis

Characters and their respective states analyzed in this study are grouped according to the region of the body with which they are associated.

#### Neurocranium

**1.** Ventral depression at anterior tip of mesethmoid: (0) absent; (1) present (CI = 100; RI = 100).

The mesethmoid of loricariids varies considerably in shape but usually its posterior portion is relatively elongate, narrow, and cylindrical. The lateral projections (cornuas) at the anterior tip of the ossification may be extremely reduced or absent (Schaefer, 1990: 175; 1998: 394) and the median anteroventral portion is usually thin and lacks a groove or cavity.

Uniquely among taxa examined, the mesethmoid of *L. filamentosus*, *L. llanero*, and *L. maracaibero* possesses an anteroventral depression (Fig. 15a). A strong, anteriorly directed ligament attaches to this groove and is, apparently, connected to plates on the snout tip.

**2.** Tissue adhered to anterior tip of mesethmoid: (0) present; (1) absent (CI = 50; RI = 0).

A thick layer of tissue, strongly adhered to the anterior tip of the mesethmoid, which may be covered by plates, is present in all taxa examined except *Farlowella* and *Pseudoloricaria*. This feature was previously described by Rapp Py-Daniel (1997: character 8).

**3.** Shape of mesethmoid disk: (0) robust, circular in lateral view with margins of disk much broader than central portion; (1) laminar shaped, circular in lateral view; (2) laminar shaped, rectangular to triangular in lateral view, similar to a keel (CI = 66; RI = 83).

The ventral surface of the mesethmoid of astroblepids and loricariids possesses a vertical process on the median longitudinal line close to the premaxillae and is referred to as the mesethmo-premaxillary articular condyle or mesethmoid disk (Schaefer, 1987: 5; 1998: 384). Ligaments that sustain the premaxillae are inserted on this process and enable their ample mobility (Schaefer, 1987).

In *Lamontichthys*, *Harttia*, *Hypostomus*, *Neoplecostomus*, *Pterosturisoma*, and *Sturisomatichthys*, the mesethmoid disk is robust, circular in lateral view and with the margins of the



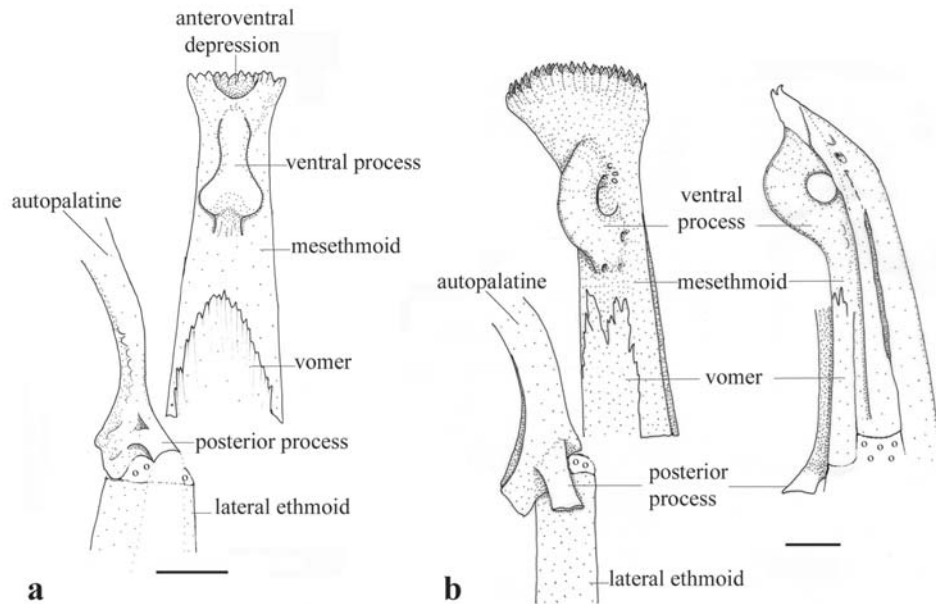
**Fig. 14.** *Lamontichthys stibaros*, INHS 84111, 100.1 mm SL. Dorsal, lateral and ventral views.

disk much broader than the central portion (Figs. 15 and 16a). In the two conditions considered as derived, the mesethmoid disk is more delicate (Fig. 16b-c). In *Farlowella* and *Sturisoma*, although the disk is also approximately circular in lateral view it is laminar shaped. In *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, the mesethmoid disk is also laminar shaped, but the lamina is thin and rectangular to triangular in lateral view, similar to a keel.

**4.** Position of mesethmoid disk relative to anterior mesethmoid margin: (0) terminal, on anterior margin of mesethmoid; (1)

subterminal, at short distance from anterior margin of mesethmoid; (2) non-terminal, far from anterior margin of mesethmoid (CI = 50; RI = 33).

The position of the mesethmoid disk relative to the anterior mesethmoid margin is variable within the Loricariidae (Schaefer, 1991; 1998: 384; Armbruster, 2004). The Ancistrinae, a few Hypoptopomatinae, Hypostominae, and *Neoplecostomus* possess the mesethmoid disk located at the terminal anterior margin of the mesethmoid, a condition shared with the Astroblepidae (Fig. 16a, Schaefer, 1987: fig. 3; 1991: 7). Other loricariids possess the mesethmoid disk in a non-terminal



**Fig. 15.** Ventral view of mesethmoid, lateral ethmoid, anterior portion of vomer, and posterior portion of autopalatine of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a), and *L. avacanoeiro* (MZUSP 61974, 113.7 mm SL, paratype) (b, left). Lateral view of these structures (b, right). Scale bar = 1 mm.

position, at varying distances from the anterior margin of the bone (Figs. 15 and 16b-c). The distance between the mesethmoid disk and the anterior margin of the mesethmoid is short in *Lamontichthys*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, and *Rineloricaria*, and longer in *Farlowella*, *Sturisoma*, and *Sturisomatichthys*.

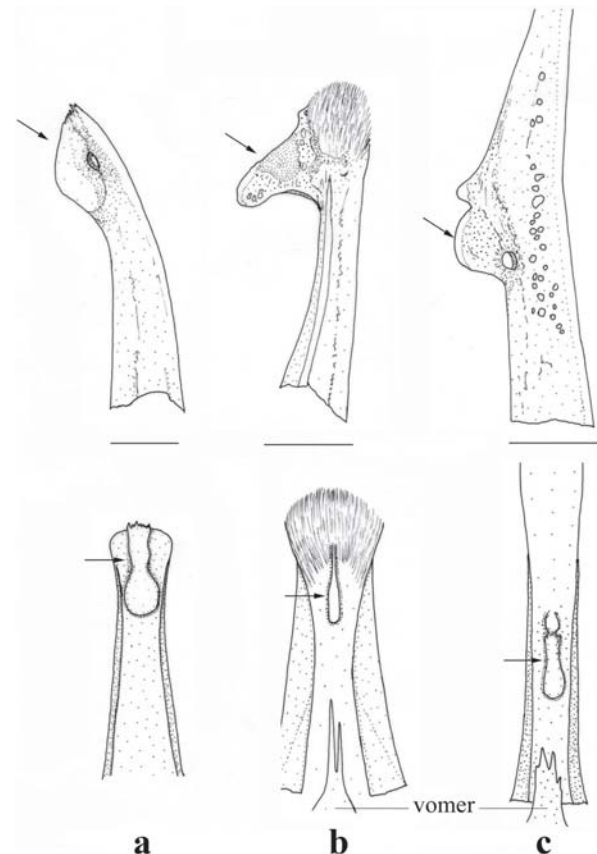
**5.** Anterior portion of vomer: (0) thick, with short anterior prolongations; (1) elongate, with one or two long and narrow prolongations (CI = 50; RI = 83).

In Loricariids the vomer is elongate with reduced lateral wings, and is sutured anteriorly to the mesethmoid and posteriorly to the parasphenoid (Schaefer, 1987: 5). The anterior portion varies in shape and the posterior portion is tapered at the end, forming an elongate tip (Rapp Py-Daniel, 1997: character 9).

In *Lamontichthys*, *Harttia*, *Neoplecostomus*, and *Sturisomatichthys* the vomer has a thick anterior portion, with very short anterior prolongations (Fig. 15). In the derived condition, present in *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisoma* the anterior portion of the vomer is elongate, and has one or two long and narrow prolongations (Fig. 16b-c). Schaefer (1987: 5; 1997a: 23) observed a similar condition in *Hypostomus plecostomus* (Hypostominae) and in *Otocinclus* (Hypoptopomatinae).

**6.** Dorsal projection (or lateral wall) on dorsolateral region of lateral ethmoid: (0) extending along entire lateral border of bone; (1) extending approximately from posterior half of lateral border of bone (CI = 33; RI = 60).

The lateral ethmoid in loricariids encapsulates the nasal organ from below (Howes, 1983; Schaefer, 1991). Anteriorly,



**Fig. 16.** Lateral (upper) and ventral (lower) views of the mesethmoid of *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL) (a), *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL) (b), and *Farlowella nattereri* (MZUSP 57658, 112.9 mm SL) (c). Arrow points to the mesethmoid disk, anterior to top. Scale bar = 1 mm.

the lateral ethmoid has a concave face, with cartilage, that articulates with the autopalatine. Posteriorly, the lateral (vertical), ventral (horizontal) and medial (vertical) walls of the capsule are open only dorsally. The meeting of these walls shape part of the anterior border of the orbit.

In the Callichthyidae (except *Aspidoras*, *Brochis*, and *Corydoras*) and most loricariids, including *Neoplecostomus*, the lateral wall is formed by the anterior condyle of the lateral ethmoid that completely encapsulates the nasal organ (Howes, 1983: 331; Schaefer, 1998: 394). This condition occurs in *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, and *Sturisomatichthys*.

In *Lamontichthys*, *Harttia*, *Pterosturisoma*, and *Sturisoma* the lateral wall of the lateral ethmoid is formed more posteriorly, leaving anteriorly a small portion lacking an ossified wall (Fig. 17; Howes, 1983: 331), a condition shared with the Hypoptopomatinae (Schaefer, 1998: 394).

*Pterosturisoma microps* possesses the dorsal border of the nasal fossa circular, while in the other taxa the border is oval. This condition was not codified in the present analysis, however it may be tentatively proposed as autapomorphic for this species.

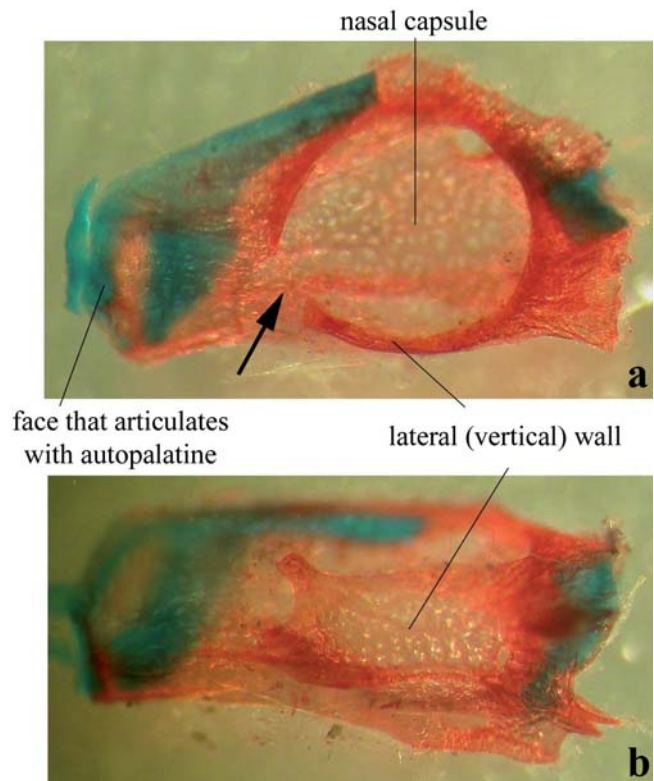
**7. Type of contact between lateral ethmoid and dorsal border of metapterygoid:** (0) through posterior process; (1) through posterior process and anterior short suture; (2) through interdigitating margins, with no process (CI = 66; RI = 66).

Among the Siluriformes, only in the family Loricariidae the ventral surface of the lateral ethmoid contacts the dorsal border of the metapterygoid (Schaefer, 1987). In *Lamontichthys*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* this contact is limited to the posterior portion of the dorsal border of the metapterygoid, which articulates with the lateral ethmoid by processes present on both ossifications, a condition shared with *Neoplecostomus* and most loricariids (Fig. 18a). In the derived condition, *Farlowella* and *Hypostomus* possess an additional contact characterized by a short suture in the anterior portion of the metapterygoid (Fig. 18c). In *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, the dorsal border of the metapterygoid contacts the lateral ethmoid by an interdigitating type of contact (Fig. 18b).

Schaefer (1991: 7; 1998: 394) reported the presence of a vertical lamina in the lateral ethmoid contacting the metapterygoid in various loricariids (Ancistrinae, most Hypoptopomatinae, Hypostominae, most Loricariinae, and *Neoplecostomus*), however, he did not describe variation in the type of contact between these structures.

**8. Lateral process of sphenotic:** (0) long; (1) short; (2) inconspicuous or absent (CI = 66; RI = 0).

Located lateral to the supraoccipital, the sphenotic forms the dorsoposterior portion of the orbit in the majority of the Loricariidae and bears part of the temporal laterosensory canal (Schaefer, 1987: 6). The sphenotic of loricariids is usually square-shaped with one long lateral process. Schaefer (1987: 6) considered the lateral process of the sphenotic in loricariids



**Fig. 17.** Dorsal (a) and lateral (b) views of the lateral ethmoid of *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL). Arrow points to anterior portion of lateral ethmoid that lacks an ossified wall.

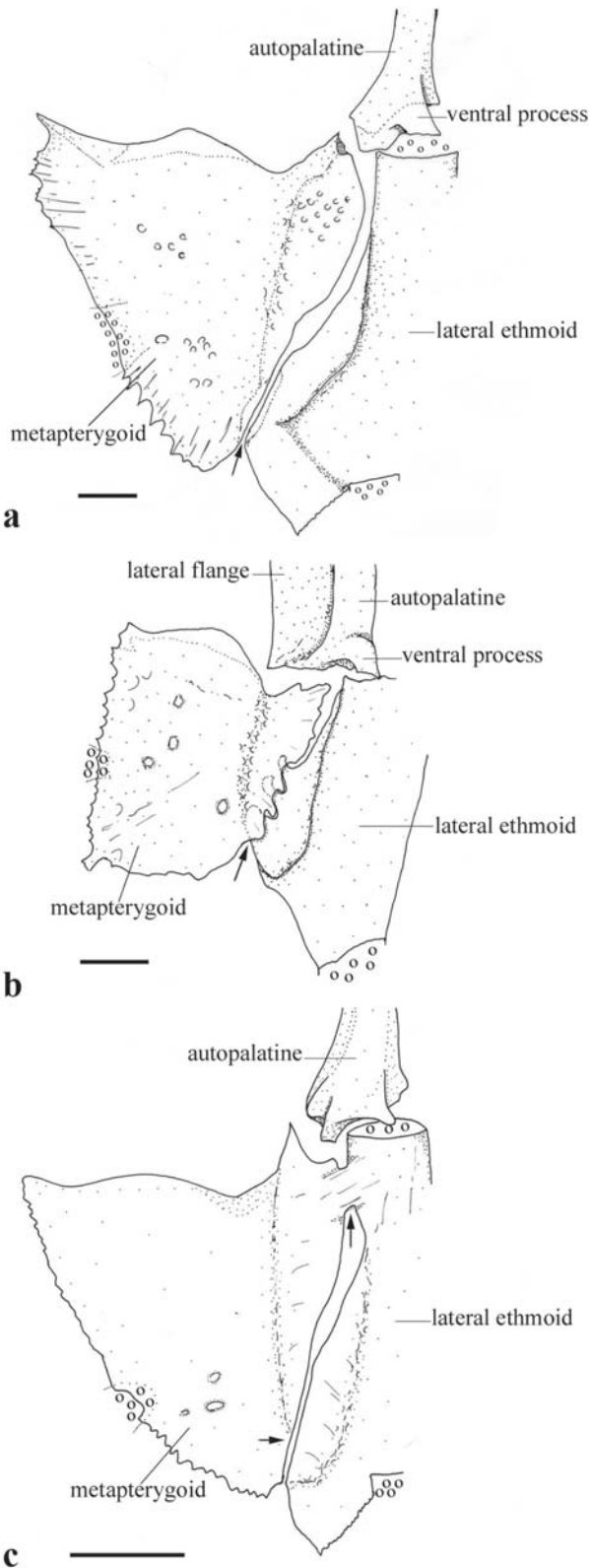
as homologous to the prominent “lateral spine” representative of the Siluriformes in general. However, Howes (1983: 95) considered that the lateral spine present in the sphenotic of primitive Teleostei is absent in Siluriformes, including the Diplomystidae (Arratia, 1987: 92), Scoloplacidae (Schaefer, 1990: 180) and the Loricariidae.

Astroblepids and many loricariids possess a long lateral process of variable width on the sphenotic (Armbruster, 2004: 26), while other loricariids possess a relatively short and wide or inconspicuous process. Variation in the size of this process is accompanied by several degrees of participation of the sphenotic in the margin of the orbit.

*Lamontichthys*, *Farlowella*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, and *Sturisomatichthys* possess a long sphenotic process of variable width, a condition shared with other loricariids such as *Hypostomus* and *Neoplecostomus* (Fig. 19). In this condition, the sphenotic contributes with 1/5 or more to the dorsoposterior margin of the orbit.

*Sturisoma* possesses a short and wide lateral process, and the sphenotic contributes with approximately 1/5 of the border of the orbit, and in *Pterosturisoma* this process is much shorter and the sphenotic has little or no contribution to the margin of the orbit (Fig. 20).

Observation of this character is better accomplished with



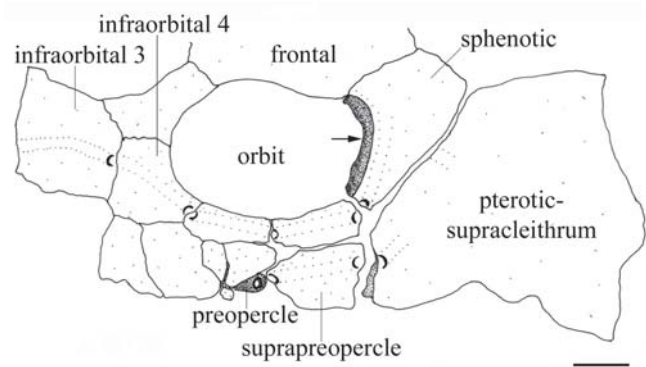
**Fig. 18.** Ventral view of region of contact between the lateral ethmoid and dorsal border of metapterygoid of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a), *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL) (b) and *Farlowella nattereri* (MZUSP 57658, 112.9 mm SL) (c). Arrows points to the region of contact between the two ossifications. Scale bar = 1 mm.

the sphenotic separate from the rest of the neurocranium.

**9.** Orbital notch in sphenotic: (0) absent; (1) present (CI = 100; RI = 100).

The orbital notch is formed by an anteroventral laminar expansion of the sphenotic, in the region where the sphenotic forms the posterior margin of the orbit, and its presence is considered derived within loriciariids and proposed as autapomorphic for the tribe Loriciariini (Boeseman, 1971: 17).

Among examined taxa, the presence of an orbital notch is restricted to the clade that includes members of the Loriciariini, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* (Fig. 19).



**Fig. 19.** Lateral view of left side of bones surrounding orbit of *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL). Arrow points to orbital notch. Scale bar = 1 mm.

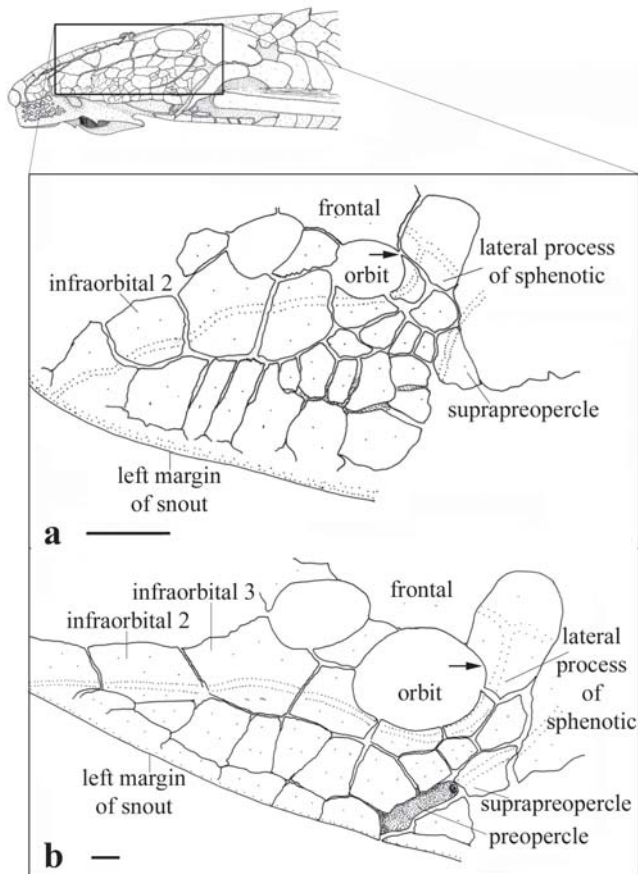
**Hyoid Arch and Branchial Arches**

**10.** Relative width of ventral laminar expansion along posterior border of anterior ceratohyal: (0) widens abruptly in lateral portion; (1) widens gradually from medial to lateral portion, narrow; (2) widens gradually from medial to lateral portion, broad (CI = 50; RI = 66).

