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

Andrea de Carvalho Paixão and Mônica Toledo-Piza

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 rio Orinoco basin; *L. maracaibero* in the lago Maracaibo basin; and *L. stibaros* in the upper rio 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 parccimônia, 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 monofilia 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 monofilietismo e as relações do gênero monotypico *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 rio 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, Isbrucker & Nijssen, Harttiella, Boeseman, Harttia, Steindachner, Pterosturisoma, Isbrucker & Nijssen, Sturisoma, and Sturisomatichthys Isbrucker & Nijssen (1978). 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. Isbrucker & 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; Isbrucker & Nijssen, 1976), described L. stibaros, based on two specimens from Ecuador, and redescribed Lamontichthys filamentosus (LaMonte). Harttia filamentissima Eigenmann & Allen was provisionally considered by Isbrucker & 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 investigation of the meaning of such variation. More recently, Taphorn & Liljestrom (1984) described two new species of Lamontichthys, L. maracaibero and L. llanero, from the lago Maracaibo drainage and the rio 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 & Liljestrom (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), Isbrucker & Nijssen (1978a) and Taphorn & Liljestrom (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
and *L. ilanero* 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

Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ).

Formal descriptions are provided only for the new species. Redescriptions of *Lamontichthys filamentosus,* *L. ilanero,* *L. maracaibo,* 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 ventralview 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. Pecaudal 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

---

**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.
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 (DETRAN) 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, Río Preto de Eva, Río Preto de Eva; *Farlowella nattereri*: MZUSP 57658, 1vs. 112.9, Amazonas, rio Madeira; *Harttia*: *H. carvalhoi*: MZUSP 48598, 1vs. 62.6, 5alc, 69.6-76.6, São Paulo, Pindamonhangaba, tributary of Ribeirão Grande; *H. kornei*: MZUSP 62390, 1vs. 59.9, São Paulo, Ribeira, Iporanga, rio Betari; *H. leiopleura*: MZUSP 42701, 2vs. 52.7-58.6, Minas Gerais, Nova Lima, rio das Velhas, tributary of rio Mutuca, paratypes; *H. loricariformis*: MZUSP 66187, 1vs. 67.7, Minas Gerais, Muriá, rio Glória; *H. punctata*: MZUSP 40825, 1vs. 68.0, Tocantins, upper Tocantins, rio Bezerra; MNRJ 12726, 1vs. 59.8, 19 (of 120) alc, Goiás, upper Tocantins, córrego Bateias; *Harttia sp.:* MZUSP 100919, 1vs. 58.8, 2alc, São Paulo, Tietê, Perus, córrego Laranjeiras; *H. torrenticola*: MZUSP 37170, 1vs. 54.4, Minas Gerais, rio das Velhas, tributary of rio Paraopeba, paratype; *Pseudoloricaria punctata*: MZUSP 100921, 1vs. 58.7, 1alc, no locality data; *Loricaria punctata*: MZUSP 23847, 1vs. 124.2, Pará, igarapé Açu, near São Domingos do Capim; *Neoplecostomus ribeirensis*: MZUSP 100920, 1vs. 45.3, 1alc, São Paulo, Ribeira dos Laranjeiras; *Pseudoloricaria punctata*: MZUSP 34542, 1vs. Roraima, rio Branco, Cachoeira do Bom-querer; *Pterosturisoma microps*: MZUSP 79909, 1vs. 75.9, Amazonas, rio Solimões below rio Iça; *Rineloricaria darioha*: MZUSP 23748, 1vs. 91.5, 16alc, Pará, Oriximiná; *Sturisoma sp.:* MZUSP 50112, 1vs. 115.2, Acre, rio Purus. **Colombia:** *Sturisomaticthys leigthoni*: ANSP 84179, 1vs. 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. avacaneo*, 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 darioha* 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 darioha* 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 loricariids: 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 Loricariinae. 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 rio Ucayali, rio Marañon and rio Napo, the upper regions of rio Purus and rio Juruá, rio Madeira and rio Tocantins basins. It also occurs in the middle and upper rio Orinoco basin, and in the lago Maracaibo drainage (Fig. 2).

---

**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. 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.

**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. (lago Maracaibo drainage) ........................................................ \textit{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

Fig. 5. Ventral view of pelvic region of \textit{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) ................................................ \textit{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) ................. \textit{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) ........................................................ \textit{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. 7. Ventral view of distal tip of caudal peduncle of \textit{Lamontichthys parakana} (INPA 3010, 112.7 mm SL, holotype) (a) and \textit{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.