In the Astroblepidae and Loriciariidae the anterior and posterior ceratohyals possess a ventral laminar expansion along their posterior borders, forming an angle of approximately 90° with the remaining of the hyoid arch (anterohyal of Schaefer, 1987: 12). Schaefer & Lauder (1986) discussed various specializations in the musculature and osteology of the hyoid arch in the Astroblepidae and Loriciariidae associated with the life-style of members of these families. These fishes continue to respire while maintaining the suck pressure of the oral disk (Alexander, 1965: 136). In addition, the ceratohyal of the Loriciariidae possesses expansions forming a broad surface for the attachment of the associated musculature (Schaefer & Lauder, 1986: 500).

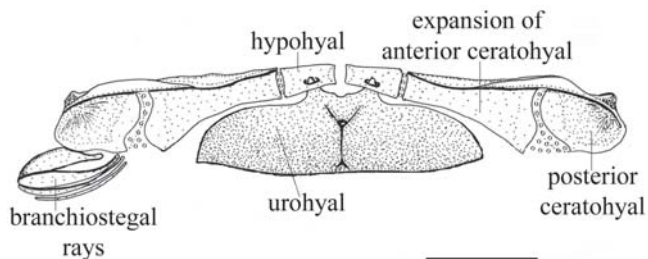
The ventral expansion of the posterior border of the anterior ceratohyal varies among loriciariids. In *Farlowella*, *Hypostomus*, *Loricaria*, *Neoplecostomus*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisomatichthys* the laminar expansion widens abruptly in the lateral portion of the bone.

In *Lamontichthys* (except *L. avacanoeiro*), *Harttia*, and



**Fig. 20.** Lateral view of region of snout and orbit (left side) of *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL) (a) and *Sturisoma* sp. (MZUSP 50112, 115.2 mm SL) (b). Arrow points to margin of sphenotic that borders the orbit. Scale bar = 2 mm.

*Sturisoma*, the ventral expansion of the anterior ceratohyal is relatively narrow overall, and it widens gradually along the extension of the bone (Fig. 21). Although in *L. avacanoeiro* the ventral expansion of the anterior ceratohyal also widens gradually along the extension of the bone the ossification is relatively broad, distinctly wider than the expansion in the other species of *Lamontichthys*.



**Fig. 21.** Anterior view of hyoid and branchial arches of *Lamontichthys stibaros* (FMNH 84111, 62.4 mm SL). Branchial filaments not represented. Scale bar = 2 mm.

**11.** Ossification in basibranchial 3: (0) absent; (1) present (CI = 100; RI = 100).

The first basibranchial commonly present in the Otophysi is absent in the Siluriformes (Arratia, 1987: 41). The branchial arches of the Loricariidae possess three basibranchials (2, 3 and 4), with basibranchial 2 being ossified, basibranchial 4 cartilaginous, and basibranchial 3 having variable degrees of ossification among taxa (Schaefer, 1987: 12). The Ancistrinae, many Hypoptopomatinae, Hypostominae and *Neoplecostomus* possess the basibranchial 3 cartilaginous (Schaefer, 1987: 12), a condition herein observed in *Hypostomus* and *Neoplecostomus*.

The presence of ossification in basibranchial 3 is considered derived within the Loricariidae and occurs in *Lamontichthys*, *Farlowella*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*.

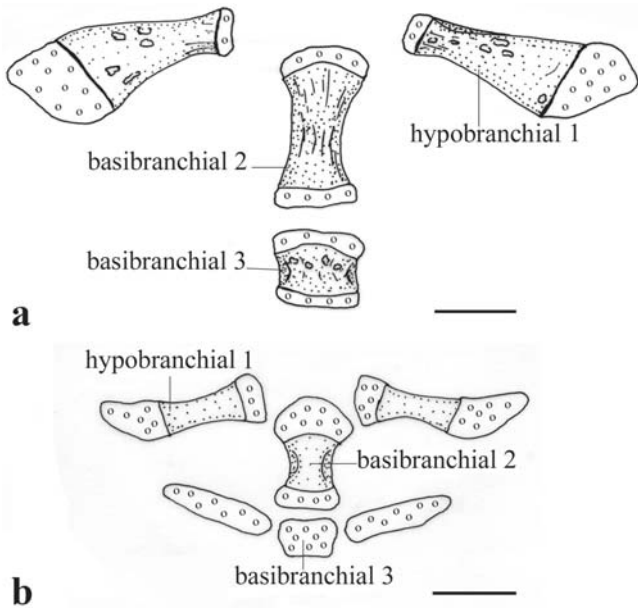
**12.** Shape of first hypobranchial: (0) stick-shaped; (1) fan-shaped (CI = 100; RI = 100).

Loricariids possess five pairs of hypobranchials, the first pair is ossified and the others cartilaginous (Schaefer, 1987: 12). The first hypobranchial in loricariids is usually stick-shaped and slightly wider in the medial tip. However, some loricariids possess a derived condition, wherein the lateral portion of the first hypobranchial is considerably broader than the medial portion resulting in a fan-shaped ossification (Armbruster, 2004: 11). In the present study, a fan shaped first hypobranchial was observed only in *Loricaria* and *Pseudoloricaria*. In the other loricariids examined, including *Lamontichthys*, the first hypobranchial is stick-shaped, gradually widening towards the lateral margin (Fig. 22).

**13.** Shape of lower pharyngeal plate: (0) stick-shaped, slightly expanded; (1) triangular; (2) approximately rectangular, with posterior border parallel to anterior border, medial and lateral borders of similar length; (3) quadrangular, medial and lateral borders parallel, medial border approximately same length of posterior border and slightly longer than lateral border; (4) trapezoidal, medial and lateral borders almost parallel, medial border larger than the posterior border and at least twice larger than the lateral border (CI = 100; RI = 100).

The fifth ceratobranchial in the Otophysi is modified into a plate-like ossification with teeth, and within the Loricariidae there is wide variation in the shape of the pharyngeal plate (Schaefer, 1987: 12). The fifth ceratobranchial in *Neoplecostomus* is a somewhat broad ossification with a narrow dorsal end, a condition considered plesiomorphic for the Siluriformes (Fig. 23; Arratia, 1987: 41).

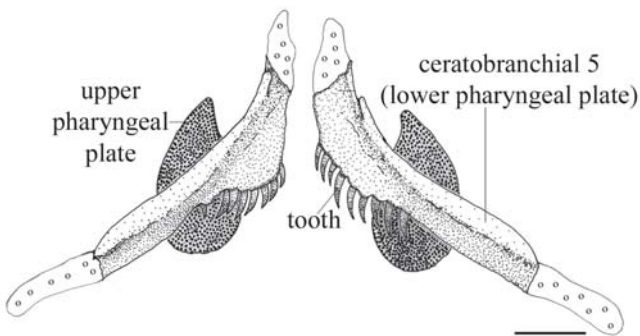
Armbruster (2004: 9) characterized the shape of the lower pharyngeal plate of most Loricariinae as widened at least anteriorly to form a hatchetlike structure. In the present study, four different conditions may be further distinguished regarding the lower pharyngeal of the Loricariinae. *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisomatichthys* possess the lower



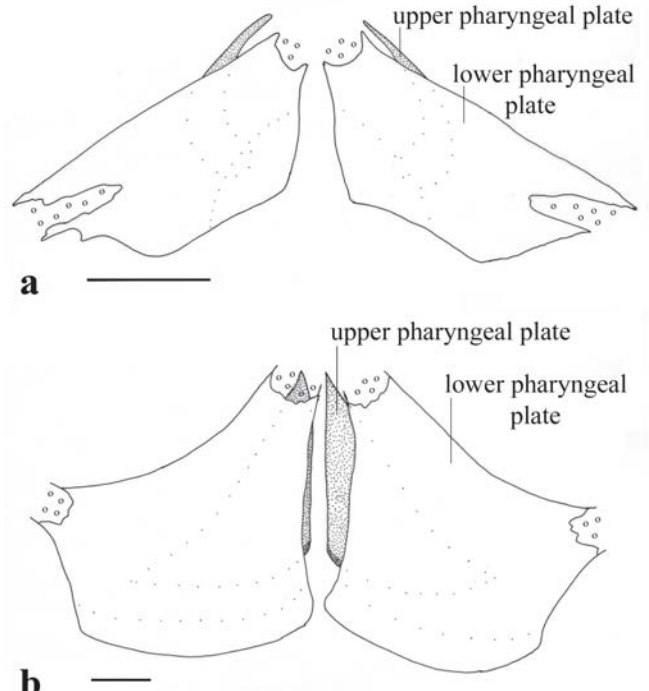
**Fig. 22.** Dorsal view of hypobranchial 1 and basibranchials 2 and 3 of *Lamontichthys avacanoeiro* (MZUSP 61974, 113.7 mm SL, paratype) (a), and *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL) (b). Scale bar = 0.5 mm.

pharyngeal plate approximately triangular and little expanded. In *Harttia* this structure is also little expanded, however it is somewhat rectangular-shaped, with the posterior border parallel to anterior border and medial and lateral borders of similar length (Fig. 24a).

The lower pharyngeal plate is considerably enlarged in *Lamontichthys* and *Sturisoma*. In *Sturisoma* the lower pharyngeal plate is approximately quadrangular, the medial and lateral borders are parallel, and the medial border has approximately the same length of the posterior border and is slightly longer than the lateral border (Fig. 24b). In *Lamontichthys*, the lower pharyngeal plate is approximately trapezoidal, with the medial border larger than the posterior border and, at least, twice as large as the lateral border (Fig. 25a).



**Fig. 23.** Ventral view of the lower pharyngeal plate of *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL). Scale bar = 0.5 mm.



**Fig. 24.** Ventral view of the lower pharyngeal plate of *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL) (a) and *Sturisoma* sp. (MZUSP 50112, 115.2 mm SL) (b). Scale bar = 1 mm.

**14.** Posterior expansion of first epibranchial: (0) absent; (1) triangular, short; (2) triangular, relatively elongate (CI = 40; RI = 66).

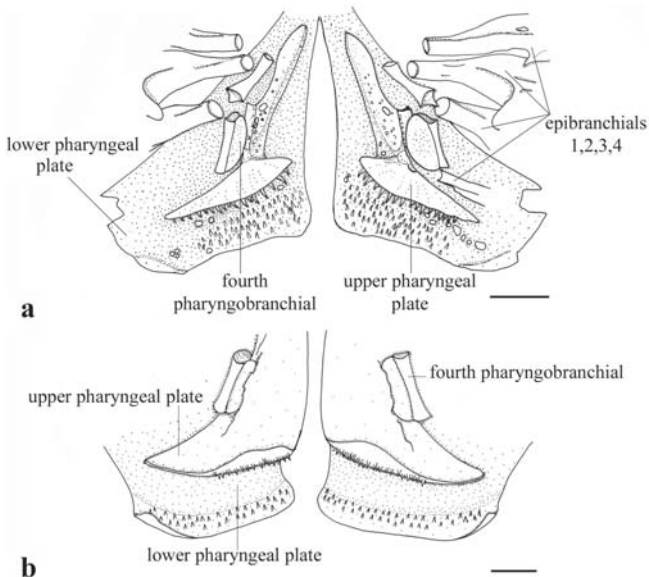
The posterior border of the first epibranchial in *Lamontichthys* has a long triangular laminar expansion that is projected medially (Fig. 26a). In the other Loricariinae examined, this projection is absent or relatively short. *Farlowella*, *Harttia*, *Loricaria*, and *Rineloricaria* do not possess any projection in the posterior border of this bone (Fig. 26c), and *Pseudoloricaria*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* possess a short laminar projection (Fig. 26b).

Schaefer (1987: 12) described the presence of a posterior process in the first epibranchial for *Hypostomus plecostomus*, and the condition of this species was coded as 1 in the present study.

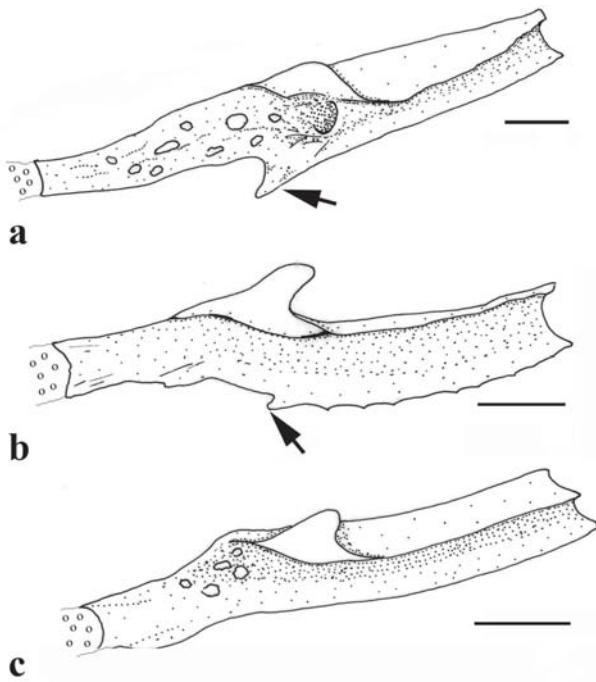
**15.** Uncinate process at posterior border of third epibranchial: (0) absent; (1) short; (2) long (CI = 50; RI = 66).

The third epibranchial in the majority of the Loricariidae possesses an uncinate process with varying degrees of development (Rapp Py-Daniel, 1997: character 75). When present, the process arises from the posteromedial border of the epibranchial, and extends into the medial portion of the brachial arches. A small dorsolateral process is present in the third epibranchial of *Hypostomus plecostomus* (Schaefer, 1987: 14) and *Harttia loricariformis* (Fig. 27).

The third epibranchial in *Lamontichthys*, *Farlowella*, *Harttia punctata*, *Neoplecostomus*, *Pterosturisoma*,

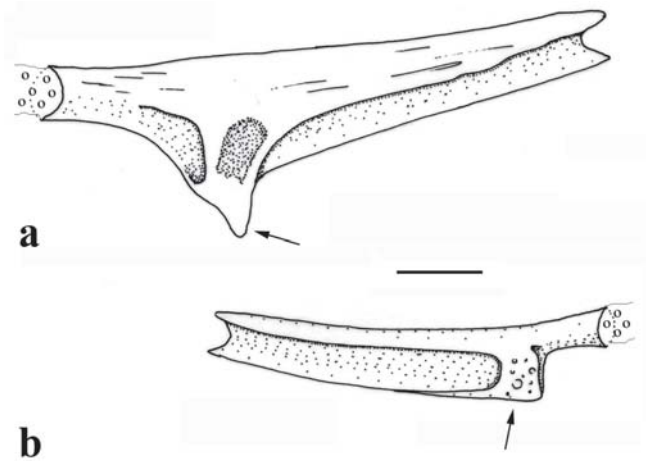


**Fig. 25.** Dorsal view of posterior portion of branchial arches of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a) and *Sturisoma* sp. (MZUSP 50112, 115.2 mm SL) (b). Cartilages not represented. Scale bar = 1 mm.



**Fig. 26.** Dorsal view of first epibranchial (right side) of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a), *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL) (b), and *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL) (c). Arrow points to posterior process of first epibranchial. Scale bar = 1 mm.

*Sturisoma*, and *Sturisomatichthys* possesses a relatively long process extending meso-posteriorly (Fig. 27), and *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* lack such a process on the third epibranchial.



**Fig. 27.** Dorsal view of third epibranchial of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (right side) (a) and *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL) (left side) (b). Arrow points to posterior process of third epibranchial. Scale bar = 0.5 mm.

**16.** Shape of upper pharyngeal tooth plate: (0) drop-shaped, anterior portion slightly narrower than posterior; (1) half-moon shaped to triangular, anterior portion much narrower; (2) circular to quadrangular, convex; (3) laminar and triangular shaped, with a fold on the posterior margin (CI = 100; RI = 100).

The Siluriformes possess a single pair of upper pharyngeal plates, connected to the fourth pharyngobranchial (Fink & Fink, 1981: 323). Teeth arranged in various patterns on the upper pharyngeal plate make contact with the dorsal surface of the fifth ceratobranchial, or lower pharyngeal plate.

The upper pharyngeal plate of *Lamontichthys*, *Harttia*, *Pterosturisoma*, and *Sturisomatichthys* possess a robust ventral surface and a dorsal laminar projection (Fig. 28a). Teeth are located on the ventral surface, which is triangular shaped with a narrow anterior portion. The upper pharyngeal plate of *Neoplecostomus* and other loricariids, such as *Acestridium discus*, lacks a dorsal laminar projection and the ventral surface is drop-shaped with a slightly narrow anterior portion, and completely covered by teeth (Figs. 23 and 28c).

The upper pharyngeal plate of *Sturisoma* is laminar and triangular shaped, and differs considerably from other examined taxa in having the teeth in a small folded area on the posterior border of the plate and along the medial border (Fig. 25b). This condition is proposed as autapomorphic for *Sturisoma*. The ventral surface, which usually has teeth in other taxa, is covered by branchial filaments, while the dorsal surface is smooth.

*Loricaria*, *Pseudoloricaria*, and *Rineloricaria* possess a relatively large pharyngeal plate, slightly convex, circular to quadrangular shaped with teeth distributed on the entire ventral face (Fig. 28b).

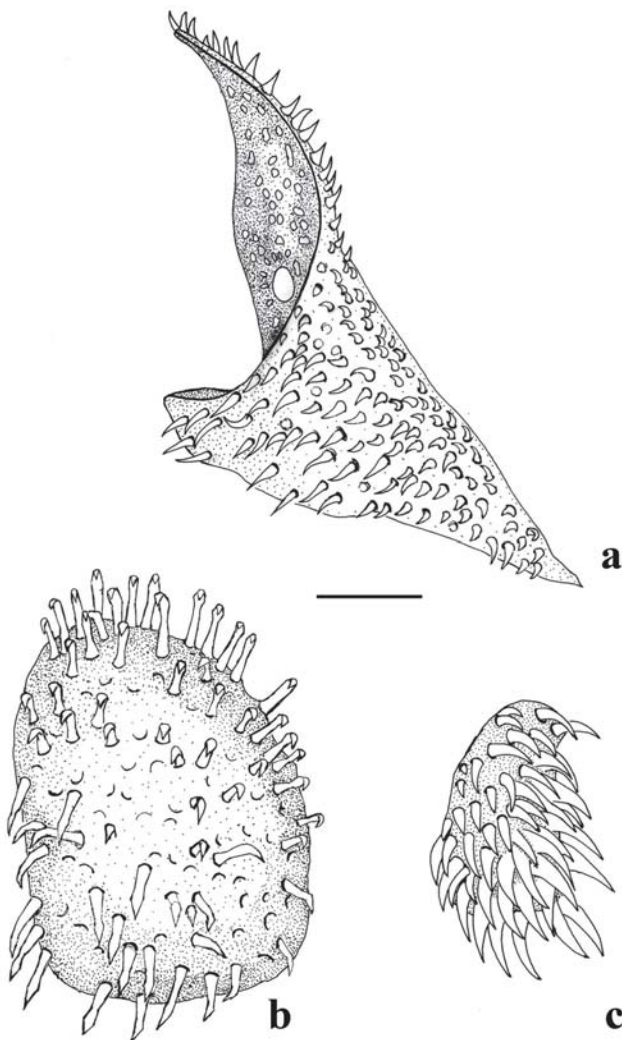
Schaefer (1991: 12; 1998: 396) described the general condition of the upper pharyngeal plates in the Loricariidae, as plane, relatively large and wedge-shaped. Members of the



Hypoptopomatinae (*Otothyris*, *Pseudotothyris*, and *Schizolecis*) alternatively have a small, compact and rounded upper pharyngeal tooth plate. Armbruster (2004: 12) described two distinct conditions of this plate in the Loricariidae. In the present study four different conditions regarding the shape of the upper pharyngeal plate among examined specimens of Loricariidae were observed.

**17. Molariform teeth on upper and lower pharyngeal plate:** (0) absent; (1) present (uninformative).

Loricariids commonly possess only conical teeth on the upper and lower pharyngeal plates. However, many members of the Loricariini possess both conical and molariform teeth in both plates (Rapp Py-Daniel 1997: character 90; Armbruster, 2004: 9), a condition observed in *Loricaria* among examined taxa.



**Fig. 28.** Ventral view of upper pharyngeal plate (left side) of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a), *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL) (b) and *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL) (c). Scale bar = 0.5 mm.

### Jaws and dentition

The Loricariidae surpasses all other Loricarioidea in the high diversity of shapes and sizes of jaws and teeth, probably a consequence of the adaptation to different kinds of microhabitats and substrates explored by these fishes. Associated with the variation of jaws and teeth, there are several other specializations in the feeding mechanisms and in the hyoid apparatus (Schaefer & Lauder, 1986: 504).