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) ........................................ \textit{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) ........ \textit{L. avacanoeiro}

Fig. 6. Schematic drawing of dorsal view of head of \textit{Lamontichthys llanero} (a) and \textit{L. filamentosus} (b). The “x” indicates interorbital distance and “y” indicates distance from orbit to exposed border of cleithrum.
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, 1 cs*, 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 Trairãs, 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.
(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 into 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 end of head ellipse shaped in dorsal view. Dorsal profile of head posteriorly to caudal-fin base and, anteriorly, to snout tip. Through dorsal-fin origin, gradually more depressed 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 odontodes. 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                                      | *L. avacanoeiro* | *L. filamentosus* |
|-----------------------------------------------|------------------|-------------------|
|                                               | Holotype         |                  |
|                                               | N                | Range            |
| Standard length (mm)                          | 150.5            | 47.6-159.9       |
| Percents of standard length                   |                  |                  |
| Head length                                   | 20.9             | 19.8-25.3        |
| Predorsal length                              | 29.9             | 28.4-33.0        |
| Postanal length                               | 49.9             | 47.7-52.7        |
| Abdominal length                              | 16.9             | 15.2-17.7        |
| Thoracic length                               | 16.9             | 13.7-16.9        |
| Dorsal-fin length                             | 21               | 20.5-26.0        |
| Pectoral-fin length                           | 19.3             | 18.2-22.0        |
| Pelvic-fin length                             | 17.7             | 17.7-20.6        |
| Anal-fin length                               | 17.3             | 16.9-20.3        |
| Body depth at dorsal-fin origin               | 11.8             | 9.3-12.5         |
| Caudal peduncle depth                         | 1.5              | 1.3-1.8          |
| Body width at dorsal-fin origin               | 16.6             | 13.5-16.9        |
| Body width at anal-fin origin                 | 12.9             | 10.2-13.1        |
| Body width at caudal-fin origin               | 2.7              | 2.4-2.9          |
| Percents of head length                       |                  |                  |
| Head width                                    | 97.7             | 85.6-100.9       |
| Interorbital distance                         | 27.3             | 25.4-29.4        |
| Orbital diameter                              | 13.8             | 13.6-16.2        |
| Snout length                                  | 62.2             | 60.6-64.8        |
| Dentary length                                | 20.8             | 18.4-23.4        |
| Lower lip width                               | 14.8             | 13.0-21.2        |
| Meristic data                                 |                  |                  |
| Lateral plates of median series               | 32               | 31-34            |
| Lateral plates of mid-ventral series          | 19               | 14-20            |
| Ventrolateral thoracic plates                 | 7                | 6-9              |
| Premaxillary teeth                            | 96               | 60-100           |
| Dentary teeth                                 | 83               | 50-87            |
| Dorsal-fin rays                               | 41.7             | 11.7             |
| Pectoral-fin rays                             | 1.7              | 1.7              |
| Pelvic-fin rays                               | 1.5              | 1.5              |
| Anal-fin rays                                 | 1.5              | 1.5              |
| Caudal-fin rays                               |                  |                  |

Systematics of *Lamontichthys* with the description of new species.
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. Anterioventral 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 upper lip. Lateral border of head covered with large dorsal plates anteroventrally curved.

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.

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 filamentosus 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].

**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]; Barzanti & Oldani, 1976: 130-137 [incorrect identification; based on four specimens of probably, Loricaria sp., Loricariinae; Argentina, rio Paraná basin - specimens not examined].

**Harttia filamentosa** Miranda-Ribeiro, 1939: 12 [original description of genus; designation of type-species]; Gosline, 1945: 108 [listed]; Isbrücker & Oldani, 1976: 88 [listed]; 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,..
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 sympathy with L. stibaros in the drainages of rio Ucayali and rio 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 rio 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) 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 rio Muyumanu. Brazil: Acaraé: 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, rio Napo. Peru: Amazonas: LACM 41724-9, 10, 120.2-150.8, Marañón, rio Santiago; LACM 41705-9, 11, 130.7-153.3; LACM 41729-29, 13, 128.2-154.1, Marañón, rio Santiago in La Poza; LACM 41741-9, 13, 82.5-169.0, Lacs*, 119.4, LACM 42001-7, 1, 162.8, LACM 41740-13, 1, 167.4, confluence of rio Marañón with rio Nieva; LACM 42005-6, 1, 155.8, Marañón, near Caterpiza; LACM 39884-7, 1, 139.2, Marañón, Galileia, rio 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, rio 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.
Systematics of *Lamontichthys* with the description of new species

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), 117.5-144.0, río Portuguesa, 3 km NE El Barriendo; 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, rio Motatán in el...
Puente Tres de Febrero”; paratypes from rio Motatán and rio Ariguísâ; Taphorn & Liljestrom, 1984b: 17, 29 [key and common name; lago Maracaibo, Venezuela]; Galvis et al., 1997: 88 [description, habits, common names, illustrations, rio 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].