**18. Length of posterior process of palatine:** (0) short, not extending beyond anterior condyle of lateral ethmoid; (1) long, extending beyond anterior condyle of lateral ethmoid (CI = 50; RI = 0).

The palatine in loricariids is narrow and cylindrical. Anteriorly there is a cartilaginous tip that articulates with the maxilla and posteriorly there is an articular surface for the lateral ethmoid (Arratia, 1990: 209). Medial to this latter articular surface is a ventral posterior process, extremely reduced in loricariids in comparison to other Siluriformes (Fig. 15a; Schaefer, 1987: 10; Schaefer, 1997: 25; Reis, 1998: 124). *Lamontichthys avacanoeiro* and *Loricaria*, in contrast, possess a long posterior process compared to other loricariids (Fig. 15b). In these two species, the posterior process of the palatine extends ventrally beyond the anterior condyle of the lateral ethmoid. In other loricariids, the posterior process fails to reach the condyle of the lateral ethmoid.

According to Schaefer (1990: 185), in loricariids, one of the two subdivisions of the *extensor tentaculi* muscle inserts on the posterior process of the palatine.

**19. Lateral flange of palatine:** (0) absent; (1) present and incomplete; (2) present and complete (CI = 66; RI = 66).

In loricariids, the palatine is usually a cylindrical bone lacking lateral edges (Schaefer, 1997: fig. 12e; Armbruster, 2004: 17). In a few taxa there is a flange projecting from the lateral border of the bone that is already present early in ontogeny (Arratia, 1990: 209). In many members of the Loricariini the flange extends along the entire lateral margin of the autopalatine, a condition observed in *Pseudoloricaria* and *Rineloricaria*. In *Loricaria*, exclusively, the flange is somewhat shorter extending along 2/3 of the lateral margin of the autopalatine (Rapp Py-Daniel, 1997: character 23).

**20. Palatine splint:** (0) present; (1) absent (CI = 50; RI = 50).

The palatine splint is an ossification of questionable homology that occurs in the Astroblepidae, Scoloplacidae, Loricariidae, some Trichomycteridae and Callichthyidae (Schaefer, 1987: 10; 1997: 25; Reis, 1998: 124). In loricariids the ossification is thin, elongate and straight with a wide anterior tip, and contacts the anterior cartilage of the autopalatine (Fig. 29). Posteriorly, it extends parallel to the autopalatine, and reaches the lateral ethmoid.

The palatal splint is present in all examined taxa except *Farlowella*, *Loricaria*, and *Pseudoloricaria*.

**21. Length of cup-shaped portion of premaxilla relative to**

cup shaped portion of dentary: (0) similar; (1) distinctly longer; (2) distinctly shorter (CI = 100; RI = 100).

The premaxilla and dentary in the Loricariidae are distinctly cup-shaped anteriorly and contain several rows of teeth (Schaefer, 1987: 11; 1997: 25). The relative length of the cup-shaped region of the premaxilla compared to that of the dentary varies among examined taxa. *Lamontichthys avacanoeiro*, *L. maracaibero*, *L. stibaros*, *Farlowella*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* have these regions of similar length (Fig. 29), a condition shared with *Hypostomus* and *Neoplecostomus*.

*Loricaria*, *Pseudoloricaria*, and *Rineloricaria* have the cup-shaped region of the premaxilla distinctly shorter than that of the dentary. In contrast, *L. filamentosus* and *L. llanero* have the cup-shaped region of the premaxilla distinctly longer than that of the dentary.

*Lamontichthys parakana*, not included in this analysis, has the cup-shaped region of the premaxilla only slightly

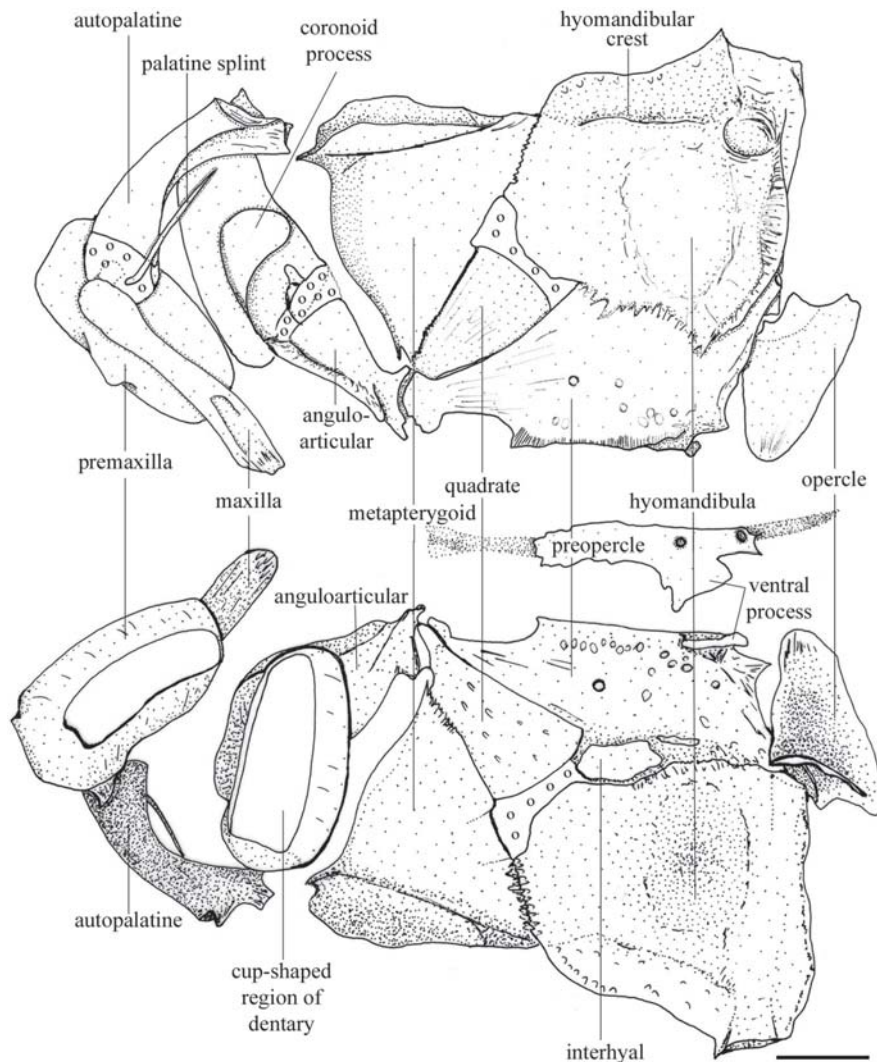
longer than that of the dentary (state 0).

**22.** Length versus width of cup-shaped region of premaxilla: (0) two to three times longer than wide; (1) length and width equivalent. (CI = 100; RI = 100).

The cup-shaped region of premaxilla in *L. avacanoeiro*, *L. filamentosus*, *L. llanero*, *L. maracaibero*, *L. stibaros*, and in the outgroups *Farlowella*, *Harttia*, *Hypostomus*, *Neoplecostomus*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* is rectangular shaped, with the length twice to three times longer than its width (Fig. 29). In the derived condition present in *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, it is approximately square shaped.

**23.** Coronoid process of dentary: (0) large, with small robust area; (1) large, with large robust area; (2) small; (3) absent (CI = 100; RI = 100).

The dentary of most siluriforms possesses a well



**Fig. 29.** Dorsal view (upper) and ventral view (lower) of left mandibular arch, suspensorium, opercle, and interhyal of *Lamontichthys stibaros* (FMNH 84111, 62.4 mm SL). Lateral view of preopercle (centre). Scale bar = 1 mm.

developed and conspicuous coronoid process for insertion of the *adductor* muscles (Schaefer, 1987). The coronoid process in loricariids, when present, is usually strong and concave posteriorly (Howes, 1983). In *Farlowella*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* the coronoid process is large and has a small heavily ossified and robust area along its posterior margin (Fig. 30), a condition shared with *Hypostomus* and *Neoplecostomus*.

Three derived conditions of the coronoid process were observed among examined taxa. *Lamontichthys* also possesses a large coronoid process, but in this genus the robust area is more developed and occupies almost the entire posterior region of the coronoid process (Fig. 31b). Species of *Harttia* possess a relatively small coronoid process (Fig. 31a), and *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* lack a coronoid process in the dentary.

**24.** Posteroventral lamina of dentary: (0) present; (1) absent (CI = 100; RI = 100).

The dentary of loricariids usually has a long posteroventral lamina of bone that overlies the posterior face of the anguloarticular (Schaefer, 1987: 12). Among the Loricariinae, this condition was observed in *Lamontichthys avacanoeiro*, *L. filamentosus*, *L. llanero*, *L. maracaibero*, *L. stibaros*, and in the outgroups *Farlowella*, *Harttia*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* (Fig. 31). *Pseudoloricaria* and *Loricaria* lack a posteroventral lamina of bone in the dentary.

**25.** Process on posteroventral lamina of bone of dentary: (0) absent or very narrow; (1) present, relatively distant from main body of dentary; (2) present, close to main body of dentary (CI = 100; RI = 100).

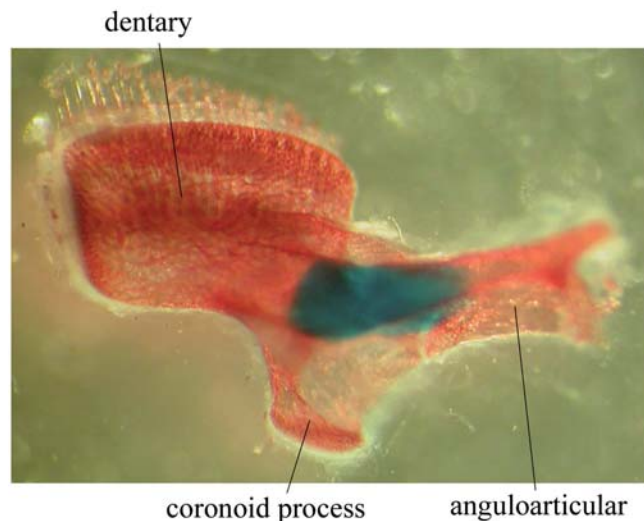
As detailed under the previous character, the dentary of many loricariids possesses a posteroventral lamina of bone that overlaps the anguloarticular. The *geniohyoideus* muscle

inserts on this lamina and provides high mobility of the dentary and of the hyoid arch (Schaefer & Lauder, 1986: 499). In *Lamontichthys*, *Hypostomus*, *Neoplecostomus*, *Pseudoloricaria*, *Pterosturisoma*, *Sturisoma*, *Sturisomatichthys*, and *Rineloricaria* the muscle is inserted directly on the posteroventral lamina of the dentary. In *Harttia* there is a small laminal process located at the anterior portion of the posteroventral lamina of the dentary onto which the *geniohyoideus* muscle is inserted (Fig. 31a). *Farlowella* possesses a similar process, which is instead situated posteriorly on the posteroventral lamina of the dentary.

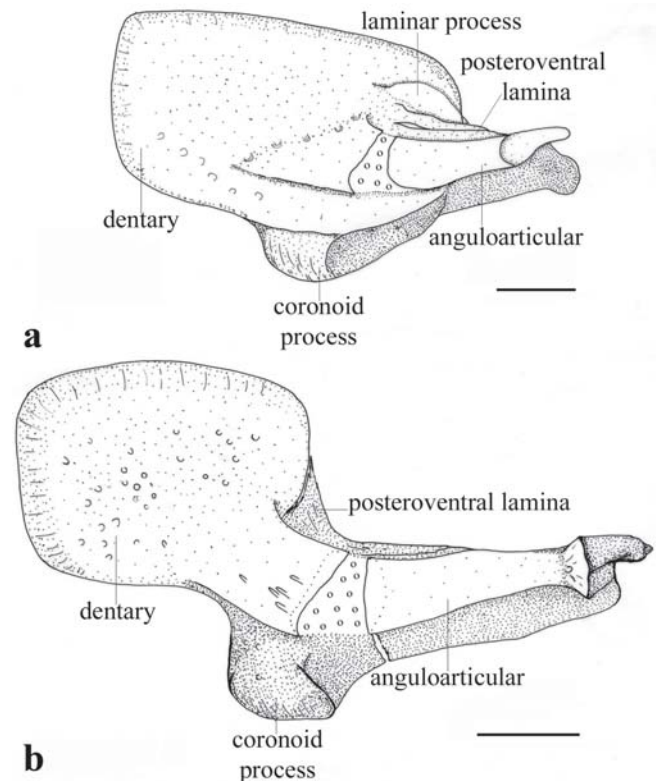
*Pseudoloricaria* and *Loricaria*, that lack the posteroventral lamina of the dentary (character 24), were not coded for this character.

**26.** Shape of maxillary teeth: (0) teeth delicate, long and narrow, tooth cusp forming angle of approximately 90° with longer axis of tooth and ventrally directed; (1) teeth robust, relatively short and wide, tooth cusp forming an angle of approximately 180° with the longer axis of tooth and medially directed (CI = 100; RI = 100).

Loricariid fishes are primarily herbivorous, benthic algae scrapers and greatly exceeds all other loricarioides in the arrangement, number, shape and size of teeth (Schaefer &



**Fig. 30.** Dorsal view of dentary and anguloarticular (left side) of *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL).



**Fig. 31.** Dorsal view of dentary and anguloarticular (left side) of *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL) (a), and *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (b). Scale bar = 1 mm.

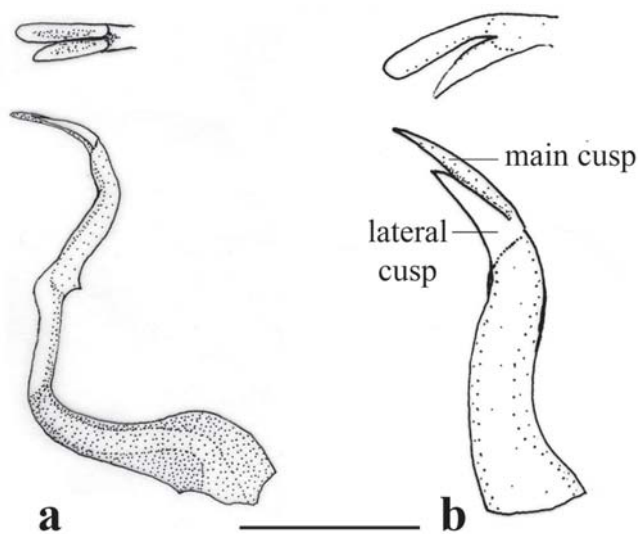
Lauder, 1986). The most common pattern of dentition in the family, present in *Lamontichthys*, *Farlowella*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys*, is that of delicate, long and narrow setiform teeth, bicuspid and strongly curved (Fig. 32a; Isbrücker, 1981; Schaefer, 1987; Müller & Weber, 1992). The cusps, when observed from a lateral view, form an angle of approximately 90° with the longer axis of the tooth.

In contrast, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* possess relatively strong, short and wide teeth, with only a gentle curvature (Fig. 32b). In addition, the tooth cusps form an angle of approximately 180° with the longer axis of the tooth.

**27.** Size of tooth cusps: (0) long, main cusp approximately twice as large and broad than lateral cusp; (1) short, main cusp slightly larger and wider than lateral cusp (CI = 50; RI = 80).

Bicuspid teeth are present in the families Scoloplacidae, Loricariidae and Astroblepidae, but only members of the Loricariidae possess asymmetric cusps (Schaefer, 1990: 185). In the most common condition found in loricariids, the main cusp is longer and wider than the lateral cusp (Müller & Weber, 1992). Although differences in cusp size have not been utilized in phylogenetic analysis of loricariids, Isbrücker & Nijssen (1978b: 70) illustrated teeth of representatives of the Loricariinae, in which it is possible to clearly distinguish between short and long cusps.

*Lamontichthys stibaros*, *L. avacanoeiro*, *Harttia*, and *Sturisomatichthys* share with *Hypostomus* and *Neoplecostomus* teeth with long cusps (Fig. 3a). *Hypostomus* and *Neoplecostomus* have teeth with the main cusp twice as large and wide than the lateral cusp. *Harttia* has teeth with



**Fig. 32.** Lateral view of left premaxillary tooth of *Lamontichthys avacanoeiro* (MZUSP 61974, 113.7 mm SL, paratype) (a) and *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL) (b). Detail of cusps in anterior view. Scale bar = 0.5 mm.

the main cusp twice as large and only slightly broader than the lateral cusp, and the remaining species of *Lamontichthys* have teeth with cusps of similar size, or with the main cusp only slightly longer and wider than the lateral cusp. The latter condition is also present in *L. parakana*, a species not included in the analysis. The variation in cusp size is relatively continuous among taxa and therefore it was not coded as distinct character states.

*Lamontichthys filamentosus*, *L. llanero*, *L. maracaibero*, *Farlowella*, *Pterosturisoma*, and *Sturisoma* possess teeth with short cusps, with the main cusp usually slightly longer and wider than the lateral cusp (Fig. 3b).

*Loricaria*, *Pseudoloricaria*, and *Rineloricaria* were not coded for this character due to their distinct tooth morphology (character 26).

**28.** Number of teeth in each premaxilla or dentary: (0) more than 50; (1) between 20 and 50; (2) fewer than 20 (CI = 66; RI = 88).

The number of teeth in each premaxilla or dentary in loricariids is highly variable and Boeseman (1971: 10) was the first author to propose groupings within the Loricariinae based on variation on the number of jaw teeth. Among the non-loricariine Loricariidae, Schaefer (1997: 109) considered the presence of 12 to 18 teeth in each jaw as plesiomorphic for the Hypoptopomatinae. Garavello *et al.* (1998) showed that variation in the number of teeth could be used to diagnose species of the genus *Otothyris*.

*Lamontichthys*, *Harttia*, and *Sturisomatichthys* possess between 50 and 100 teeth in each premaxilla or dentary. *Farlowella*, *Pterosturisoma*, and *Sturisoma* possess between 20 and 50 teeth in each premaxilla or dentary, a condition shared with *Hypostomus* and *Neoplecostomus*. In *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* the number of jaw teeth rarely reaches 20.

There is a slight difference between the number of teeth in the premaxilla and in the dentary of loricariids. However, such difference is included within the range of variation of the states defined for this character. The number of teeth in the premaxilla and dentary of loricariids increases with growth. In the present study only adult specimens were considered for this character.

### Suspensorium

**29.** Projection of posterior border of hyomandibula: (0) present; (1) absent (CI = 50; RI = 0).

The hyomandibula of loricariids is a relatively large, square shaped bone. The posterior border is usually straight, with a crest for the insertion of the *adductor mandibulae* muscle (Schaefer, 1987: 8). In *Lamontichthys* and in the outgroups *Farlowella*, *Harttia*, *Loricaria*, *Neoplecostomus*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisomatichthys*, the crest is in direct contact with the pterotic-supracleithrum. In *Hypostomus* and *Sturisoma* the hyomandibula extends posteriorly to this crest, and the contact with the pterotic-supracleithrum is made via this posterior projection.

**30.** Contribution of pterotic-supracleithrum to hyomandibula-cranium articulation: (0) wide, as large as contribution of prootic; (1) short, less than contribution of prootic; (2) absent, with exclusive participation of prootic (CI = 100; RI = 100).

Schaefer (1997: 104) proposed that a contribution of the pterotic-supracleithrum and of the prootic in the hyomandibula-cranium articulation is plesiomorphic for the Loricariidae and this condition is present in *Neoplecostomus*, the Loricariinae, Ancistrinae, many Hypostominae, and in the tribe Otothyirini (Hypoptopomatinae). However, that author did not indicate the degree of participation of each ossification to this articulation and proposed that the lack of contribution of the prootic to the hyomandibula-cranium articulation in members of the Hypostominae and in the tribe Hypoptopomatini (Hypoptopomatinae) as a derived condition. The lack of contribution of the prootic to the hyomandibula-cranium articulation reported for some loricariids (Armbruster, 2004: 13) was not observed in taxa examined in the present study.

Three different conditions regarding the contribution of the pterotic-supracleithrum to the hyomandibula-cranium articulation occur among examined taxa. *Lamontichthys*, *Harttia*, *Hypostomus*, and *Neoplecostomus* possess an equivalent contribution of the prootic and pterotic-supracleithrum to the facet of the hyomandibula-cranium articulation (Fig. 33a). *Farlowella*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* possess a smaller contribution of the pterotic-supracleithrum to the facet of the hyomandibula-cranium articulation relative to that of the prootic (Fig. 33b). In *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, the pterotic-supracleithrum is excluded from this articulation, and only the prootic connects to the hyomandibula. Although in *Farlowella*, the contribution of the pterotic-supracleithrum to the hyomandibula-cranium articulation is particularly small, the ossification is still present in the facet of the hyomandibula and that species was therefore coded as having state 1.