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

| Variable                     | L. llanero | L. maracaibero |
|------------------------------|------------|---------------|
| Standard length (mm)         | N | Range | Mean | SD |
| Head length                  | 37 | 17.4-23.2 | 19.0 | 1.4 |
| Percents of standard length  |   |   |   |   |
| Head length                  | 37 | 82.6-96.9 | 92.4 | 3.1 |
| Interoctal distance          | 37 | 29.4-35.0 | 31.9 | 1.4 |
| Orbital diameter             | 37 | 15.0-19.4 | 17.5 | 1.1 |
| Snout length                 | 37 | 54.8-61.8 | 59.3 | 1.4 |
| Lower lip width              | 37 | 13.6-16.5 | 14.5 | 0.9 |
| Meristic data                |   |   |   |   |
| Lateral plates of median series | 36 | 32.33 | 32.7 | 0.5 |
| Lateral plates of mid-ventral series | 36 | 15.17 | 15.9 | 0.6 |
| Premaxillary teeth           | 34 | 33.75 | 58.2 | 9.8 |
| Dentary teeth                | 32 | 27.60 | 47.3 | 7.4 |
| Dorsal-fin rays              | 37 | II,7 | II,7 | 0.0 |
| Pectoral-fin rays            | 37 | I,1 | I,1 | 0.0 |
| Pelvic-fin rays              | 37 | I,1 | I,1 | 0.0 |
| Anal-fin rays                | 37 | I,1 | I,1 | 0.0 |
| Caudal-fin rays              | 36 | I,1,1,1 | I,1,1 | 0.0 |

**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. avacaneiro, 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. avacaneiro, 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, rio Catatumbo, crío 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, rio 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 Tucurui, 31 Ago 1984,
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. ilanero 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 18th to 19th 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.
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 I,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

---

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 | *L. parakana* | *L. stibaros* |
|----------|---------------|---------------|
| Standard length (mm) | Holotype 112.7  Range 72.2-119.0  Mean 101.3  SD | N 25  Range 27.2-172.8  Mean 73.7  SD |
| 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 | 25  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  0.0 | 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 | 25  24-109  60.9  16.6 |
| Dentary teeth | 64-67  49-67  55.5  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 | 25  i,12,i  i,12,i  0.0 |
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

**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 having more than one lower lip connective to plates on the snout tip. *Lamontichthys stibaros* differs from *L. parakana* in having more than one lower lip connective to plates on the snout tip.

*lamontichthys* differs from all other species of the genus in having more than one lower lip connective to plates on the snout tip.

*Farlowella* and *Pseudoloricaria* possesses an anterointernal (vs. anterointernal) 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).

The presence of 19 to 20 lateral plates along the mid-ventral series (vs. 14 to 18) and the longer denticary (18.6-23.2%, vs. 11.5-17.3% HL) in specimens larger than 70 mm SL.

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 astrolepids 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 a typical feature of the group is the presence of a keel-like prominence on the mesethmoid (Schaefer, 1987: 5). This feature was previously described by Rapp Py-Daniel (1997: character 8).

Character 4:

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

Astrolepids and loricariids are characterized by a bony keel-like prominence on the mesethmoid, which may be covered by plates, is present in all taxa examined except *Farlowella* and *Pseudoloricaria*. This feature is also reported in *Lamontichthys stibaros*. The presence of this keel-like prominence is a diagnostic character of the family Astrolepididae and is used for the identification of the species in this study.
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
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,
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 Loriciaridae 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 Loriciaridae 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 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 Diplomyistidae (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
A. de C. Paixão & M. Toledo-Piza

539

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 loricariids and proposed as autapomorphic for the tribe Loricariini (Boeseman, 1971: 17).

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

---

**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.

**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 Loricariidae 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 Loricariidae 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 Loricariidae 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 loricariids. 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
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.

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 Hypoptopomatininae, 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...
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).

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,
Systematics of *Lamontichthys* with the description of new species

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

Fig. 25. Dorsal view of posterior portion of branchial arches of *Lamontichthys filamentosus* (LACM 41741-9, 119.4 mm SL) (a) and *Sturisoma* (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.

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.

**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. 12c; 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...
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. \textit{Lamontichthys} avacanoeiro, \textit{L.} maracaibero, \textit{L.} stibaros, Farlowella, Harttia, Pterosturisoma, Sturisoma, and Sturisomatichthys have these regions of similar length (Fig. 29), a condition shared with \textit{Hypostomus} and \textit{Neoplecostomus}.

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

\textit{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 \textit{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 \textit{L.} avacanoeiro, \textit{L.} filamentosus, \textit{L.} llanero, \textit{L.} maracaibero, \textit{L.} stibaros, and in the outgroups Farlowella, Harttia, \textit{Hypostomus}, \textit{Neoplecostomus}, Pterosturisoma, Sturisoma, and \textit{Sturisomatichthys} is rectangular shaped, with the length twice to three times longer than its width (Fig. 29). In the derived condition present in \textit{Loricaria, Pseudoloricaria,} and \textit{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 madibular arch, suspensorium, opercle, and interhyal of \textit{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. 30). 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 avancanoiero, 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 laminar 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, Loriciaridae and Astroblepidae, but only members of the Loriciaridae 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 (1992) showed that the presence of 12 to 18 teeth in each jaw as plesiomorphic for the loricariine Loricariidae, Schaefer (1997: 109) considered the first author to propose groupings within the Loricariinae based on variation in the number of jaw teeth. Among the non-loricariine Loriciaridae, 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 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 Loriciarinae based on variation in the number of jaw teeth. Among the non-loricariine Loriciaridae, 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.

---

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.
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 Otothyrini (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 Hypoptopomatinii (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. Therfore, 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.
Systematics of Lamontichthys with the description of new species

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, Haritia, Loricaria, Pseudoloricaria, Pterosturisoma, Rineloricaria, Sturisoma, and Sturisomachtys 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. ilanero, L. maracaibo, L. stibaros, Farlowella, Haritia, Loricaria, Pseudoloricaria, Pterosturisoma, Rineloricaria, Sturisoma, and Sturisomachtys, 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. avacaneiro and L. parakana, there is a plate that lacks a laterosensory canal that is situated between infraorbital 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, Haritia, Pterosturisoma, Sturisoma, and Sturisomachtys 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 Loricariididae 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 (Fig. 38).

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.
of this structure and in Lamontichthys, Farlowella, Harttia, Loricaria, Pseudoloricaria, Rineloricaria, Sturisoma, and Sturisomaticthys, 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
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 (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 pointed and lack any type of contact with the ventral plates (Fig. 39). 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 pointed and lack any type of contact with the ventral plates (Fig. 39). This character does not apply to Hypostomus and Neoplecostomus because these taxa lack ventrally directed bilateral projections.

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.

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.
subfamily Loricariinae and the genera *Acestridium*, *Niobichthys*, and *Oxysops* (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 (Hypoptominae 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...
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).

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-
Systematics of Lamontichthys with the description of new species

556

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 Sturisomatchthys 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 Hypoptopominae 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 Hypoptopominae. 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, Hypostomus, Neoplecostomus, Pterosturisoma, Sturisoma, and Sturisomatchthys, 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 avacaneiro, 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).

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

In the Loricariidae each basipterygium possess a pair of anterior processes, one internal and one lateral (Schaefer, 1987: 19) or anteromesial and anterolateral processes, respectively (Armbuster, 2004: 37). Different types of contact between the anteromesial processes of the basipterygia 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 basipterygium: (0) antero-medial; (1) medial (CI = 100; RI = 100).

Harttia possesses the anteromesial processes of the basipterygium 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 basipterygium: (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 basipterygium 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 basipterygium considerably wider than the ventral.

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

The lateropterygium is a bony structure that is connected with the lateral margin of the basipterygium 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 lateropterygium among loricariids. Due to the difficulty in coding the variation observed in the format of the lateropterygium 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 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 Sturisomatischthys, 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 (Schaefer, 1991: 17). Lundberg & Baskin, 1969: 35; Schaefer, 1987: 17; 1991: 17).

Lamontichthys, Harttia, Pterosturisoma, Sturisoma, and Sturisomatischthys 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 Sturisomatischthys, 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 avacanoero 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. avacanoero, 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 Sturisomatischthys.

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 hyprural plate (Fig. 43b; Schaefer, 1991: 16).

In Lamontichthys filamentosus, L. Ilanero, L. maracaibero, L. stibaros, L. avacanoeiro, Harttia, Hypostomus, Loricaria, Pseudoloricaria, 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 Rhinelepis (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 anterioventral 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 = 60).