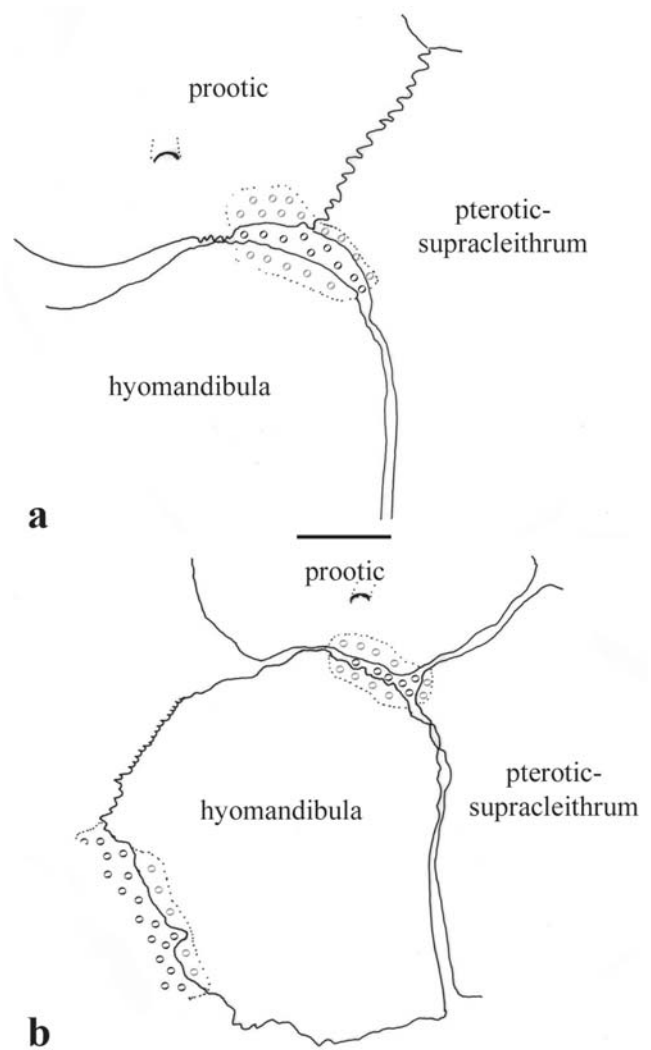
**31.** Crest on lateral surface of hyomandibula for insertion of *levator arcus palatini* muscle: (0) present; (1) absent (CI = 50; RI = 0).

Most Siluriformes including loricariids possess a crest on the hyomandibula, where the *levator arcus palatini* muscle is inserted (Arratia, 1987; Armbruster, 2004: 15). This muscle originates in the sphenotic, and connects the hyomandibula with the lateral border of the skull (Howes, 1983). The *levator arcus palatini* muscle is extremely reduced in *Farlowella*, *Hypostomus*, *Loricaria*, and *Neoplecostomus*, and it is absent in some species of the latter genus (Howes, 1983: 322). In the Hypoptopomatinae the reduction of this muscle is directly proportional to the reduction of the extension of the hyomandibular crest (Schaefer, 1991: 10)

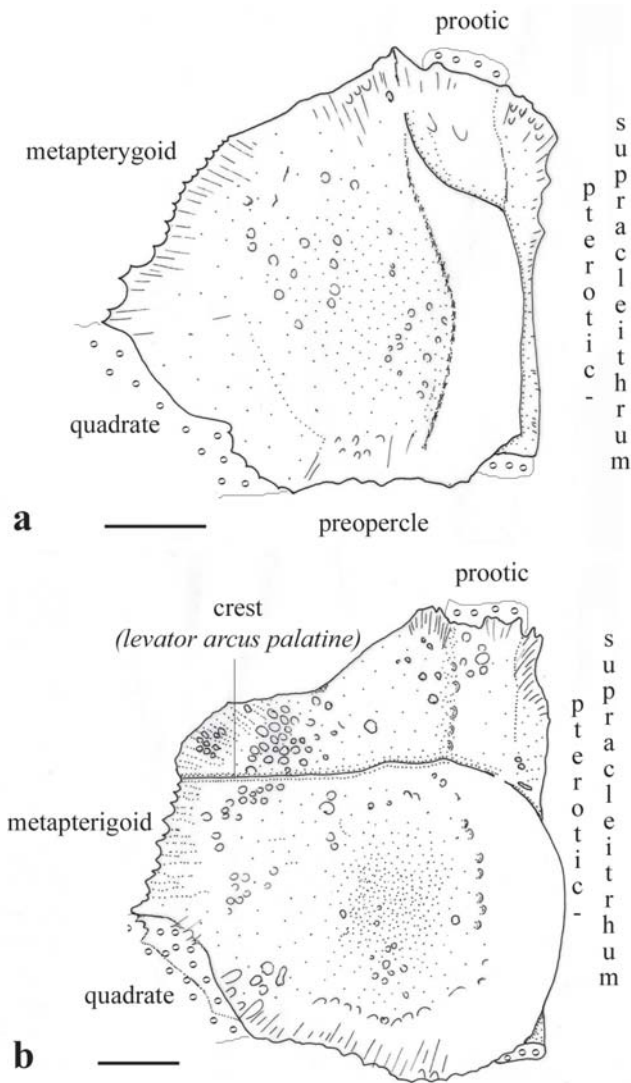
Among the Loricariinae, *Lamontichthys*, *Farlowella*, *Harttia*, *Pseudoloricaria*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* possess the lateral face of the hyomandibula with a very narrow crest, while in *Loricaria*

and *Pterosturisoma* the crest is absent (Fig. 34).

In the single specimen of *L. stibaros* examined (FMNH 84111, 62.4 mm SL) the hyomandibula crest does not cross the entire extension of the hyomandibula. The single specimen of *L. maracaibero* examined (MCNG 3593, 83.8 mm SL) possesses a complete crest, a condition present in the other species of the genus examined in the present study, all represented by larger specimens. Arratia (1987) reported that juveniles of *Diplomystes* possess a rudimental crest, while in the adult it is well developed, except in the adult of *D. camposensis*. The lack of both juveniles and adults of all species of *Lamontichthys* in the present study did not allow comparison of the degree of development of the crest of the homandibula within the genus. Therefore, only the presence or absence of the crest on the lateral face of the hyomandibula was considered in the present study.



**Fig. 33.** Ventral view of the suspensorium-neurocranium articulation of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a) and *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL) (b). Scale bar = 1 mm.



**Fig. 34.** Dorsal view of the hyomandibula (left side) of *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL) (a), and *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (b). Bones that articulate with the hyomandibula are indicated around the illustration. Scale bar = 1 mm.

- 32.** Ventral process of preopercle: (0) inconspicuous or absent; (1) well developed (CI = 50; RI = 75).

The preopercle of loricariids is usually an elongate ossification, with the anterior and posterior tips narrower, and it bears a branch of the laterosensory canal (Schaefer, 1991: 11). The anterior portion of the dorsal border of the preopercle of loricariids is sutured with the quadrate and the posterior portion is sutured with the hyomandibula. The posterior portion of the ventral border of the preopercle in some Loricariinae has a ventral process that articulates with a bony plate (Rapp Py-Daniel, 1997: character 53), which bears a branch of the laterosensory canal ("canal-bearing plate" of Schaefer, 1987: 22). This process occurs in *Lamontichthys*, and in the outgroups *Farlowella*, *Harttia*, *Pterosturisoma*,

*Sturisoma*, and *Sturisomatichthys* (Fig. 29). On the other hand in *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* the ventral process of the preopercle is absent or inconspicuous, a condition that also occurs in *Hypostomus* and *Neoplecostomus*.

- 33.** Exposed region on posterodorsal portion of preopercle: (0) present; (1) absent, totally covered by skin (CI = 33; RI = 60).

The Siluriformes usually possess the preopercle covered by skin, lacking any exposed surface (Reis, 1998: 143) a condition observed in *Lamontichthys* and the outgroups *Farlowella*, *Harttia*, *Pterosturisoma*, and *Sturisomatichthys* (Fig. 20a). Reis (1998: 143) reported the presence of a partially exposed preopercle in members of the family Callichthyidae. Similarly, *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, and *Sturisoma* possess the posterodorsal portion of the preopercle exposed and usually ornamented with odontods, a condition shared with *Hypostomus* and *Neoplecostomus* (Fig. 20b).

#### Laterosensory canal system

- 34.** Position of canal-bearing cheek plate on head: (0) lateral; (1) ventrolateral; (2) ventral (CI = 66; RI = 66).

Members of the Loricariidae possess a plate anterior to the opercle that receives the terminus of the preopercular laterosensory canal ("canal-bearing plate" of Schaefer, 1987: 22; 1991: 11; "canal-bearing cheek plate" of Schaefer, 1991: 20).

*Lamontichthys*, *Farlowella*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* possess the canal-bearing cheek plate located ventrally on the head (Fig. 1), while in *Rineloricaria*, *Loricaria*, and *Pseudoloricaria* it occupies the lateral region of the head. In *Neoplecostomus*, part of the canal-bearing cheek plate occupies the lateral region of the head and part the ventral region.

- 35.** Orientation of laterosensory canal on canal-bearing cheek plate: (0) cranium-caudal; (1) medial; (2) laterolateral (CI = 66; RI = 66).

The laterosensory canal on the canal-bearing cheek plate of loricariids (see plate in Fig. 1), commonly travels anteriorly from the posterolateral to the anterolateral portion, running close to the lateral margin of the cheek-plate (Rapp Py-Daniel, 1997: character 161). This condition occurs in *Lamontichthys*, *Farlowella*, *Harttia*, *Pterosturisoma*, and *Sturisomatichthys* among examined members of the subfamily Loricariinae. A different condition occurs in *Hypostomus*, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, in which the laterosensory canal is directed laterally and travels along the median line of the cheek plate, from its dorsal to its ventral border. In *Sturisoma*, the laterosensory canal travels from the posterolateral portion of the cheek plate, running anteromedially to reach the anterolateral portion.

- 36.** Laterosensory canal on supracaudal plates: (0) absent; (1) present (CI = 100; RI = 100).

The plesiomorphic condition for the Siluriformes is to have a continuous and complete laterosensory canal on the body, that extends near to or lateral to the hypural plate, is partially

included in ossicles, and gives off numerous short tubules that open in the skin by diminutive pores (Arratia & Huaquin, 1995: 90).

In *Lamontichthys*, *Farlowella*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* the lateral line continues on the elongate plate posterior to the hypural plate. In *Hypostomus* and *Neoplecostomus*, the lateral line falls short of the elongate plate posterior to the hypural plate (Fig. 35).

According to Schaefer (1991: 20), in *Neoplecostomus*, some Hypoptopomatinae, and in the majority of the other loricariids the lateral line is complete and extends from the pterotic-supracleithrum, posteriorly to the last lateral plate of the median series on the base of the caudal-fin. Schaefer (1991: 20) and Armbruster (2004: 23) reported that the lateral line of Callichthyidae, Astroblepidae and many loricariids (Hypoptopomatinae, *Neoplecostomus*, and some members of the other loricariid subfamilies) terminates anteriorly to the hypural plate, while in some Hypostominae, Ancistrinae and many Loricariinae it terminates lateral to the hypural plate. Armbruster (2004: 75) proposed the presence of laterosensory canal on the elongate plate posterior to the hypural plate as synapomorphic for the Loricariinae.

#### Infraorbital series

Loricariids possess between five and six infraorbitals (Schaefer, 1987: 8), modified into bony plates and usually covered by odontods (Fink & Fink, 1981: 315; Arratia, 1987: 96). Five infraorbitals are present in *Neoplecostomus* and in the Hypoptopomatinae and six infraorbitals is a condition shared with the Astroblepidae (Schaefer, 1997: 23).

**37.** Plate between infraorbital 2 and 3: (0) absent; (1) present (uninformative).

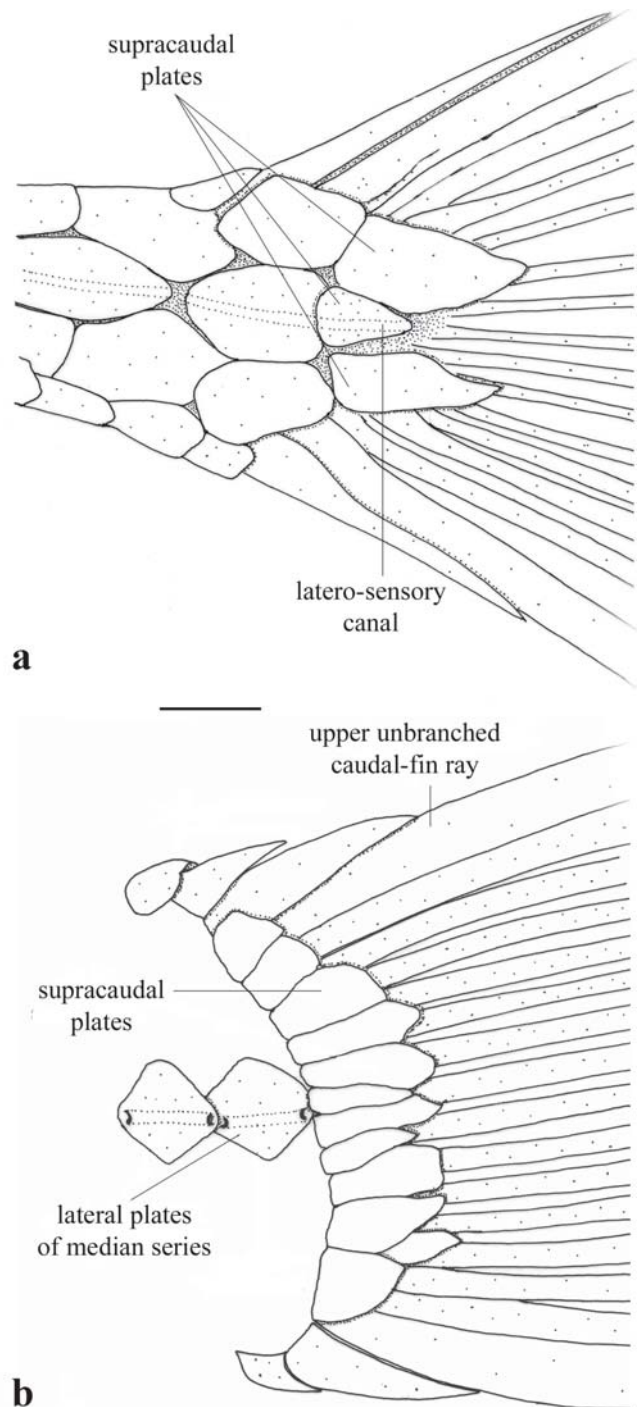
In *Lamontichthys filamentosus*, *L. llanero*, *L. maracaibero*, *L. stibaros*, *Farlowella*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*, the posterior border of infraorbital 2 contacts the anterior border of infraorbital 3 along its entire extension, and there is no plate between these two ossifications (Fig. 20). In the derived condition, present in *L. avacanoeiro* and *L. parakana*, there is a plate that lacks a laterosensory canal that is situated between infraorbitals 2 and 3, and restricts the contact between these two ossifications (Fig. 36).

#### Weberian apparatus and Axial skeleton

**38.** Suture between basioccipital and Baudelot's ligament: (0) present; (1) absent (CI = 100; RI = 100).

The Siluriformes, in general, possess the Baudelot's ligament ossified, arising from a small process of the supracleithrum and inserting directly on the basioccipital (Chardon, 1968: 190; Fink & Fink, 1981: 335). *Lamontichthys*, *Farlowella*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* possess a ventral and lateral prolongation of the posterior portion of the basioccipital that is in contact with Baudelot's ligament. In *Loricaria*, *Pseudoloricaria*,

and *Rineloricaria*, a ventral prolongation of the posterior border of the exoccipital is situated between the basioccipital and the Baudelot's ligament (Fig. 37). These different conditions were previously described by Rapp Py-Daniel (1997: character 18).



**Fig. 35.** Lateral view of caudal-fin, procorrents rays, and supracaudal plates (left side) of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a), and *Hypostomus* sp. (MZUSP 100921, 58.7 mm SL) (b). Scale bar = 1 mm.

**39.** Flange on lateral region of seventh precaudal vertebra: (0) absent; (1) present, anteriorly directed; (2) present, posteriorly directed (CI= 100; RI = 100).

Members of the subfamily Loricariinae have a flange projecting from the dorsolateral side of the seventh precaudal vertebra that extends dorsally along the side of the neural spine. In all examined members of the Loricariinae except *Lamontichthys avacanoeiro*, the flange is directed anteriorly (Fig. 38a). In *L. avacanoeiro*, this flange is directed posteriorly. Members of the Loricariidae in general seem to lack a lateral flange on the seventh precaudal vertebra (Fig. 38b).

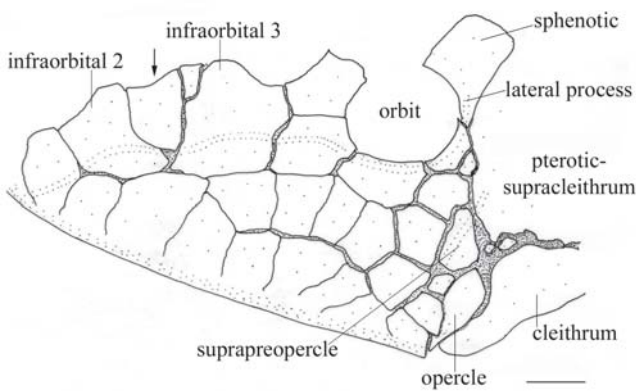
**40.** Hemal spine on last precaudal vertebra: (0) absent; (1) present, shorter or same length of associated vertebral centrum; (2) present, longer than associated vertebral centrum (uninformative).

*Pterosturisoma* possesses the hemal spine of the last precaudal vertebra considerably elongate and narrow distally,

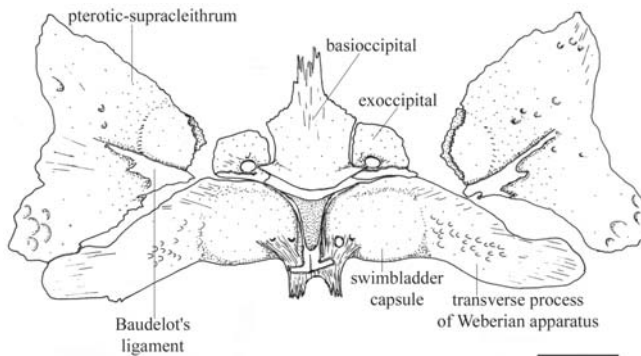
with a length of approximately twice that of the corresponding vertebral centrum (Fig. 39). In *Neoplecostomus* and in the great majority of the Loricariinae (*Lamontichthys*, *Farlowella*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*) this spine is considerably shorter, its length equal or less than the length of the corresponding vertebral centrum (Figs. 40 and 41).

**41.** Bifid hemal spine on first caudal vertebra: (0) very short, almost inconspicuous; (1) medium, length approximately 1/2 width of corresponding vertebra; (2) long, approximately, as long as corresponding vertebra (CI = 100; RI = 100).

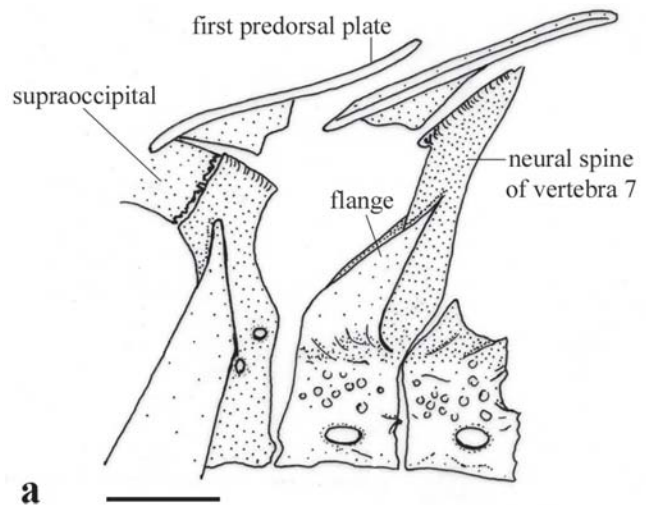
In *Hypostomus*, the hemal spine of the first caudal vertebra is very short and only its distal posterior tip is split to receive the first anal-fin pterygiophore. The bifid hemal spine of the first caudal vertebra in *Neoplecostomus* is longer, its length approximately 1/2 of the corresponding vertebral width (Fig. 41). In members of the Loricariinae there is a further elongation



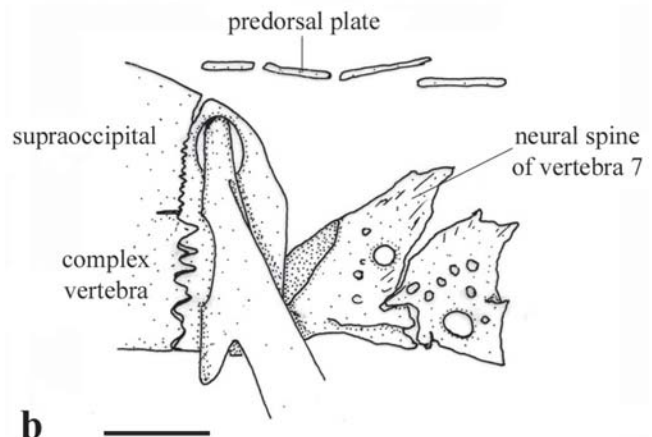
**Fig. 36.** Lateral view of region of snout and orbit (left side) of *Lamontichthys avacanoeiro* (MNRJ 18553, 98.1 mm SL, paratype). Arrow points to plate between infraorbitals 2 and 3. Scale bar = 2 mm.