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, diminate 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. Ilanero, 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
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 bucal 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* (MNJ 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-
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.

**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 avacaneiro and L. stibaros**

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

**Autapomorphies of Lamontichthys avacaneiro**

Character 10 (1>2): Broad ventral laminar expansion along
Table 4. Character matrix for species of Lamontichthys, representatives of the Loricarinae, 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 |
|-------------------------------|----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Lamontichthys avacanoeiro     | 0001000002 | 1042110100 | 0010000000 | 011201102 | 211001111 | 021010101 | 002011212 | 2311113111 | 12121110 |
| Lamontichthys filamentosus    | 1001010001 | 1042110000 | 1010001000 | 0112010011 | 211001111 | 012010101 | 002101212 | 2311013112 | 12121111 |
| Lamontichthys llanero         | 1001111010 | 1021000100 | 1101010111 | 011201102 | 211001111 | 021010101 | 021011212 | 2311013112 | 12121111 |
| Lamontichthys maracaibero     | 1001010001 | 1042110000 | 0010000010 | 0112010011 | 211001111 | 021010101 | 002101212 | 2311013112 | 12121111 |
| Lamontichthys stibaros        | 0100110011 | 1101010111 | 0112010011 | 211001111 | 021010101 | 021011212 | 2311013112 | 12121111 |
| Farlowella nattereri           | 0112101000 | 1101010111 | 0112010011 | 211001111 | 021010101 | 002101212 | 2311022113 | 11312110 |
| Harttia loricariformis         | 0001000001 | 1200010000 | 0020001010 | 0112010011 | 211201111 | 1210010000 | 021121111 | 2210101100 | 02121110 |
| Harttia punctata               | 0001000001 | 1200010000 | 0202000010 | 0112010011 | 211201111 | 1210010000 | 021121111 | 2210101100 | 02121110 |
| Loricia sp.                   | 0021102010 | 1111100011 | 21331-1-12 | 100210111 | 211001111 | 1220101100 | 1210221112 | 2311013112 | 01311110 |
| Pseudoloricaria punctata       | 0121102010 | 1111200011 | 21331-1-12 | 000210111 | 211001111 | 1220101100 | 1210221112 | 2311013112 | 01311110 |
| Pterosturisoma microps         | 0001101200 | 1011100000 | 0000001111 | 1112010012 | -111011112 | 012011212 | 2311013112 | 00321110 |
| Rinoloricaria sp.             | 0021102010 | 1010000010 | 2133001-212 | 000210111 | 211001111 | 1220101100 | 1210221112 | 2311013112 | 01311110 |
| Sturisoma sp.                 | 0012110100 | 1031100000 | 00000101101 | 0102110011 | 211010111 | 1210101100 | 021012111 | 2311013111 | 11311110 |
| Sturisomatichthys leightoni   | 0002000000 | 1110111000 | 00000001001 | 011012101 | 211001111 | 1210101100 | 021012111 | 2311013111 | 11311110 |
| Hypostomus sp.                | 0001111000 | 0011010000 | 00000001100 | 002010000 | 000-01000 | 2000000000 | 0010001000 | 10001-1000 | 01021000 |
| Neoplecostomus ribeirensis     | 0000000000 | 0000100000 | 00000001100 | 001000000 | 010000000 | 0100000000 | 0100000000 | 0000000000 | 00000000 |

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

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

Character 37 (0>1): Presence of one dermal plate between infraorbitalis 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, Rinelorica, and Sturisoma.

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

**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 Rinelorica 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 occurs in Harttia leitopleura and Rinelorica daraha, but all other species of Harttia and Rinelorica 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 1, 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 loricariines. 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 sympathy with *L. filamentosus* in the drainages of rio Ucayali and rio 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 Tucurui 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.

**Acknowledgements**

A previous version of this work was part of a dissertation submitted by the first author in partial fulfillment of a Master’s degree in Zoology at Instituto de Biociências of Universidade de São Paulo. The latter institution and Museu de Zoologia da Universidade de São Paulo provided work space and access to all facilities. We are indebted to the following individuals and institutions for the loan of specimens, information, and other types of assistance: John G. Lundberg and Mark Sabaj Pérez (ANSP); Jaime Sarmiento (Colección Boliviana de Fauna, La Paz); Flávio Bockmann (FFCLRP/LIRP-USP); Barry Chernoff and Mary Anne Rogers (FMNH); José Ivan Mojica (ICMHN); Larry Page and Mike Retzer (INHS); Lúcia Rapp Py-Daniel, Marcelo Rocha and Maria A. S. Brazil (INPA); Jeff A. Siegel (LACM); Francisco Provenzano (MBUVC); Donald Taphorn (MCNG); Roberto E. Reis and José F. P. Silva (MCP); Wolmar B. Wosiacki and Cristiano Trinca (MPEG); Paulo A. Buckup, Marcelo R. Britto, Arion T. Aranda (MNRJ); Osvaldo T. Oyakawa, José L. de Figueiredo, and Vivian Oliveira (MZUSP); Richard Winterbottom (ROM); Érica Caramaschi and Renata Bartolette (UFRJ); and Richard P. Vari (USNM). Eduardo Baena prepared photographs of figures 8, 10, 11 and 13. Carlos Magenta provided help with image editing. The maps of South America are based on a map prepared by Marilyn Weitzman. Flávio C. T. Lima and Alexandre Ribeiro kindly provided access to an unpublished version of a manuscript on the biogeography of South American freshwater fishes. For helpful discussions and suggestions on many topics related to the present study we thank Flávio C. T. Lima, Marcelo R. Britto, Mario de Pinna, and especially, Osvaldo T. Oyakawa. This manuscript greatly benefited from the suggestions of Lúcia Rapp Py-Daniel and an anonymous
reviewer. Financial support for this project was provided by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 02/01341-1), PRONEX - FINEP/CNPq (661058/1997-2), and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

**Literature Cited**

Alexander, R. M. 1965. Structure and function in the catfishes. Journal of Zoology, 148: 88-152.

Amorim, D. S. 2002. Elementos básicos de sistemática filogenética. São Paulo, Sociedade Brasileira de Entomologia, 154p.

Armbruster, J. W. 1998. Modifications of the digestive tract for holding air in loricariid and scoloploid catfishes. Copeia, 1998(3): 663-675.

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

Arratia, G. 1987. Development and diversity of the suspensorium of the trichomycterids and comparison with loricarioids (Teleostei: Siluriformes). Journal of Morphology, 205: 193-218.

Arratia, G. & L. Huaquin. 2005. Morphology of the lateral line system and of the skin of diplomyistid and certain primitive loricariid catfishes and systematic and ecological considerations. Bonner Zoologische Monographien, 36: 5-109.

Baensch, H. A. & R. Riehl. 1997. Aquarium Atlas, Band. 5. Germany, 3222: 1-19.

Bailey, R. M. & J. N. Baskin. 1976. Scolopax dicra, a new armored catfish from the Bolivian Amazon. Occasional Paper of the Museum of Zoology of the University of Michigan, 674: 1-14.

Barriga, R. 1991. Peces de agua dulce (Ecuador). Politiêcnica - Biologia 3, 14(3): 7-88.

Barzanti, J. M. & N. O. Oldani. 1976. *Lamontichthys filamentosus* (LaMonte, 1935) (Pisces, Loricariidae). Una nueva cita para la fauna de peces de la República Argentina. Physis B, 35(91): 131-137.

Begossi, A., R. A. M. Silvano & O. T. Oyakawa. 1999. Use of local resources by fishers and hunters in an extractive reserve (upper Juruá, Acre, Brazil). Environmental, Development and Sustainability, 1: 73-93.

Boeseman, M. 1971. The “comb-toothed” Loricariinae of Surinam, with reflections on the phylogenetic tendencies within the family Loricariidae (Siluriformes, Siluroidae). Zoologische Verhandelingen, 116: 1-56.

Boeseman, M. 1976. A short review of the Surinam Loricariinae; with additional information on Surinam Harttiinae, including the description of the new species (Loricariidae, Siluriformes). Zoologische Mededelingen, 50(11): 153-177.

Bonaparte, C. L. J. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Giornale Arcadico di Scienze, 49: 1-77.

Buckup, P. A. N. A. Menezes & M. S. Ghazzi. 2007. Catálogo das espécies de peixes de água doce do Brasil. Rio de Janeiro, Museu Nacional, Série Livros 23, 195p.

Burgess, W. E. 1989. An atlas of freshwater and marine catfishes. A preliminary survey of the Siluriformes. New Jersey, T.F.H. Publications, 784p.

Chardon, M. 1968. Anatomie comparée de l’appareil de Weber et des structures connexes chez les Siluriformes. Musée Royal de l’Afrique Centrale, Annales, Série 8, Sciences Zoologiques, n.169, 277p.