**Fig. 37.** Ventral view of posterior portion of neurocranium and anterior portion of Weberian apparatus of *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL). Bones were disarticulated to allow better visualization of features mentioned in the text. Scale bar = 2 mm.



**a**



**b**

**Fig. 38.** Lateral view of sixth, seventh and eighth vertebra and predorsal plates (right side) of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a, scale bar = 2 mm), and *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL) (b, scale bar = 1 mm).



of this structure and in *Lamontichthys*, *Farlowella*, *Harttia*, *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*, the bifid hemal spine of the first caudal vertebra is as long as the corresponding vertebral width (Fig. 40).

In *Pterosturisoma* two very long contralateral projections originate from the proximal region of the hemal spine (Fig. 39). It is not clear whether these processes are homologous to the bifid hemal spines or represent distinct structures (Rapp Py-Daniel, 1997: 64) and this species was therefore coded as “?”.

42. Presence of completely expanded, hemal spines on caudal vertebrae: (0) from first caudal vertebra; (1) from fifth, sixth or

seventh caudal vertebra (uninformative).

*Neoplecostomus* and members of the Loricariinae possess completely expanded hemal spines ranging from the fifth, sixth or seventh caudal vertebrae (vertebrae 20 to 23), to the last body vertebra (Figs. 39-41). According to Schaefer (1987: 17), in *Hypostomus plecostomus* the hemal spines are completely expanded along their length in all caudal vertebrae (posterior to vertebrae 14), a condition observed in the specimens of *Hypostomus* examined in the present study.

43. Bilateral projections on vertebrae: (0) absent; (1) present (CI = 100; RI = 100).

Members of the Loricariinae possess ventrally directed

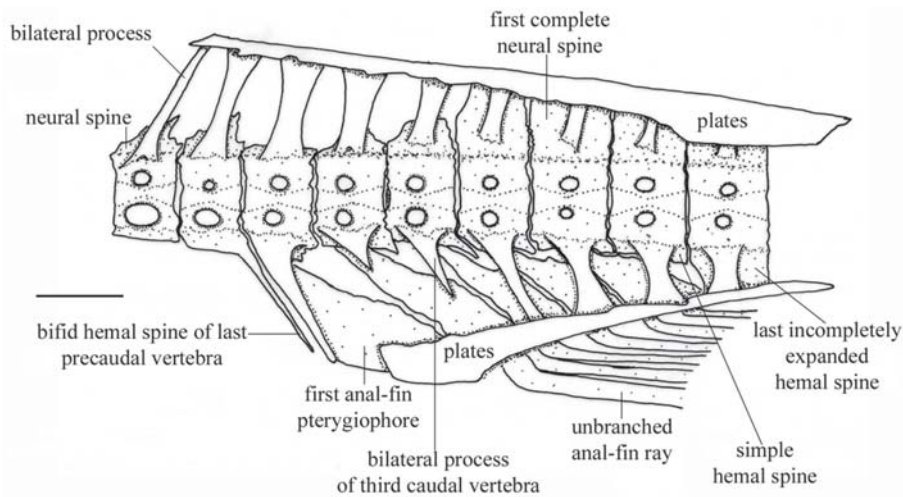


Fig. 39. Lateral view of the portion of the axial skeleton associated with the anal-fin pterygiophores (right side) of *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL). Dorsal-fin pterygiophores not represented. Scale bar = 2 mm.

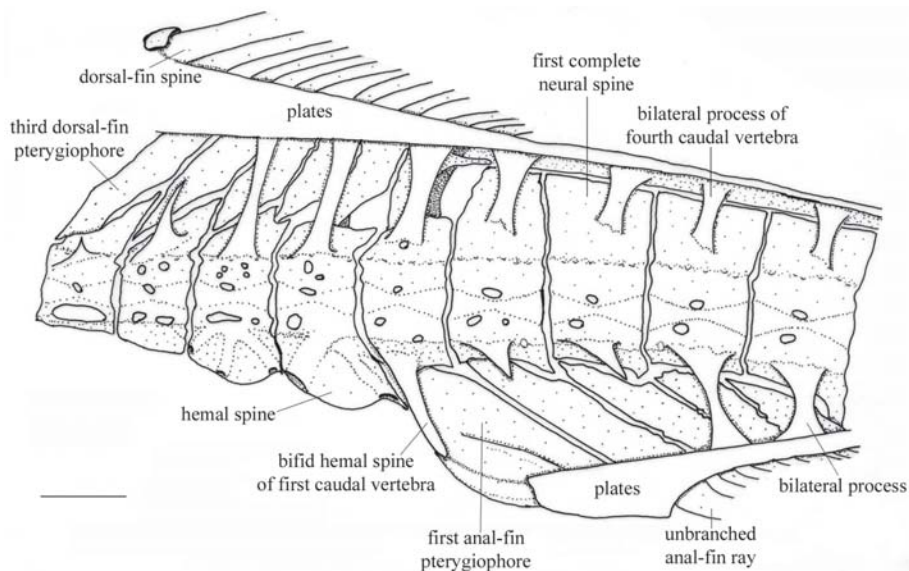
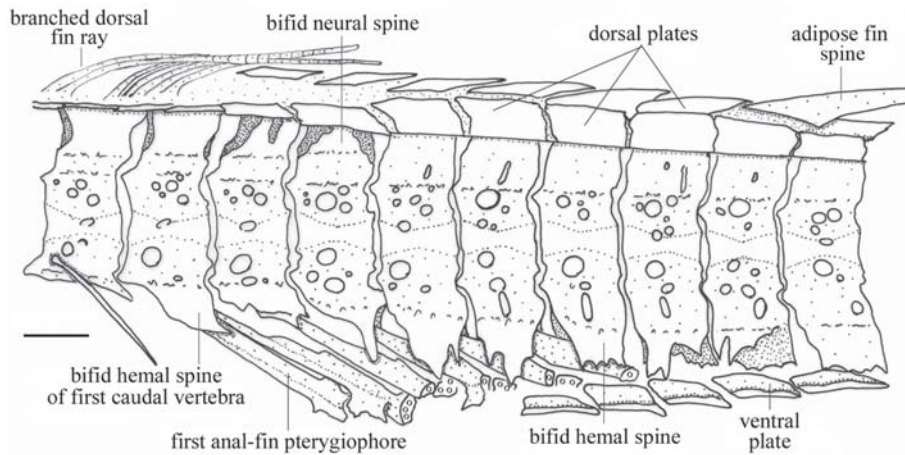


Fig. 40. Lateral view of the portion of the axial skeleton associated with the dorsal and anal-fin pterygiophores (right side) of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL). Scale bar = 3 mm.



**Fig. 41.** Lateral view of the portion of the axial skeleton associated with the anal-fin pterygiophores (right side) of *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL). Dorsal-fin pterygiophores and anal-fin rays not represented. Scale bar = 3 mm.

bilateral projections on the proximal portion of the hemal spines, as well as dorsally directed bilateral projections on the proximal portion of the neural spines, a feature previously described by Rapp Py-Daniel (1997: 106) as a synapomorphy for Loricariinae. These projections are strong and narrow, their length not exceeding one third of the vertebral width (Figs. 39 and 40). The two anterior most pairs of these projections usually do not contact the body plates, while the more posterior ones possess the distal tips firmly sutured to these plates. The dorsally directed bilateral projections are present from vertebrae 9 to 11, and the ventrally directed bilateral projections, from approximately vertebrae 13 to 15.

**44.** Orientation of ventrally directed bilateral projections on second caudal vertebra: (0) ventral to slightly anteriorly or posteriorly directed; (1) distinctly posteriorly directed; (2) distinctly anteriorly directed (CI = 66; RI = 66).

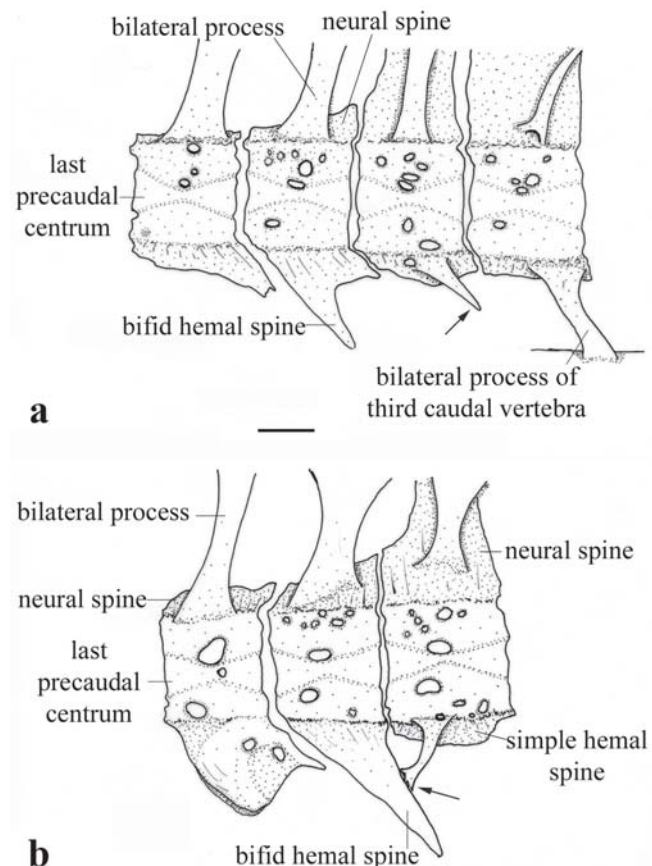
The ventrally directed bilateral projections of the second caudal vertebra of the majority of the Loricariinae are directed ventrally or only slightly anterior or posterior and their distal tips lack any type of contact with the body plates. In *Harttia* the ventrally directed bilateral projections of the second caudal vertebra are directed posteriorly and their distal tips also lack any type of contact with the body plates (Fig. 42a). *Lamontichthys llanero* has the ventrally directed bilateral projections of the second caudal vertebra anteriorly directed and the distal tips are strongly sutured to the hemal spine of the first caudal vertebra (Fig. 42b).

This character does not apply to *Hypostomus* and *Neoplecostomus* because these taxa lack ventrally directed bilateral projections.

**45.** Contact between ventrally directed bilateral projections of third caudal vertebra and ventral plates of body: (0) absent; (1) present (uninformative).

The ventrally directed bilateral projections of the third caudal vertebra of the majority of Loricariinae (except *Harttia*

*loricariformis*) possess their distal tips pointed and lacking any type of contact with the ventral plates (Fig. 39). In *Harttia loricariformis*, the distal tips of these projections are strongly



**Fig. 42.** Lateral view of part of the axial skeleton (right side) of *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL) (a), and *Lamontichthys llanero* (INHS 29957, 105.2 mm SL) (b). Arrow points to distal portion of the parahemal spine of second caudal vertebra. Scale bar = 1 mm.

attached to the ventral plates of the body (Fig. 42a).

*Hypostomus* and *Neoplecostomus* were not coded for this character due to lack of bilateral projections on the vertebrae of these taxa.

**46.** Length of posterior process of hemal spine of second preural centrum: (0) long; (1) short (CI = 100; RI = 100).

The hemal spine of the second preural centrum in all examined taxa extends posteriorly as a process along the ventral margin of the hypural plate (Fig. 43).

In all members of the Loricariinae this process is short not extending beyond half the length of the hypural plate. Alternatively, in *Hypostomus* and *Neoplecostomus* this process is long almost reaching the vertical through the posterior margin of the hypural plate.

**47.** Cartilage on posterior tip of hemal spine of second preural centrum: (0) present; (1) absent (CI = 100; RI = 100).

*Harttia*, *Hypostomus*, and *Neoplecostomus* among examined taxa possess cartilage on the posterior tip of the hemal spine of the second preural centrum. This feature was previously reported in members of the Astroblepidae, Ancistrinae, Hypoptopomatinae, Hypostominae, and Neoplecostominae, and in *Harttia* among the Loricariinae by Rapp-Py Daniel (1997: character 135).

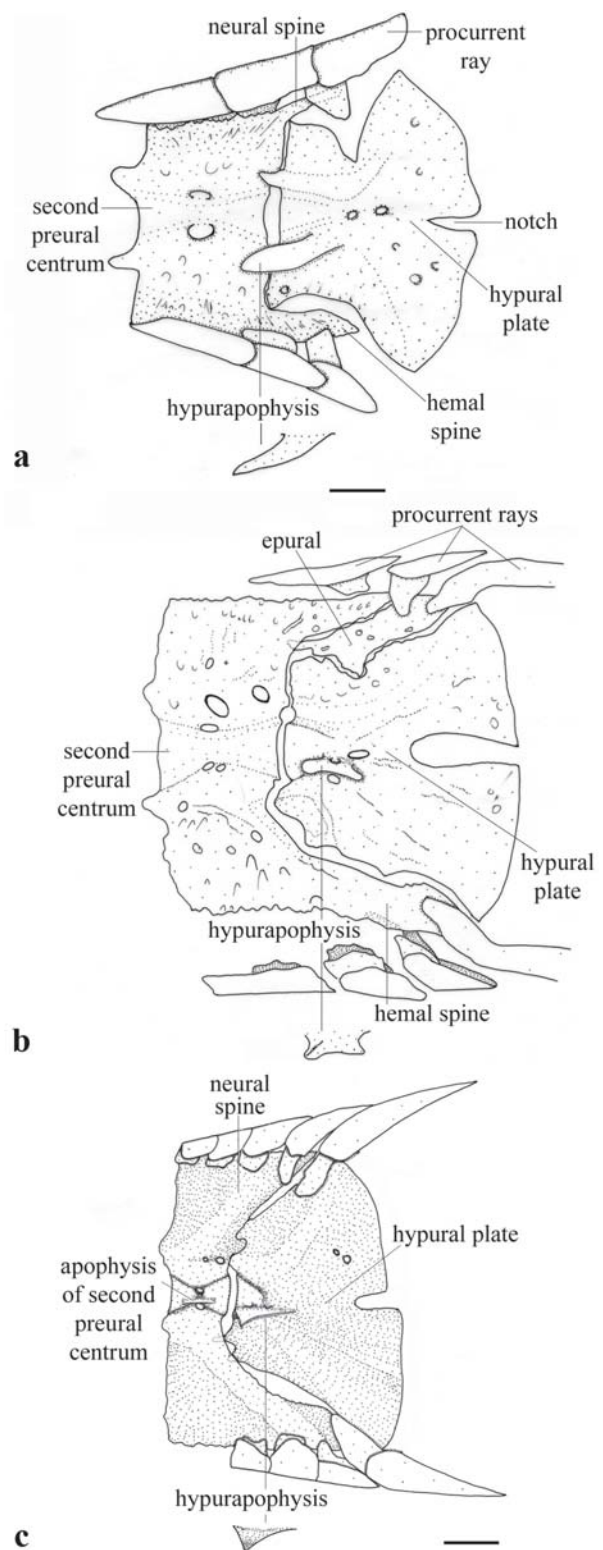
**48.** Relative length of neural spine of second preural centrum: (0) reaches vertical through posterodorsal tip of hypural plate; (1) reaches vertical through 1/2 to 3/4 length of hypural plate; (2) reaches vertical through 1/3 length of hypural plate (CI = 100; RI = 100).

Three different conditions of the relative length of the neural spine of the second preural centrum were described by Rapp-Py-Daniel (1997: character 134) for the Loricariidae. Among examined taxa, *Hypostomus* possess an elongate neural spine of the second preural centrum that extends parallel to the dorsal border of the hypural plate to the vertical through its posterodorsal tip (Fig. 43c). In all other examined taxa the neural spine of the second preural centrum is shorter. In *Lamontichthys*, *Harttia*, *Neoplecostomus*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys*, the neural spine of the second preural centrum reaches the vertical through 1/2 to 3/4 length of the hypural plate (Fig. 43). In *Farlowella*, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* the neural spine of the second preural centrum reaches the vertical through 1/3 the length of the hypural plate.

**49.** Caudal peduncle depth: (0) cylindrical or moderately depressed; (1) depressed (CI = 100; RI = 100).

According to Alexander (1965: 142), one of the main modifications along the evolution of the Siluriformes was the depression of the body in adaptation to a bottom-feeding habit.

One extreme of this modification occurs in the Loricariidae, whose members have the ventral surface of the body very flat. In addition, the caudal peduncle of loricariids is slightly depressed, though still cylindrical in overall shape. The



**Fig. 43.** Lateral view of second preural centrum and caudal-fin skeleton (right side) of *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL) (a, scale bar = 0.5 mm), *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL) (b, scale bar = 0.5 mm), and *Hypostomus* sp. (MZUSP 100921, 58.7 mm SL) (c scale bar = 1 mm). Detail of each illustration show dorsal view of hypurapophysis.

subfamily Loricariinae and the genera *Acestridium*, *Niobichthys*, and *Oxyropsis* (Hypoptopomatinae) possess the caudal peduncle extremely depressed. Schaefer (1987: 20) hypothesized a depressed caudal peduncle to be a synapomorphy for the subfamily Loricariinae. This feature has been used to diagnose the Loricariinae since the original recognition of this taxon (Bonaparte, 1831; Eigenmann & Eigenmann, 1890).

**50.** Number of precaudal vertebrae: (0) 14 or more; (1) 13; (2) 12; (3) 11 (CI = 100; RI = 100).

The Loricariidae possess 26 to 42 vertebrae between the basioccipital and the hypural plate (Schaefer, 1987: 24; 1990: 190; 1997: 105). The increase in the total number of vertebrae is derived within loricariids (Schaefer, 1987: 24), with the greatest number present in the subfamily Loricariinae, with 33-37 vertebrae (*vs.* 30 or fewer). The Astroblepidae and Callichthyidae possess 16-18 precaudal vertebrae and the Loricariidae 12-16 (Hypostominae and Ancistrinae with 13-16; Hypoptopomatinae and Loricariinae with 12) (Schaefer, 1987: 24). Within the Loricariinae there is a secondary reduction in the number of precaudal vertebrae. *Lamontichthys* and *Harttia* possess 13 precaudal vertebrae, *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisoma* possess 12 precaudal vertebrae, and *Sturisomatichthys* has 11 precaudal vertebrae (Rapp Py-Daniel, 1997: character 110).

**51.** Number of caudal vertebrae: (0) 23-25; (1) 19-22; (2) 12-18 (CI = 50; RI = 75).

Among examined taxa *Hypostomus* and *Neoplecostomus* possess 12 to 18 caudal vertebrae and all members of the Loricariinae possess 19 or more. *Harttia*, *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, and *Sturisomatichthys* possess 19 to 22 caudal vertebrae and *Lamontichthys*, *Farlowella*, *Pterosturisoma*, and *Sturisoma* possess 23 to 25 caudal vertebrae (Rapp Py-Daniel, 1997: character 111).

### Dorsal-fin

**52.** Spinelet: (0) shaped as strong and short spine, articulated with first pterygiophore; (1) shaped as small plate; (2) absent (CI = 50; RI = 33).

The majority of the Siluriformes possess the first element of the dorsal-fin (often termed the spinelet, Schaefer, 1987: 17) shaped as a strong, short, and spine-like element that acts as a locking system for the second much longer dorsal-fin spine (Alexander, 1965), a condition observed in *Hypostomus*, among examined taxa. The spinelet is variably reduced or lost in several members of the Loricariidae (Schaefer, 1987: 18; Armbruster, 2004: 33).

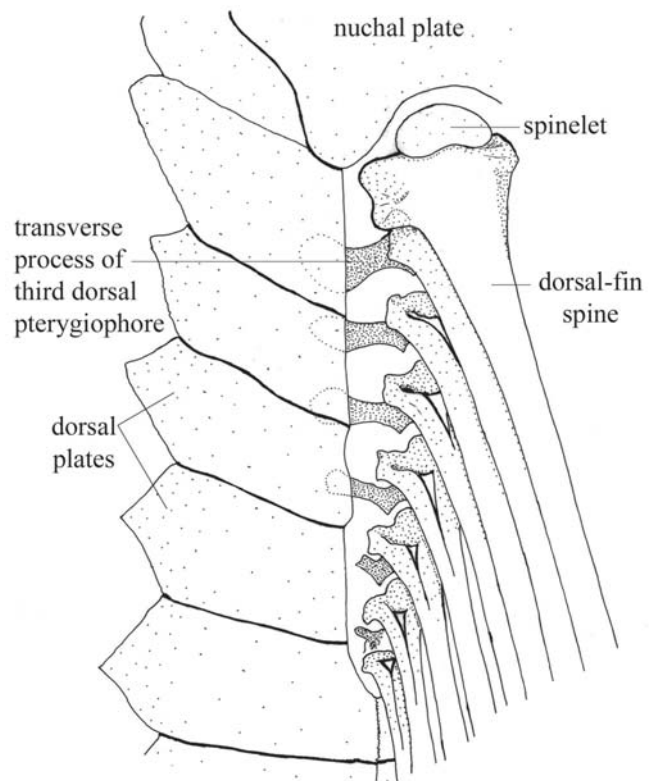
In *Lamontichthys* (including *L. parakana*), *Harttia punctata*, *Neoplecostomus*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* the spinelet is shaped as a plate-like structure (Fig. 44), and *Farlowella*, *Harttia loricariformis*, *Loricaria*, and *Pseudoloricaria* lack the spinelet.