Chernoff, B., P. W. Willink, J. Sarmento, S. Barrera, A. Machado-Allison, N. Menezes & H. Ortega. 1999a. Fishes of the rios Tahuamanu, Manuripi and Nareuda, Depto. Pando, Bolivia: Diversity, distribution, critical habitats and economic value. Pp. 39-46. In: Chernoff, B. & W. Willink (Eds.). A Biological Assessment of the Aquatic Ecosystems of the Upper río Orthon Basin, Pando, Bolivia. Bulletin of Biological Assessment 15, 145p.

Chernoff, B., P. W. Willink, J. Sarmento, S. Barrera, A. Machado-Allison, N. Menezes & H. Ortega. 1999b. Geographic and macrohabitat partitioning of fishes in the Tahuamanu-Manuripi region, upper río Orthon basin, Bolivia. Pp. 51-67. In: Chernoff, B. & W. Willink (Eds.). A biological assessment of the aquatic ecosystems of the upper río Orthon basin, Pando, Bolivia. Bulletin of Biological Assessment 15, 145p.

Conci, C. & M. Michelangelo. 1974. Catalogo dei tipi del Museo Civico di Storia Naturale di Milano. I. I tipi dei pesci, con note storiche sulla collezione ittologica. Atti della Società italiana di Scienze naturali e del Museo Civico di Storia naturale di Milano, 115(3-4): 213-237.

Covain, R. & S. Fisch-Muller. 2007. The genera of the Neotropical armored catfish subfamily Loricariinae (Siluriformes: Loricariidae): a practical key and synopsis. Zootaxa, 1462: 1-40.

Cunha, M. C. & M. B. Almeida. 2002. Enciclopédia da Floresta: o Alto Juruá: práticas e conhecimentos das populações. São Paulo, Companhia das Letras, 735p.

Eigenmann, C. H. & W. R. Allen. 1942. Fishes of western South American. Lexington, University of Kentucky, 494p.

Eigenmann, C. H. & R. S. Eigenmann. 1890. A revision of the South American Nematognathi or cat-fishes. Occasional Papers California Academy of Sciences, 1: 1-508.

Eschmeyer, W. N. 1998. Catalog of Fishes. Center for Biodiversity Research and Information, Spec. Publ. 1. California Academy of Sciences, 1: 1-2905.

Ferraris C. J., Jr. 2003. Loricariidae: Loricariinae. Pp. 330-350. In: Reis, R. E., S. O. Kullander & C. J. Ferraris Jr. (Eds.). Check list of the freshwater Fishes of South and Central America. Porto Alegre, Edipucrs, 729p.

Ferraris, C. J., Jr. 2007. Checklist of catfishes, recent and fossil (Osteichthyes, Siluriformes), and catalogue of siluriform primary types. Zootaxa, 1418: 1-628.

Ferraris, C. J., Jr. & R. Vari. 1992. Catalog of type specimens of recent fishes in the National Museum of Natural History, Smithsonian Institution, 4: Gonorynchiformes, Gymnotiformes, and Siluriformes (Teleostei: Ostariophysi). Smithsonian Contributions to Zoology, 535: 1-52.

Fink, S. V. & W. L. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei). Zoological Journal of the Linnean Society, 72: 297-353.

Fowler, H. W. 1945. Los peces del Peru. Boletim Museo Historia Natural Javier Prado, 8: 1-298.

Galvis, G. J. I. Mojica & M. Camargo. 1997. Peces del Catatumbo. Bogotá, Asociación Cravo Norte, 118p.

Garavello, J. C., H. A. Britski & S. A. Schaefer. 1998. Systematics of the genus *Otolithys* Myers 1927, with comments on geographic distribution (Siluriformes: Loricariidae: Hypoptopomatinae). American Museum Novitates, 3222: 1-19.
Rapp Py-Daniel, L. H. & I. Fichberg. 2008. A new species of *Rineloricaria* (Siluriformes: Loricariidae: Loricariinae) from rio Daraá, rio Negro basin, Amazon, Brazil. Neotropical Ichthyology, 6(3): 339-346.

Reed, H. D. 1924. The morphology and growth of the spines of siluroid fishes. Journal of Morphology, 38: 431-451.

Reis, R. E. 1998. Anatomy and phylogenetic analysis of the Neotropical callichthyid catfishes (Ostariophysi, Siluriformes). Zoological Journal of the Linnean Society, 124: 105-168.

Reis, R. E. 1998. Systematics, biogeography, and the fossil record of the Callichthyidae: a review of the available data. Pp. 351-362. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. Lucena & C. A. S. Lucena (Eds.). Phylogeny and classification of Neotropical fishes. Porto Alegre, Edipucrs, 603p.