**53.** Type of articulation between proximal portion of dorsal-fin spine and second dorsal-fin pterygiophore: (0) through condyle on dorsal region of pterygiophore; (1) through simple contact with pterygiophore, with no condyle; (2) via chain-link structure (CI = 66; RI = 50).

The second element of the dorsal-fin in the Siluriformes is usually modified into a defensive spine (Reed, 1924), and the proximal end of this spine articulates with a dorsal condyle of the second pterygiophore (Fig. 45a; Schaefer, 1987: 23), a condition observed in *Hypostomus*, among examined taxa.

In *Lamontichthys*, *Farlowella*, *Harttia punctata*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* the dorsal-fin spine articulates with the second pterygiophore via a chain-like structure (Fig. 45b), a condition proposed as synapomorphic for the Loricariinae by Schaefer (1987: 23) and posteriorly corroborated by Armbruster (2004: 33). In *Harttia loricariformis* and *Neoplecostomus* the dorsal surface of the second pterygiophore is flat, lacking any structure for articulation.

The dorsal-fin pterygiophores of the majority of loricariids possess transverse processes, which provide support for the dermal body plates. Usually, the processes of the anterior most pterygiophores are long, and decrease in size posteriorly (Schaefer, 1991: 18). The number of dorsal-fin pterygiophores



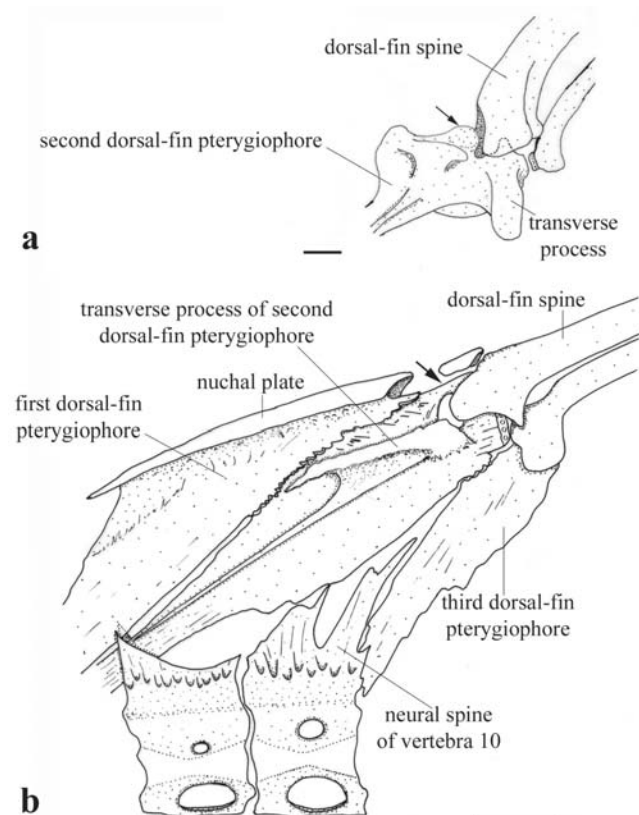
**Fig. 44.** Dorsolateral view of the dorsal-fin of *Lamontichthys stibaros* (FMNH 84111, 62.4 mm SL). Cartilages not represented. Scale bar = 1 mm.

bearing transverse processes varies within the Loricariidae (Armbruster, 2004: 33). Variations pertaining to the dorsal-fin pterygiophores observed in the present study are discussed under characters 54 to 59.

**54.** Length of transverse process of first dorsal-fin pterygiophore relative to second dorsal-fin pterygiophore: (0) shorter; (1) of similar length (uninformative).

The first and the second dorsal-fin pterygiophores of loricariids possess a pair of relatively long transverse processes, involved in the support of the nuchal plate and first rays of the dorsal-fin (Schaefer, 1991: 18). In *Neoplecostomus* these processes are of similar length, and in the other loricariid examined, the lateral processes of the first dorsal-fin pterygiophore are shorter than those of the second. This character was previously described by Rapp-Py Daniel (1997: character 120).

**55.** Orientation of transverse process of second dorsal-fin pterygiophore: (0) lateral at proximal portion and anterolateral at distal portion; (1) anterolateral throughout entire extension; (2) anterolateral at proximal portion and anterior at distal portion (CI = 66; RI = 83).



**Fig. 45.** Lateral view of portion of the dorsal-fin and associated elements (left side) of *Pterygoplichthys* sp. (modified from of Schaefer, 1987: fig. 17c) (a), and *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL) (b). Arrow points to condyle (a) and chain-like structure (b). Scale bar = 1 mm.

Different types of orientation of the lateral process of the second dorsal-fin pterygiophore were described for the Loricariidae by Rapp Py-Daniel (1997: character 118). The condition in which the lateral process of the second dorsal-fin pterygiophore is directed anterolaterally along its entire extension occurs in *Lamontichthys*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* (Fig. 46a). The lateral process of the second dorsal-fin pterygiophore directed anterolaterally at its proximal portion and anteriorly at its distal portion occurs in *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* (Fig. 46b). The lateral process of second dorsal-fin pterygiophore directed lateral at its proximal portion and anterolateral at its distal portion occurs in *Farlowella*, *Harttia*, *Hypostomus*, and *Neoplecostomus* (Fig. 46c).

**56.** Contact between transverse process of third and fourth dorsal-fin pterygiophores and dorsal body plates: (0) present; (1) absent (uninformative).

In the majority of the loricariids examined (with the exception of *Neoplecostomus*) the lateral processes of the third and fourth dorsal-fin pterygiophores are long and contact the ventral surface of the dorsal body plates (Fig. 44). According to Schaefer (1991: 18) *Neoplecostomus* lacks transverse processes on the third and fourth pterygiophores, however, two very short processes are present in the specimen of *N. ribeirensis* examined in the present study and they fail to reach the dorsal plates.

**57.** Transverse process on fifth dorsal-fin pterygiophore: (0) absent; (1) present (CI = 50; RI = 50).

The majority of the Loricariinae examined possess a transverse process on the fifth dorsal-fin pterygiophore (Fig. 44). *Sturisomatichthys* lacks these processes, a condition that also occurs in *Hypostomus* and *Neoplecostomus*.

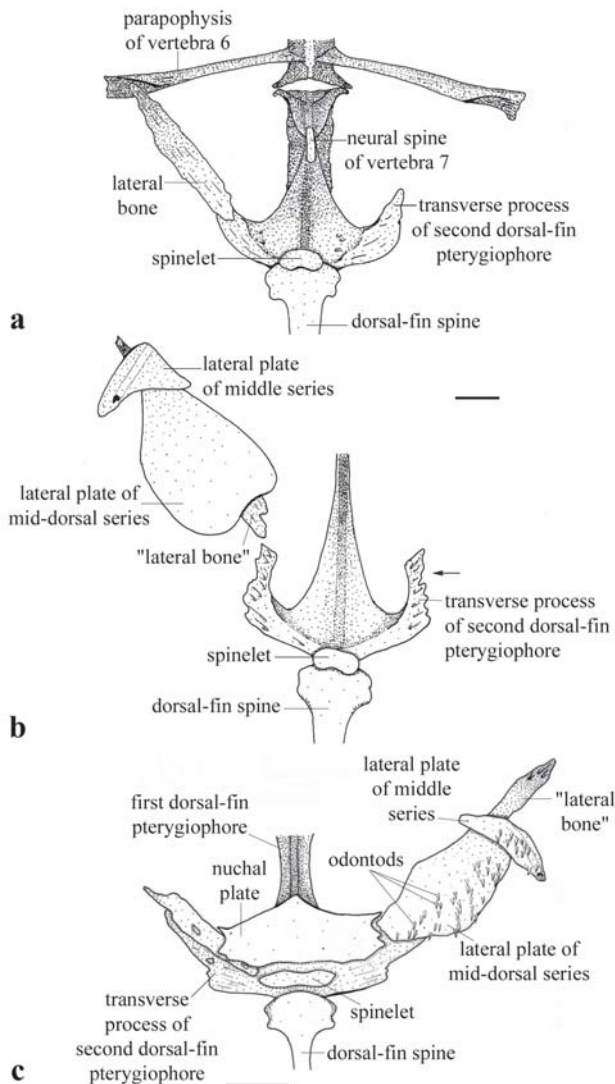
**58.** Transverse process of sixth dorsal-fin pterygiophore: (0) absent; (1) present (CI = 50; RI = 75).

*Harttia*, *Hypostomus*, *Neoplecostomus*, and *Sturisomatichthys* lack a transverse process on the sixth dorsal-fin pterygiophore. Small transverse processes are present in *Lamontichthys*, *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisoma* (Fig. 44).

**59.** Connecting bone: (0) present, contacting first or second dorsal-fin pterygiophore; (1) present, not contacting any pterygiophore; (2) absent (CI = 50; RI = 50).

The connecting bone or lateral bone (Bailey & Baskin, 1976; Schaefer, 1987: 26) is a laminar ossification located between the parapophysis of the sixth vertebra and the first or second dorsal-fin pterygiophore that is present in many loricariids, the Astroblepidae and the Scoloplacidae and occurs as an unossified tendon in callichthyids (Schaefer, 1990: 193; Armbruster, 2004: 32).

In the Astroblepidae, Scoloplacidae, and many loricariids the posterior tip of the lateral bone contacts the second dorsal-



**Fig. 46.** Dorsal view of second dorsal-fin pterygiophore, spinelet, dorsal-fin spine and lateral bone of *Lamontichthys stibaros* (FMNH 84111, 62.4 mm SL) (a), *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL) (b), and *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL) (c). Scale bar = 1 mm.

fin pterygiophore (Bailey & Baskin, 1976; Schaefer, 1987: 26). This condition occurs in *Lamontichthys*, *Harttia*, *Hypostomus*, *Loricaria*, and *Neoplecostomus* among examined taxa (Fig. 46a).

In *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* although present, the posterior tip of the lateral bone does not contact any pterygiophore (Fig. 46b). *Farlowella* lacks a connecting bone.

#### Pectoral fin and girdle

**60.** Number of branched pectoral-fin rays: (0) 6; (1) 7 (CI = 100; RI = 100).

The majority of the Siluriformes, including the more basal taxa, have eight or more branched rays in the pectoral-fin (de Pinna, 1996: 37). However, in the Loricariidae there is a

reduction of this number to five to seven rays. *Neoplecostomus*, the Hypostominae, the Ancistrinae and the majority of the members of the Loricariinae and Hypoptopomatinae possess six branched rays in the pectoral-fin (Schaefer, 1987, 1998). Schaefer (1998: 399) considered the presence of seven branched rays in the pectoral-fin as a derived condition within the Hypoptopomatinae. Among the Loricariinae, all species of *Lamontichthys* (including *L. parakana*), *Harttia leiopleura*, and *Rineloricaria daraha* (Rapp Py Daniel & Fichberg, 2008) possess seven branched rays, while some species of *Farlowella* possess only five (Boeseman, 1971). The presence of seven branched rays in the pectoral-fin was originally proposed as a diagnostic character for *Lamontichthys* by Isbrücker & Nijssen (1976, 1978b).

**61.** Length of cleithrum symphysis relative to coracoid symphysis: (0) similar to twice as short; (1) twice as long (CI = 100; RI = 100).

The cleithrum and coracoid in loricariids articulate with their counterparts by means of interdigitating sutures along their symphyses, the extension of which is variable, a feature previously observed by Rapp-Py Daniel (1997: character 142).

In *Lamontichthys*, *Harttia*, *Farlowella*, *Hypostomus*, *Neoplecostomus*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys*, the length of the symphysis of the cleithrum is approximately equal to twice as short as the coracoid symphysis (Fig. 47). Alternatively, in *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, the symphysis of the cleithrum is twice as long as the coracoid symphysis.

**62.** Bony lamina on ventrolateral portion of coracoid: (0) absent; (1) present (CI = 50; RI = 75).

The ventral surface of the pectoral girdle of loricariids possesses a fossa between the cleithrum and coracoid, termed the abductor fossa or arrector fossa that lodges the *arrector ventralis profundus* and *arrector ventralis superficialis* muscles, responsible for the movement of the pectoral fin (Schaefer, 1987: 24; 1991: 18).

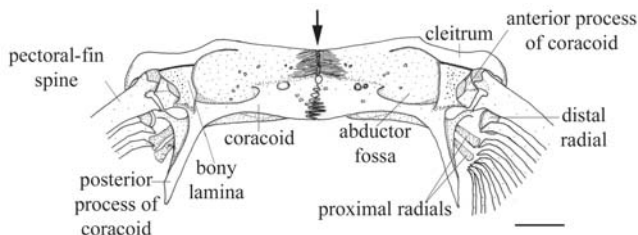
In *Lamontichthys avacanoeiro*, *L. parakana* (the latter species not included in the analysis), *Harttia*, *Hypostomus*, and *Neoplecostomus*, there is no bony lamina covering the fossa, resulting in a complete exposure of the arrector fossa (Fig. 48a).

Within the Loricariinae, *Lamontichthys filamentosus*, *L. llanero*, *L. maracaibero*, *L. stibaros*, *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* possess a bony lamina on the ventrolateral region of the coracoid that covers the lateral portion of the arrector fossa (Figs. 47 and 48b). This lamina connects the cleithrum anteriorly to the coracoid posteriorly and it was previously discussed by Schaefer (1987: 24).

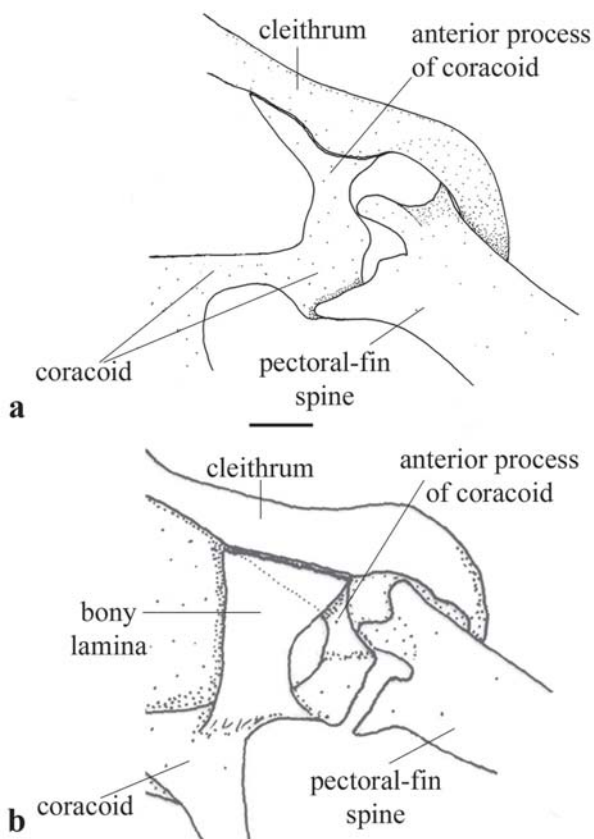
A third condition of this character was proposed by Schaefer (1987: 24; 1991: 18; 1998: 397) as synapomorphic for the Hypoptopomatinae a taxon not included in the present study.

Although *Lamontichthys avacanoeiro* and *L. parakana* lack a bony lamina in the ventrolateral portion of the coracoid,

these two species possess a thin bony plate, covered by odontods, embedded in the skin and firmly attached to the coracoid in the same position as the osseous lamina in the other taxa. These two species were coded as “0”.



**Fig. 47.** Ventral view of the pectoral girdle of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL). Arrow points to region of cleithrum and coracoid symphyses. Cartilages not represented. Scale bar = 3 mm.



**Fig. 48.** Ventral view of ventrolateral portion of the pectoral girdle of *Lamontichthys avacanoeiro* (MZUSP 61974, 113.7 mm SL, paratype) (a), and *L. filamentosus* (LACM 41741-9, 119.4 mm SL) (b). Scale bar = 1 mm.

### Pelvic fin and girdle

**63.** Contact between internal anterior processes of basiptyerygium: (0) in contact along their entire medial margins; (1) in contact anteriorly and posteriorly at midline, with a small foramen in between; (2) not in contact, with distal tip of

each process close to each other or connected by ligaments (uninformative).

In the Loricariidae each basiptyerygium possess a pair of anterior processes, one internal and one lateral (Schaefer, 1987: 19) or anteromesial and anterolateral processes, respectively (Armbruster, 2004: 37). Different types of contact between the anteromesial processes of the basiptyerygia occur among examined taxa.

In members of the subfamily Loricariinae, the contralateral anteromesial processes are either not in contact, or contact each other only at their distal tips (Fig. 49a, b). The remaining loricariids possess additional regions of contact and in *Neoplecostomus* they are in contact along their entire medial margins (Fig. 49c).

In *Lamontichthys stibaros*, the distal tips of the anteromesial processes are connected by ligaments.

**64.** Orientation of anteromesial processes of basiptyerygium: (0) antero-medial; (1) medial (CI = 100; RI = 100).

*Harttia* possesses the anteromesial processes of the basiptyerygium medially directed, a condition previously reported by Rapp Py-Daniel (1997: character 152) for the genus.

**65.** Relative width of two laminar expansions of anterolateral process of basiptyerygium: (0) dorsal wider than ventral; (1) dorsal and ventral of similar widths; (2) dorsal narrower than ventral (CI = 100; RI = 100).

In loricariids, the anterolateral process of the basiptyerygium possesses two laminar expansions for the attachment of the *arrector dorsalis* muscles (external process ridge of Shelden, 1937). One of these expansions is oriented ventral or ventrolaterally, and the other dorsal or dorsolaterally. Rapp Py-Daniel (1997: character 155) previously reported differences in the relative width of these laminar expansions in the Loricariinae.

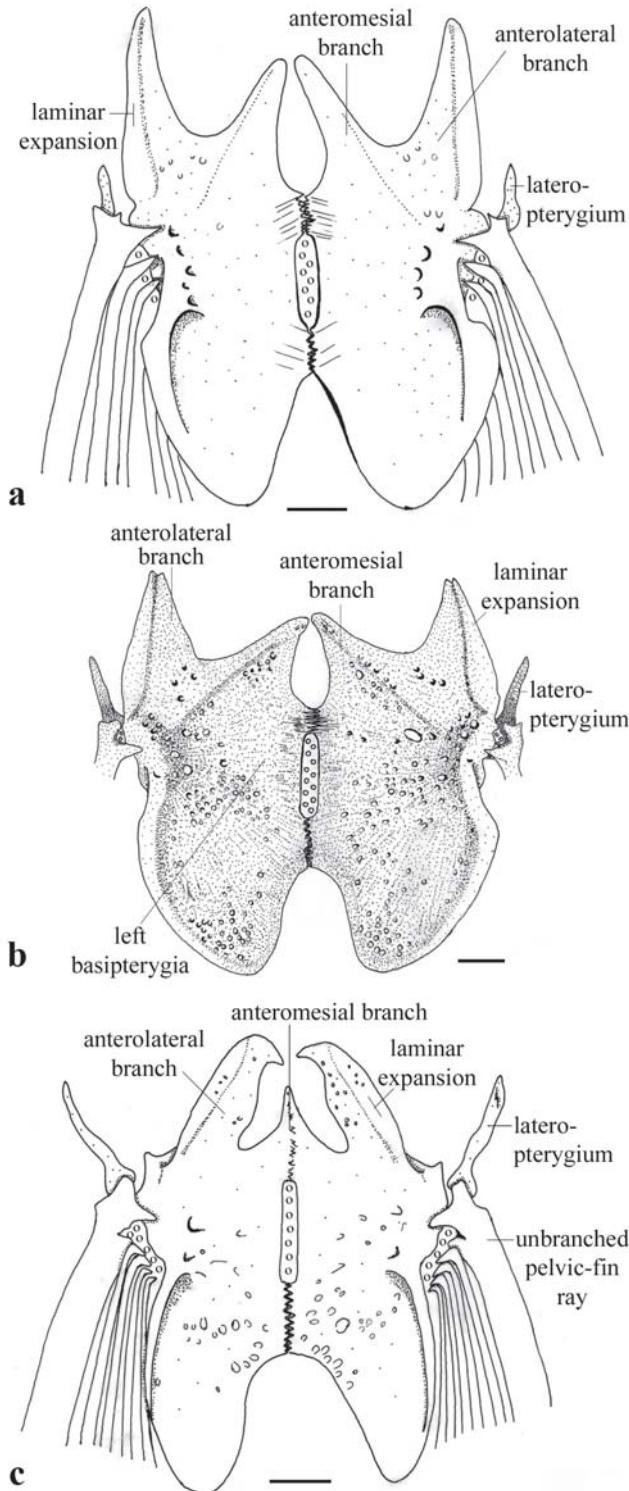
In *Lamontichthys*, *Farlowella*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* both expansions are well developed and of similar widths. In *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*, the dorsal expansion is considerably narrower than the ventral. *Hypostomus* and *Neoplecostomus* have the dorsal expansion of the anterolateral process of the basiptyerygium considerably wider than the ventral.

**66.** Presence and relative size of lateroptyerygium: (0) large; (1) medium; (2) small; (3) absent (CI = 100; RI = 100).

The lateroptyerygium is a bony structure that is connected with the lateral margin of the basiptyerygium dorsal to the insertion of the pelvic-fin rays, and is present in the Astroblepidae and Loricariidae (Shelden, 1937; Howes, 1983: 336). Armbruster (2004: 39) observed variation in the form of the lateroptyerygium among loricariids. Due to the difficulty in coding the variation observed in the format of the lateroptyerygium in the taxa examined in this study, such variation was coded in terms of differences in the relative size of the structure.

*Neoplecostomus* and *Hypostomus* possess a relatively

large lateropterygium, its size approximately twice the length of that structure in *Lamontichthys* and *Harttia* (coded as having a medium sized lateropterygium) (Fig. 49). In the latter



**Fig. 49.** Dorsal view of the pelvic girdle and lateropterygium of (a) *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL), (b) *Lamontichthys stibaros* (FMNH 84111, 62.4 mm SL), and (c) *Neoplecostomus ribeirensis* (MZUSP 100920, 45.3 mm SL). Scale bar = 1 mm.

two genera the lateropterygium is twice the size of that structure in *Farlowella*, *Loricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*, taxa with a considerably small lateropterygium.

Howes (1983: 336) proposed that the lack of a lateropterygium is derived in the subfamily Loricariinae, a condition herein observed in *Pseudoloricaria*.

#### Anal-fin

The anal-fin in the majority of loricariids is formed by one relatively large anterior unbranched ray, followed by four branched rays, all supported by five pterygiophores. The anal-fin pterygiophores have the proximal and medial radials fused, with only the distal radial present as a separate element (Schaefer, 1987: 18).

**67.** First anal-fin pterygiophore: (0) completely covered by skin; (1) with small exposed area; (2) with large exposed area (uninformative).

*Neoplecostomus* possesses the first anal-fin pterygiophore completely covered by skin, lacking any exposed surface and *Hypostomus* possesses only one small exposed area. In all examined taxa of the Loricariinae the first anal-fin pterygiophore has a relatively large exposed area that supports dermal plates.

**68.** Centrum of articulation of first anal-fin pterygiophore: (0) centrum 15; (1) centra 12, 13 or 14 (CI = 100; RI = 100).

The articulation of the first anal-fin pterygiophore with the vertebral column in all examined taxa of the Loricariinae is on centra 12, 13 or 14. In *Farlowella*, *Loricaria*, *Sturisomatichthys*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisoma*, the articulation is on centra 12 or 13 and in *Lamontichthys* and *Harttia* the articulation is slightly posterior, on centra 13 or 14. In both cases, most often, the articulation is on centrum 13.

In the Astroblepidae and Callichthyidae, the articulation of the first anal-fin pterygiophore with the vertebral column is on centra 17, 18 or 19 and in the Loricariidae it varies from centra 13 to 17 (Schaefer, 1987: 25). Within loricariids, in the Hypostominae and Ancistrinae the articulation varies from centra 14 to 17, while in the Hypoptopomatinae and Loricariinae on centrum 13. This latter condition was proposed by that author as synapomorphic for the family Loricariidae.

**69.** Relative distance of adjacent proximal portions of first three anal-fin pterygiophores: (0) relatively distant; (1) relatively close; (2) in contact (CI = 66; RI = 80).

The anal-fin pterygiophores of the majority of loricariids are expanded along the anteroposterior axis. The degree of separation among the proximal region of the first three anal-fin pterygiophores varies among taxa, and three distinct conditions were defined by Rapp Py-Daniel (1997: character 122). *Hypostomus* has the proximal tips of the first three anal-fin pterygiophores relatively separate from each other (Schaefer, 1987: fig. 11a). In *Harttia*, *Loricaria*,



*Neoplecostomus*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*, the proximal regions of the first three anal-fin pterygiophores are less separate, but are not in contact, while in *Lamontichthys* and *Farlowella* the proximal tips of the first three anal-fin pterygiophores are in (or almost) in contact (Figs. 39-41).

#### Caudal-fin

**70.** Number of principal caudal-fin rays: (0) 16 (i,7+7,i); (1) 14 (i,6+6,i); (2) 11-12 (i,5+5,i; i,5+4,i) (CI = 100; RI = 100).

There is a trend toward a reduction in the number of principal caudal-fin rays within the Siluriformes. Diplomystidae has 18 principal rays, but most Siluriformes possess 17 or fewer principal rays in the caudal-fin (Lundberg & Baskin, 1969: 35). Members of the Loricariidae usually possess 16 principal rays in caudal-fin (Schaefer, 1991: 17). In the subfamily Loricariinae there is a reduction of this number to 11-14 principal rays (Lundberg & Baskin, 1969: 35; Schaefer, 1987: 17; 1991: 17).

*Lamontichthys*, *Harttia*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* possess 14 principal caudal-fin rays. *Farlowella*, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* possess 11-12 principal caudal-fin rays.

**71.** Relative length and shape of upper and lower lobes of hypural plate: (0) symmetric, posterior border vertically aligned; (1) asymmetric, lower lobe extending beyond posterior margin of upper lobe; (2) symmetric, posterior border "V"-shaped (uninformative).

In the Loricariidae, the five hypurals and the uroneural are fused forming the "hypural plate", the parahypural is fused to hypurals 1 and 2; the uroneural and/or the epural are fused to hypurals 3, 4 and 5.

Within the Loricariidae there is variation in the shape of the posterior border of the hypural elements (Schaefer, 1987: 25). *Neoplecostomus* possesses a vertical posterior border with symmetric caudal lobes. In the Loricariinae the caudal fin-lobes are also symmetric, however the posterior border is "V" shaped due to the more posteriorly elongate median portion of the hypural plate. This condition was proposed by Schaefer (1987: 25) as synapomorphic for the subfamily Loricariinae.

Asymmetric caudal lobes occur in most loricariids including members of the Hypostominae (Schaefer, 1987: 25), represented in this study by *Hypostomus*.

**72.** Shape of hypurapophysis: (0) short, robust, approximately triangular; (1) short, robust, approximately quadrate; (2) relatively elongate, robust, keel-shaped; (3) broad, laminar, wing-shaped (CI = 100; RI = 100).

The hypurapophyses are projections on the parahypural and first and second hypurals of the caudal-fin skeleton of the Siluriformes, which serve as the insertion site for muscles involved in the movement of the caudal-fin rays (Schaefer, 1987: 17). Loricariids possess hypurapophysis type C (Lundberg & Baskin, 1969: 14), the most common among the Siluriformes in which the primary hypurapophysis is continuous with a secondary hypurapophysis on hypurals 1 and 2.

In the present study, four different conditions regarding shape of the hypurapophysis are recognized. *Neoplecostomus* and many loricariids possess a short and robust hypurapophysis, triangular to approximately quadrate-shaped. Within the Loricariinae, *Harttia* possesses a robust hypurapophysis, relatively wide and keel-shaped, and in *Lamontichthys*, *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*, the structures are broad, laminar and wing-shaped (Figs. 43 and 50).

**73.** Relative length of hypurapophysis: (0) short, not projecting to second preural centrum; (1) long, projecting to second preural centrum (CI = 100; RI = 100).

In loricariids in general, the hypurapophysis is short and does not project anteriorly to the second preural centrum. However, in all taxa of the Loricariinae examined the hypurapophysis extends anteriorly to the second preural centrum (Figs. 43 and 50).

**74.** Process on ventral surface of hypurapophysis: (0) absent; (1) present (uninformative).

The ventral surface of the hypurapophysis of *Lamontichthys avacanoeiro* possesses a narrow ossified process posteroventrally oriented, probably serving as an additional site for the attachment of the caudal-fin musculature (Fig. 50; Schaefer, 1987: 17). There are no reports of any process on the hypurapophysis of other Siluriformes.

**75.** Presence and relative size of epural: (0) large, length approximately equal to height of lower lobe of hypural plate; (1) small, length shorter than 1/2 of height of lower lobe of hypural plate; (2) absent as a separate element (CI = 40; RI = 25).

The Siluriformes primitively possess a single epural, relatively large, separate from the dorsal hypurals (Lundberg & Baskin, 1969: 11). Among loricariids, this condition occurs in the Neoplecostominae, Hypoptopomatinae, and some Hypostominae, while in the Loricariinae and many Hypostominae there is a tendency of fusion of the epural to hypurals or reduction in epural size (Fig. 43; Schaefer, 1987: 17). Rapp Py-Daniel (1997: character 127) previously reported variation on the relative size of the epural in the Loricariinae.

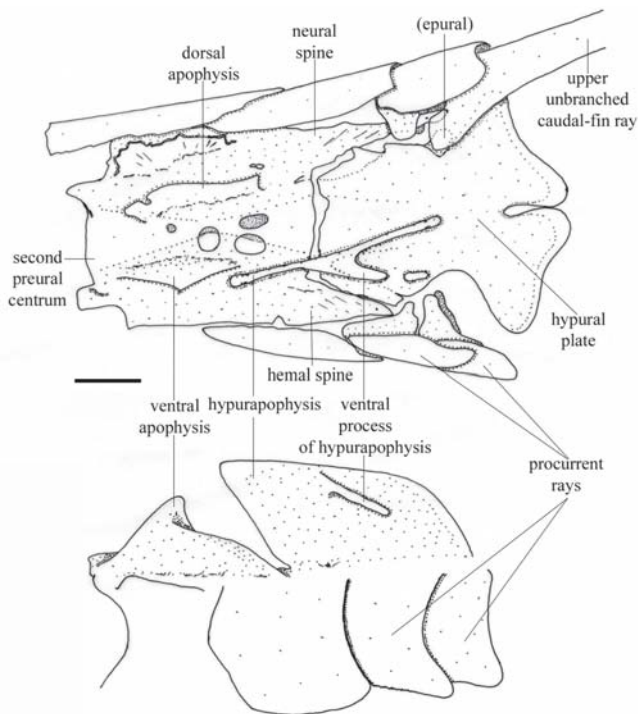
*Lamontichthys filamentosus*, *L. llanero*, *L. stibaros*, *L. avacanoeiro*, *Harttia*, *Pseudoloricaria*, *Pterosturisoma*, and *Sturisoma* possess a separate epural. However, it is a relatively small ossification, shorter than half the height of the lower lobe of the hypural plate (Fig. 50). The epural is lacking as a separate element in *L. maracaibero*, *Farlowella*, *Loricaria*, *Rineloricaria*, and *Sturisomatichthys*.

**76.** Notch at median posterior border of hypural plate: (0) present, elongate, extending to 1/2 of length hypural plate; (1) present, extending to approximately 1/4 length of hypural plate; (2) extremely reduced or absent (uninformative).

The hypural plate of loricariids possesses a notch at its posterior median border, demarcating the separation between

the upper and lower lobes (Schaefer, 1987: 17). There is a wide degree of variation in the extent of this notch in the family, including taxa that lack the notch. In the plesiomorphic condition for loricariids, present in *Neoplecostomus*, there is a deep notch in the hypural plate (Fig. 43b; Schaefer, 1991: 16).

In *Lamontichthys filamentosus*, *L. llanero*, *L. maracaibero*, *L. stibaros*, *L. avacanoeiro*, *Harttia*, *Hypostomus*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys*, the notch is relatively shorter extending to approximately 1/4 of the length of the hypural plate (Figs. 43a, c and 50). In *Farlowella*, the notch is extremely reduced and inconspicuous.



**Fig. 50.** Lateral view of the second preural centrum and caudal-fin skeleton (left side) of *Lamontichthys avacanoeiro* (MZUSP 61974, 113.7 mm SL, paratype). In detail (lower figure), the ventral view of hypurapophysis and lower apophysis. Cartilages not represented. Scale bar = 1 mm.

**77.** Apophysis on second preural centrum: (0) absent; (1) one; (2) two, narrow; (3) two, broad (CI = 60; RI = 60).

The second preural centrum of the Siluriformes in general lack lateral bony projections (apophyses) but Rapp Py-Daniel (1997: character 130) reported the presence of one or two apophyses, on both sides of the second preural centrum in many loricariids. These apophyses are longitudinal, flange-like, and extend along the lateral portion of the vertebral centrum. The second preural centrum of *Harttia*, *Neoplecostomus*, *Sturisoma*, and *Sturisomatichthys* lack any apophyses (Fig. 43a, b). *Farlowella* and *Pterosturisoma* possess two narrow apophyses, and *Lamontichthys*,

*Loricaria*, *Pseudoloricaria*, and *Rineloricaria* possess two broad apophyses (Fig. 50).

Schaefer (1987: 15, fig. 10) did not mention any apophysis on the second preural centrum of *Hypostomus plecostomus*, however, in the present study a single narrow apophysis was observed in the caudal skeleton of a specimen of *Hypostomus* examined (Fig. 43c).

#### Adipose fin

**78.** Adipose fin: (0) present; (1) absent (CI = 100; RI = 100).

The adipose fin, located between the dorsal-fin and the caudal-fin, is common among the Siluriformes. However, many Loricariidae lack this structure, such as the Loricariinae, members of the Hypoptopomatinae, Neoplecostominae and most of Rhineleporini (Armbruster, 2004: 31).

#### Miscellaneous

**79.** Groove on snout, anterior of nostril: (0) present, anterior portion formed by distinct fold of skin; (1) present, anterior portion not formed by distinct fold of skin; (2) absent (CI = 100; RI = 100).

Many loricariids possess a groove on the snout, extending longitudinally, from the anteriormost point of each nostril until the anteroventral border of the snout. The posterior portion of this groove runs between dermal plates or on the plates, and possess odontods along its margins. In *Lamontichthys*, *Farlowella*, *Loricaria*, *Pterosturisoma*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* the anterior region of the groove is similar to the posterior region (Fig. 51).

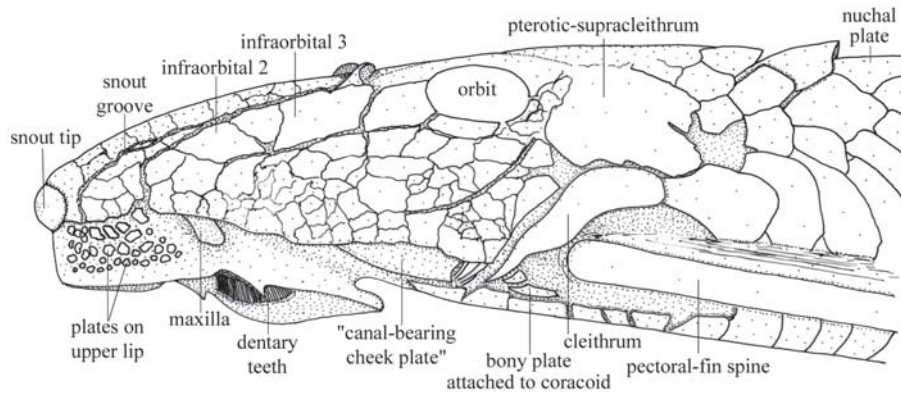
In *Harttia*, *Hypostomus*, and *Neoplecostomus*, the anterior portion of this groove is formed by a distinct fold in the skin that runs on the plates (Fig. 52). *Pseudoloricaria* lacks a groove on the snout.

**80.** Surface of snout tip: (0) without plates, with thick layer of soft connective tissue covered by papillae; (1) without plates, with thick layer of soft connective tissue without papillae; (2) with plates on thick layer of soft connective tissue; (3) with plates, without thick layer of soft connective tissue (CI = 60; RI = 66).

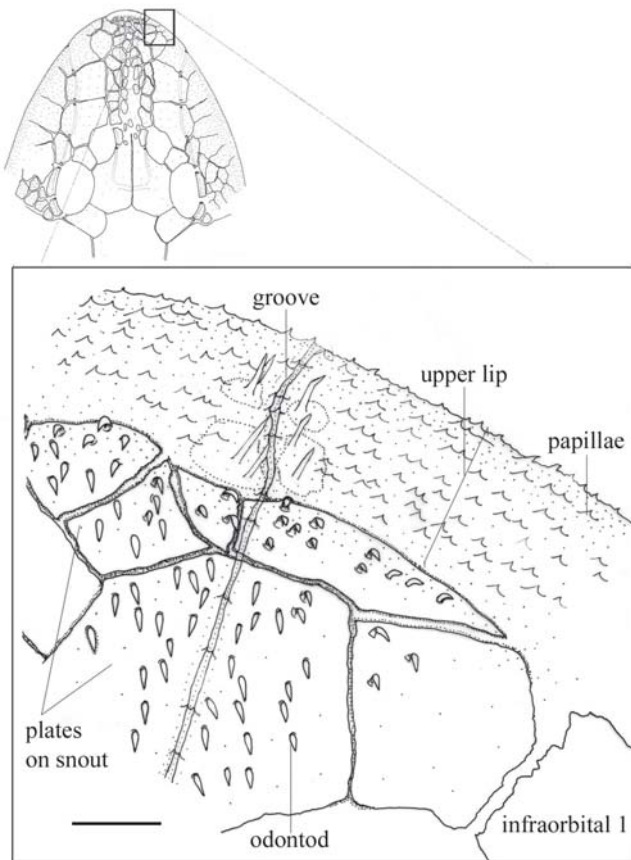
The snout of the majority of the loricariids may be completely covered by plates, or the plates may be absent exposing a thick layer of soft connective tissue attached to the anterior tip of the mesethmoid (Schaefer, 1991: 20; Armbruster, 2004: 43).

*Harttia*, *Hypostomus*, *Neoplecostomus*, *Rineloricaria*, and *Sturisoma* lack plates on the snout tip and the soft connective tissue that is exposed possesses numerous, diminute and delicate papillae. *Lamontichthys stibaros* and *L. avacanoeiro* also lack plates on the snout tip but the soft connective tissue exposed lacks papillae. *Lamontichthys parakana* (not included in the analysis) also possesses this latter condition.

*Lamontichthys filamentosus*, *L. llanero*, *L. maracaibero*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, and *Sturisomatichthys* possess small plates covering a thick layer of soft connective tissue on the snout tip. This feature is



**Fig. 51.** Lateral view of the head and anterior portion of body of *Lamontichthys avacanoeiro* (MNRJ 18553, 98.1 mm SL, paratype).



**Fig. 52.** Detail in dorsal view of anterior portion of head of *Harttia loricariformis* (MZUSP 66187, 67.7 mm SL). Scale bar = 0.5 mm.

more evident in adults. In juveniles of *L. filamentosus* the plates on the snout tip are not developed.

Although *Farlowella* has the snout tip covered by plates, it lacks the thick layer of soft connective tissue underneath the plates.

**81.** Plates on the upper lip: (0) absent; (1) present (CI = 50; RI = 83).

The majority of the Siluriformes possess lips without specializations. However, the Astroblepidae and the Loricariidae possess the lips modified into a sucking disk (Howes, 1983: 309; Armbruster, 2004: 42). The internal surface of the upper lip of loricariids is covered by papillae, but the external surface may have dermal plates.

*Harttia*, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* lack plates on the external surface of the upper lip, and in *Lamontichthys*, *Farlowella*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys*, these plates are present and covered by odontods (Fig. 51).

Although the species of *Harttia* possess a few diminutive plates on the anterior border of the snout, these plates do not cover the external surface of the upper lip.

**82.** Central buccal papillae: (0) absent; (1) present, small; (2) present, large (CI = 50; RI = 71).

Many loricariids possess a projection inside the mouth, on the median transversal line, behind the symphysis of the premaxillae. Armbruster (2004: 39) reported this structure as either absent or very small in *Astroblepus*, *Lithogenes*, and most loricariids. In the present study the presence of a small central buccal papillae and the absence of this structure were coded as different states. In *Harttia* and *Lamontichthys* (including *L. parakana*) this structure is relatively small and similar to the other papillae present in the mouth of loricariids (Fig. 9). *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Sturisoma*, and *Sturisomatichthys* share with *Hypostomus* a relatively large, tongue-like central buccal papillae, with a wide basal portion.

**83.** Odontods on lateral plates of median series: (0) covering all plate, similar to odontods of other body plates; (1) covering all plate, slightly longer on posterior border of plates; (2) long and restricted to posterior portion of plate; (3) covering all plate with one or two rows of odontods increasing in length and width along the median portion of each plate (CI = 75; RI = 75).

Members of the Loricariidae possess the body plates, fin rays, skull bones, opercular series and pectoral and pelvic girdles covered by odontods (Howes, 1983: 309).

The odontods of the lateral plates of the median series in *Hypostomus* and *Neoplecostomus* cover all plate and have similar morphology and size as the odontods of the remaining of body. The odontods of the lateral plates of the median series of the body in members of the Loricariinae examined in the present study are rather, more developed than the odontods of the remaining of the body. In *Lamontichthys*, *Farlowella*, and *Harttia*, the odontods cover all plate and are slightly larger on the posterior margin of the plate forming an inconspicuous keel along the median series of plates (Fig. 53a; state 1). The odontods of the lateral plates of the median series of *Loricaria*, *Pseudoloricaria*, *Rineloricaria*, and *Sturisoma* also cover all plate but instead, have one or two rows of odontods increasing in length and width along the median portion of each plate (Fig. 53b). In *Pterosturisoma* the odontods are restricted to the posterior portion of each lateral plate of the median series, although they may be absent in a few plates along the median series (Fig. 53c).