Reis, R. E. & E. H. L. Pereira. 2000. Three new species of the loricarid catfish genus *Loricarichthys* (Teleostei: Siluriformes) from southern South America. Copeia, 2000(4): 1029-1047.

Reis, R. E., E. H. L. Pereira & J. W. Armbruster. 2006. Delturinae, a new loricarid catfish family (Teleostei, Siluriformes), with revisions of *Delturus* and *Hemipsilichthys*. Zoological Journal of the Linnean Society, 147: 277-299.

Sarmiento, J., B. Chernoff, S. Barrera, A. Machado-Allison, N. A. Menezes & H. Ortega. 1999. Fishes collected during the AquaRAP expedition to Pando, Bolivia in September 1996. Appendix 6. Pp. 87-95. In: Chernoff, B. & W. Willink (Eds.). A Biological Assessment of the Aquatic Ecosystems of the Upper rio Orthon Basin, Pando, Bolivia. Bulletin of Biological Assessment 15, 145p.

Schaefer, S. A. 1987. Osteology of *Hyphostomus plecostomus* (Linnaeus) with a phylogenetic analysis of the Loricariid subfamilies (Pisces: Siluroidei). Contributions to Science, 394: 1-31.

Schaefer, S. A. 1990. Anatomy and relationships of the scolopacid catfishes. Proceedings of the Academy of Natural Sciences of Philadelphia, 142: 167-210.

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

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

Schaefer, S. A. 1998. Conflicts and resolution: impact of the new taxa on phylogenetic studies of the Neotropical casucudinhos (Siluriformes: Loricariidae). Pp. 375-400. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. Lucena & C. A. S. Lucena (Eds.). Phylogeny and classification of Neotropical fishes. Porto Alegre, Edipucrs, 603p.

Schaefer, S. A. & F. Provenzano R. 1998. *Niobichthys ferrarisi*, a new genus and species of armored catfish from southern Venezuela (Siluriformes: Loricariidae). Ichthyological Exploration of Freshwaters, 8(3): 221-230.

Schaefer, S. A. & G. V. Lauder. 1986. Historical transformation of functional design: evolutionary morphology of feeding mechanisms in loricarioid catfishes. Systematic Zoology, 35(4): 489-508.

Shelden, F. F. 1937. Osteology, myology and probable evolution of the nematognath pelvic girdle. Annals of New York Academy of Sciences, 37: 1-96.

Silvano, R., O. T. Oyakawa, B. Amaral & A. Begossi. 2001. Peixes do Alto rio Juruá (Amazonas, Brasil). São Paulo, Editora da Universidade de São Paulo, 298p.

Slowinski, J. B. 1993. “Unordered” versus “ordered” characters. Systematic Biology, 42: 155-165.

Sullivan, J. P., J. G. Lundberg & M. Hardman. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag 1* and *rag 2* nuclear gene sequences. Molecular Phylogenetics and Evolution, 41: 636-662.

Swofford, D. L., G. J. Olsen, P. J. Waddell & D. M. Hillis. 1996. Phylogenetic inference. Pp. 407-514. In: Hillis, D. M., C. Moritz & B. K. Mable (Eds.). Molecular Systematics. 2nd ed. Sunderland, Sinauer Associates.

Taphorn, D. C. & C. G. Liljestrom. 1984a. *Rhinodoras thomersoni*: un bagre sierra, nuevo em Venezuela (Pisces, Doradidae). Revista UNELLEZ de Ciencia e Tecnologia, 2(2): 87-92.

Taphorn, D. C. & C. G. Liljestrom. 1984b. *Lamantichthys maracaibero y L. llanero*, dos especies nuevas para Venezuela (Pisces, Loricariidae). Revista UNELLEZ de Ciencia e Tecnologia, 2(2): 93-100.

Taylor, W. R. & G. C. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium, 9(2): 107-119.

Tovar Serpa, A. 1967. Peces del oriente peruano. Algunas especies de Loricariidae con referencia especial de la “carachama” *Pterygoplichthys multiradiatus* (Hancock), ecología y utilidad. Biota, 6(50): 201-255.

Varjo, M. L., L. Koli & H. Dahlström. 2004. Kalamimiluettelo (versio 10/03). Suomen Biologian Seura Vanamo Ry.

Wiley, E. O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. New York, John Wiley & Sons, 439p.

Wiley, E. O., D. Siegel-Causey, D. R. Brooks & V. A. Funk. 1991. The Complete Cladist: A Primer of Phylogenetic Procedures. Lawrence, University Kansas Printing Service, 158p.

Accepted September 22, 2009
Published December 18, 2009