The differences in size and distribution of the odontods on the lateral plates of the median series (states 1, 2 and 3) together with those on the mid-ventral series result in longitudinal keels of various degrees of development.

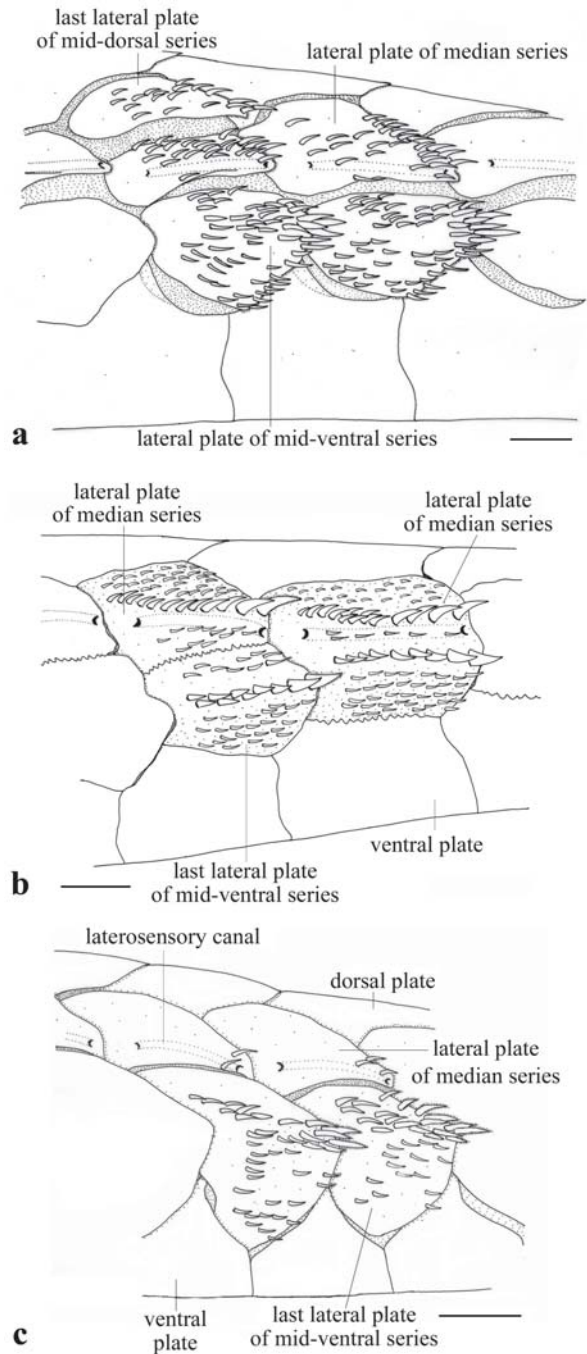
**84.** Predorsal plates between posterior tip of supraoccipital and nuchal plate: (0) three or more small plates not aligned along the midline; (1) two pairs of large plates, fused in the midline; (2) three pairs of large plates, fused in the midline; (3) six or more pairs of large plates, fused in the midline (CI = 60; RI = 0).

In the Loricariinae the predorsal plates are typically paired, large and fused in the median line of the body, while in *Neoplecostomus* these plates are relatively small and are not aligned in the median line of the body. *Lamontichthys*, *Harttia*, *Pseudoloricaria*, *Pterosturisoma*, and *Rineloricaria* possess only two paired predorsal plates. In the derived conditions, there is an increase of the number of predorsal plates. *Loricaria*, *Sturisoma*, and *Sturisomatichthys* possess three paired predorsal plates, while *Farlowella* possesses six paired predorsal plates (Fig. 54). According to Boeseman (1971: 16), members of the Loricariinae possess two plates between the supraoccipital and the nuchal plate, with a greater number in *Farlowella* (6-8) and *Sturisoma* (2-3).

**85.** Number of predorsal plates between neural spine of sixth and seventh vertebrae: (0) three; (1) two; (2) one (uninformative).

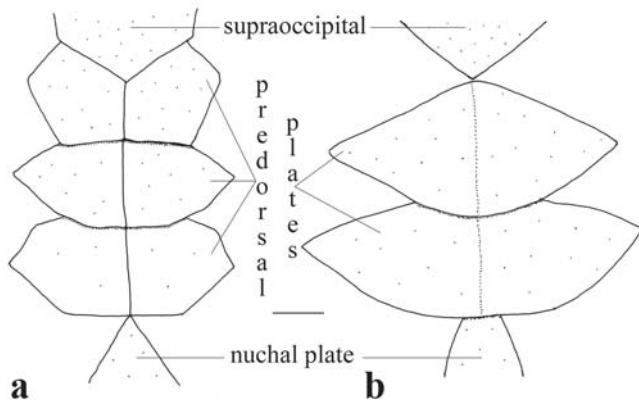
*Lamontichthys*, *Harttia*, *Loricaria*, *Pterosturisoma*, *Pseudoloricaria*, *Rineloricaria*, *Sturisoma*, and *Sturisomatichthys* possess two predorsal plates on the body in the region between the sixth and the seventh vertebra (Fig. 38). In *Farlowella*, there is a reduction of this number, and only a single plate is present in this region, a condition also present in *Acestridium discus* (Hypoptopomatinae).

**86.** Supracaudal plates: (0) short and numerous; (1) elongate and few (CI = 100; RI = 100).



**Fig. 53.** Lateral view of part of caudal peduncle of (a) *Lamontichthys avacanoeiro* (MNRJ 18553, 98.1 mm SL, paratype), (b) *Rineloricaria* sp. (MZUSP 23748, 91.5 mm SL), and (c) *Pterosturisoma microps* (MZUSP 79909, 75.9 mm SL). Odontods represented only in the complete lateral plates. Scale bar = 1 mm.

Loricariids have plates on the base of the caudal-fin, posterior to the last row of plates of the caudal peduncle (Schaefer, 1987: 25). In the Loricariinae, there are usually 3-5 supracaudal plates on each side, horizontally elongate and joined by connective tissue to the lateral region of the caudal-



**Fig. 54.** Dorsal view of the predorsal plates of (a) *Sturisoma* sp. (MZUSP 50112, 115.2 mm SL) and (b) *Lamontichthys avacanoeiro* (MNRJ 18553, 98.1 mm SL, paratype). Odontods not represented. Scale bar = 2 mm.

fin. In other loricariids these plates are short and numerous (six or more plates) (Fig. 35).

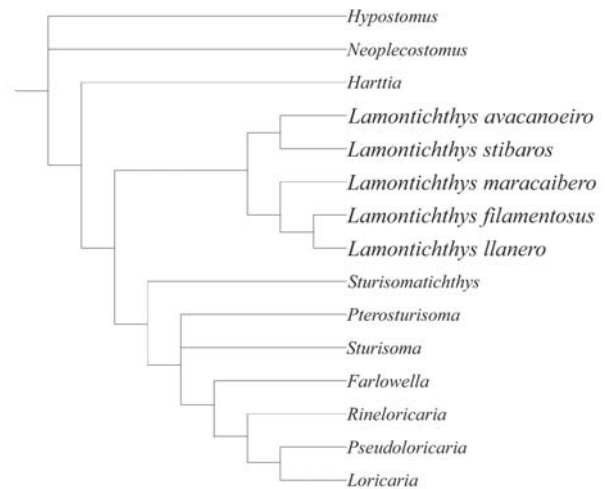
Schaefer (1987: 25) proposed the presence of elongate plates on the base of the caudal-fin as synapomorphic for the subfamily Loricariinae, but did not refer to the number of plates.

**87.** Long filament at distal tip of dorsal-fin spine: (0) absent; (1) present (CI = 100; RI = 100).

Many members of the Loricariinae possess the unbranched caudal-fin rays projecting as long filaments. There are few reports about the presence of long filaments in the other fins probably because it is a fragile structure and commonly damaged in specimens, and/or because there are relatively few taxa with long filaments in the unbranched fin-ray. Many members of the Loricariinae possess the pectoral-fin spine forming only a short filament, however *L. filamentosus* and *Pterosturisoma* possess elongate filaments.

Isbrücker & Nijssen (1974) considered the presence of a long filament in the dorsal-fin as diagnostic for *Planiloricaria*. Species of *Sturisoma* and *Loricaria* also possess this feature. Among the loricariids included in the present analysis, *L. filamentosus* and *L. llanero* possess the dorsal-fin spine projecting as a long filament sometimes longer than the standard length of the specimens.

**Phylogenetic reconstruction.** The parsimony analysis, including 87 osteological and external morphology characters of *Lamontichthys* and related groups (Table 4), resulted in three most parsimonious cladograms with 194 steps, consistency index of 0.73 and retention index of 0.78 (Fig. 55). The cladograms differ only in the hypothesized phylogenetic relationships of two outgroup taxa *Pterosturisoma* and *Sturisoma*. The list of synapomorphies that support hypothesis of the monophyly of *Lamontichthys* and relationships among its species are detailed below.



**Fig. 55.** Strict consensus of the three most parsimonious hypotheses of relationships of species of *Lamontichthys* and allied genera (L = 194; CI = 0.73; RI = 0.78, see text for considerations about relationships of outgroup taxa).

#### Monophyly of *Lamontichthys*

Character 13 (1>4): Trapezoidal shape of lower pharyngeal plate.

Character 14 (1>2): Triangular and relatively long posterior expansion of first epibranchial.

Character 23 (0>1): Large coronoid process of dentary, with large robust area, not concave.

Character 60 (0>1): Presence of I-7 pectoral-fin rays.

Character 69 (1>2): Proximal portions of first three anal-fin pterygiophores in (or almost) in contact. Independently acquired in *Farlowella*.

Character 77 (0>3): Presence of two broad apophyses on second preural centrum. Independently acquired in clade formed by *Loricaria*, *Pseudoloricaria*, and *Rineloricaria*.

Ambiguous characters:

Character 10 (0>1): Narrow ventral laminar expansion along posterior border of anterior ceratohyal gradually widening from medial to lateral portion. Also present in *Harttia* and *Sturisoma*.

Character 51 (1>0): Presence of 23-25 caudal vertebrae. Also present in *Farlowella*, *Sturisoma*, and *Pterosturisoma*.

Character 58 (0>1): Presence of transverse process on sixth dorsal-fin pterygiophore. Also present in *Farlowella*, *Pterosturisoma*, *Rineloricaria*, and *Sturisoma*.

Character 82 (1>2): Presence of large central buccal papillae. Also present in *Harttia*.

#### Monophyly of clade formed by *Lamontichthys avacanoeiro* and *L. stibaros*

Character 80 (2>1): Snout tip covered by soft connective tissue lacking papillae.

#### Autapomorphies of *Lamontichthys avacanoeiro*

Character 10 (1>2): Broad ventral laminar expansion along

**Table 4.** Character matrix for species of *Lamontichthys*, representatives of the Loricariinae, and the Loricariidae.

Taxon	Ch. 1-10	Ch. 11-20	Ch. 21-30	Ch. 31-40	Ch. 41-50	Ch. 51-60	Ch. 61-70	Ch. 71-80	Ch. 81-87
<i>Lamontichthys avacanoeiro</i>	0001010002	1042110100	0010000010	0112011021	2110011111	0120101101	0020112121	2311113111	1212110
<i>Lamontichthys filamentosus</i>	1001010001	1042110000	1010001010	0112010011	2110011111	0120101101	0120112121	2310113112	1212111
<i>Lamontichthys llanero</i>	1001010001	1042110000	1010001010	0112010011	2111011111	0120101101	0120112121	2310113112	1212111
<i>Lamontichthys maracaibero</i>	1001010001	1042110000	0010001010	0112010011	2110011111	0120101101	0120112121	2310213112	1212110
<i>Lamontichthys stibaros</i>	0001010001	1042110000	0010000010	0112010011	2110011111	0120101101	0120112121	2310113111	1212110
<i>Farlowella nattereri</i>	0112101000	1010110001	0000101111	0112010011	2110011212	0220001120	0120122122	2310222113	1113210
<i>Harttia loricariformis</i>	0001010001	1020010000	0020200010	0112010011	2112110111	1210001000	0021112111	2210110100	0212110
<i>Harttia punctata</i>	0001010001	1020110000	0020200010	0112010011	2112010111	1120001000	0021112111	2210110100	0212110
<i>Loricaria</i> sp.	0021102010	1110221121	2131-1-212	1000210111	2110011212	1220201100	1120222112	2310213112	0131110
<i>Pseudoloricaria punctata</i>	0121102010	1111220011	2131-1-212	0000210111	2110011212	1220201110	1120232112	2310113122	0132110
<i>Pterosturisoma microps</i>	0001110200	1011110000	0000001111	1112010012	-110011112	0120101110	0120122111	2310112112	1122110
<i>Rineloricaria</i> sp.	0021102010	1010220010	213001-212	0000210111	2110011212	1120201100	1120222112	2310213110	0032110
<i>Sturisoma</i> sp.	0012110101	1031130000	0000001101	0102110011	2110011112	0120101110	0120122111	2310110110	1131110
<i>Sturisomatichthys leightoni</i>	0002000000	1011110000	0000000011	0112010011	2110011113	1120100010	0120122111	2310210112	11-1110
<i>Hypostomus</i> sp.	0000111000	0011010000	0000000100	0000200000	000--01000	2000000000	0010001000	1000-11000	0102100
<i>Neoplecostomus ribeirensis</i>	0000000000	0000100000	0000000110	0001000001	110--00000	2111010000	0000000010	0100000000	0000000

posterior border of anterior ceratohyal gradually widening from medial to lateral portion.

Character 18 (0>1): Posterior process of palatine extending beyond anterior condyle of lateral ethmoid. Independently acquired in *Loricaria*.

Character 37 (0>1): Presence of one dermal plate between infraorbitals 2 and 3.

Character 39 (1>2): Presence of flange on lateral region of seventh precaudal vertebra posteriorly directed.

Character 62 (1>0): Lack of bony lamina covering part of arrector fossa on ventrolateral portion of coracoid.

Character 74 (0>1): Presence of process on ventral surface of hypurapophysis.

No autapomorphies were found to diagnose *Lamontichthys stibaros* in the present study.

#### Monophyly of clade formed by *Lamontichthys filamentosus*, *L. llanero*, and *L. maracaibero*

Character 1(0>1): Presence of ventral groove on anterior tip of mesethmoid.

Character 27 (0>1): Teeth with short cusps, main cusp slightly larger and broader than lateral cusp. Independently acquired in clade formed by *Farlowella*, *Loricaria*, *Pseudoloricaria*, *Pterosturisoma*, *Rineloricaria*, and *Sturisoma*.

#### Monophyly of clade formed by *Lamontichthys filamentosus* and *L. llanero*

Character 21 (0>1): Cup-shaped region of premaxilla distinctly longer than cup-shaped region of dentary.

Character 87 (0>1): Dorsal-fin spine projecting as long filament sometimes longer than standard length of specimens.

No autapomorphies were found to diagnose *Lamontichthys filamentosus* in the present study.

#### Autapomorphies of *Lamontichthys llanero*

Character 44 (0>1): Ventral bilateral projections on second caudal vertebra distinctly posteriorly directed and with distal

tip sutured to first anal-fin pterygiophore.

#### Autapomorphies of *Lamontichthys maracaibero*

Character 75 (1>2): Lack of epural as a separate element. Independently acquired in *Sturisomatichthys*, and clade formed by *Farlowella*, *Loricaria*, *Pseudoloricaria*, and *Rineloricaria* sp.

### Discussion

**The monophyly of *Lamontichthys*.** In the present study six characters are proposed as synapomorphic for *Lamontichthys*. One of them, the presence of seven branched pectoral-fin rays was previously proposed by Isbrücker & Nijssen (1976, 1978b) as diagnostic for *Lamontichthys*. This character state also occurs in *Harttia leiopleura* and *Rineloricaria daraha*, but all other species of *Harttia* and *Rineloricaria* possess six branched pectoral fin rays, therefore it apparently was independently acquired in the latter two species. The two species described herein, *L. avacanoeiro* and *L. parakana* also possess seven branched pectoral-fin rays. The remaining five characters are proposed as synapomorphic for the genus for the first time in the present study. Three of these synapomorphies are exclusive of *Lamontichthys* among examined taxa (characters 13, 14 and 23).

#### Phylogenetic relationships among the species of *Lamontichthys*

The present study represents the first attempt to propose a hypothesis of relationships among the species of *Lamontichthys*. Within the genus, two main clades are recognized, one formed by *L. maracaibero*, *L. filamentosus*, and *L. llanero*, and the other by *L. avacanoeiro* and *L. stibaros* (Fig. 55).

The clade formed by *L. maracaibero*, *L. filamentosus*, and *L. llanero* is supported by two synapomorphies, one of which is uniquely derived for this clade (character 1) and one homoplastic (character 27). Within this clade *L. filamentosus* is proposed as the sister taxa to *L. llanero* on the basis of two uniquely derived characters (characters 21 and 87).

The clade formed by *L. avacanoeiro* and *L. stibaros* is supported by one exclusive derived character (character 80). Although *L. parakana* was not included in the phylogenetic analysis, the presence of I, 7 pectoral-fin rays (character 60) clearly diagnose the species as a member of *Lamontichthys*.

Within *Lamontichthys*, *L. parakana* shares with *L. avacanoeiro* the presence of one plate without a laterosensorial canal between infraorbital 2 and 3 (character 37), a condition present only in these two species among all taxa examined in this study; and the lack of an osseous lamina in the ventrolateral region of the coracoid, covering the lateral portion of the abductor fossa of the pectoral girdle (character 62), a feature present in these two species and *Harttia* among examined loriciariines. Therefore, it is tentatively proposed that *L. parakana* is more closely related to *L. avacanoeiro*.

**Comments on *Pterosturisoma microps*.** The genus *Pterosturisoma* was described by Isbrücker & Nijssen (1978b) on the basis of the examination of type-specimens of *Harttia microps* Eigenmann & Allen (1942: 211) from Peru, in the upper rio Amazonas basin. In that study, the authors pointed out the similarity of this species with the then known species of *Lamontichthys*, both in the general appearance of the body and in the presence of the filamentous extension of the pectoral-fin spine. However, *Pterosturisoma* differs from *Lamontichthys* in the presence of six branched pectoral-fin rays (*vs.* seven in *Lamontichthys*), the more developed pores of the lateral line, the narrow dorsal region of the cleithrum (*vs.* wide), and the horizontal flattening of the predorsal plates.

Two autapomorphies are herein proposed for *Pterosturisoma microps*: 1) the lack of a crest on the lateral surface of hyomandibula for the insertion of the *levator arcus palatini* muscle (independently acquired in *Loricaria*) (character 31, 0>1); 2) the elongate and narrow distal portion of the hemal spine of the last precaudal vertebra (character 40, 1>2). Isbrücker & Nijssen (1978b) included *Pterosturisoma* in the tribe Harttiini based on the presence of the lateropterygium, a well developed palatine splint, and large maxillae.

In the present analysis, *Pterosturisoma* appears within a clade that includes *Sturisoma*, *Farlowella*, *Rineloricaria*, *Pseudoloricaria*, *Loricaria*, and *Sturisomatichthys* (Fig. 55), however, its phylogenetic relationships within this clade remains unresolved.

**Comments on the patterns of geographic distribution of *Lamontichthys*.** Up to the present, *Lamontichthys filamentosus* was recorded for the upper rio Amazonas basin. In the present study, the known distribution range of the species is extended eastwards to the middle Amazon basin (rio Amazonas-Solimões between the mouths of rio Purus and rio Madeira) (Fig. 2). *Lamontichthys stibaros* also occurs in the upper rio Amazonas and is found in sympatry with *L. filamentosus* in the drainages of río Ucayali and río Marañon. All other species of *Lamontichthys* have allopatric distributions. Two of them occur in Venezuela, *L. llanero* in

the upper portions of tributaries of the rio Orinoco, and *L. maracaibero*, in the lago Maracaibo system. The two remaining species of *Lamontichthys*, described in the present study, occur in the Brazilian drainage of rio Tocantins and represent a considerable extension of the known distribution range of the genus. *Lamontichthys avacanoeiro* occurs in various localities in the upper portions of that river basin and *L. parakana* is known only from the type locality in the lower rio Tocantins, below Tucuruí Dam (Fig. 2).

Based on the available information on the distribution of *Lamontichthys* (Western Amazon, rio Orinoco, and lago Maracaibo), Lima & Ribeiro (in press) characterized the distribution of the genus as clearly presenting a foreland distribution pattern, in which a foreland basin is defined as elongated, tectonically imposed lowlands, located between uplands areas of the Andean chain in the west, and the Brazilian Shield in the East. Lima & Ribeiro (in press) also commented on the fact that many fish taxa that has a lowland distribution pattern in the western-central Amazon basin also occur in the rio Tocantins system. Therefore, it is interesting to note that the two new species of *Lamontichthys* described herein also occur within that river drainage.

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