



## The genera of the Neotropical armored catfish subfamily Loricariinae (Siluriformes: Loricariidae): a practical key and synopsis

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### Abstract

The subfamily Loricariinae belongs to the Neotropical mailed catfish family Loricariidae. Members of Loricariinae are recognized by their long and flattened caudal peduncle and absence of an adipose fin. Despite important studies conducted on this group, no comprehensive generic key is presently available. A Hill & Smith (1976) analysis and cluster analysis were performed on external morphological characters taken from specimens or borrowed from the literature. The two main groups recognized correspond to the tribes Harttiini and Loricariini. Within the Loricariini, four morphological groups were found: the *Rineloricaria* group, the *Loricariichthys* group, the *Loricaria* group, and the *Pseudohemiodon* group. Results of these analyses were used to construct a practical key to thirty genera, followed by a synopsis for each genus.

**Key words:** Loricariinae, genus, morphology, multivariate analyses, identification key

### Introduction

The Neotropics contain one of the most diverse freshwater ichthyofaunas in the world with around 6,000 of the 13,000 known species (Reis *et al.* 2003). In Central and South America, the Ostariophysi are undoubtedly the largest represented group and among them, the Siluriformes exhibit the greatest diversity with around 1,647 described species (Reis *et al.* 2003) distributed in 16 families, one of which was discovered and described only recently (Rodiles-Hernández *et al.* 2005). Among the Siluriformes, the Loricariidae, or armored catfish, is the most speciose family in the world comprising 673 valid species and around 300 recognized as undescribed (Reis *et al.* 2003). Loricariids are characterized by a depressed body covered by bony

plates, a unique pair of maxillary barbels, and above all, by an important modification of the mouth structure into a sucker disk. This structural transformation enables these fishes to adhere to the substrate, even in particularly fast flowing waters. The mouth and teeth show strong adaptations to feeding by scraping submerged substrates to eat algae, small invertebrates, detritus, and even wood. Loricariids have undergone an evolutionary radiation on a subcontinental scale, from Costa Rica to Argentina, both on the Pacific and Atlantic slopes of the Andes. They have colonized nearly all freshwater habitats from the torrential waters flowing from the Andes to quiet brackish waters of the estuaries, black and acidic waters of the Guiana Shield, and subterranean systems. Schaefer & Stewart (1993) compare this radiation to that of the Cichlidae of the Great Lakes of the Rift Valley in Africa. Extremely variable color patterns and body shapes among loricariid taxa reflect their high degree of ecological specialization. Because of their highly specialized morphology loricariids have been recognized as a monophyletic assemblage in the earliest classifications of the Siluriformes (de Pinna 1998). The family comprises five or six subfamilies, depending on different authors' classifications. Isbrücker (1980), and Ferraris in Reis *et al.* (2003) divide Loricariidae into six subfamilies, the Ancistrinae, the Hypoptopomatinae, the Hypostominae, the Lithogeneinae, the Loricariinae, and the Neoplecostominae. Armbruster (2004) recognized five subfamilies placing Ancistrinae as a tribe within Hypostominae, even though this statement does not resolve paraphylies highlighted by Montoya-Burgos *et al.* (1998) within both subfamilies. Reis *et al.* (2006) followed Armbruster's (2004) classification, and described the new subfamily Delturinae according to the phylogenetic results of Montoya-Burgos *et al.* (1998), and Armbruster (2004).

Members of the subfamily Loricariinae are characterized by a long and depressed caudal peduncle and by the absence of an adipose fin. They also show dramatic variation in body shape, lip morphology and dentition. The sexual dimorphism is often pronounced and is expressed through the hypertrophy of odontodes on the pectoral-fin rays, on the snout margin, and sometimes on the predorsal area of mature males. Certain genera also show sexual differences in lip and tooth structures.

Isbrücker (1979) listed twenty-seven genera of Loricariinae, described eight as new, and classified them into four tribes and eight subtribes on the basis of morphology, without phylogenetic inferences. These include the Loricariini, including six subtribes (Loricariina, Planiloricariina, Reganellina, Rineloricariina, Loricariichthyina and Hemiodontichthyina), the Harttiini, including two subtribes (Harttiina and Metaloricariina), the Farlowellini, and the Acestridiini. The same author (1981a: p. VI, 71) voiced doubts concerning the placement of Acestridiini among Loricariinae, noting that: "The exposed cleithrum and coracoid, together with the peculiar odontodes on the unbranched pelvic fin ray ('spine') are characters otherwise occurring typically only in various members of the subfamily Hypoptopomatinae."; nevertheless, he maintained them as members of Loricariinae. In the same work he also described two new subtribes, Ricolina and Pseudoloricariina, developed the main characteristics of each rank: subfamily, tribe, subtribe, and genera, and provided a provisional key to the genera of Loricariidae. Rapp Py-Daniel (1981) described a new genus, *Furcodontichthys*, and placed it in the Loricariini, subtribe Loricariina. Martín Salazar *et al.* (1982) described *Dentectus* as a representative of the tribe Loricariini, subtribe Planiloricariina. In this paper, he completed the diagnosis of Planiloricariina, in which he transferred the genera *Rhadinoloricaria*, *Crossoloricaria*, and *Pseudohemiodon*. Isbrücker *et al.* (1983) described *Aposturisoma* as a representative of the Farlowellini. Isbrücker & Nijssen (1984, 1986a) described *Pyxiloricaria* and *Apistoloricaria*, respectively, and placed them in the Loricariini, subtribe Planiloricariina. Using phylogenetic methods, Schaefer (1986, 1987) established the monophyly of the Loricariinae on the basis of morphological data. Finally, Nijssen & Isbrücker (1987) suggested, referring to a Ferraris personal communication, that the Acestridiini were representatives of the subfamily Hypoptopomatinae. Schaefer (1991) confirmed this status and diagnosed the tribe Hypoptopomatini including, among others, the Acestridiini. Rapp Py-Daniel (1997) proposed a phylogeny of the Loricariinae based on a phylogenetic analysis of morphological characters. She confirmed the monophyly of the subfamily, and of two of the three remaining tribes *sensu* Isbrücker (1979), Harttiini and Loricariini; members of Farlowellini were placed within Harttiini. Montoya-Burgos *et al.* (1998) proposed the first molecular phylogeny of the

family Loricariidae with emphasis on the subfamily Hypostominae. Although, their analysis included only nine representatives of the subfamily Loricariinae, they partially confirmed their subdivision into two main groups, with *Farlowella*, a representative of the Farlowellini, being the sister genus of *Sturisoma*, a representative of the Harttiini, and *Harttia* located at the base of the subfamily. Outside of *Harttia*, the two main groups supported were *Farlowella* and *Sturisoma* sister group of the remaining six genera corresponding to Loricariini. Isbrücker and Isbrücker & Michels (in Isbrücker *et al.* 2001) described four new genera: *Fonchiiichthys*, *Leliella*, *Quiritixys* and *Proloricaria*, and revalidated the genus *Hemiloricaria* Bleeker, 1862 on the basis of a very restricted number of characters of questionable validity because they focus mainly on sexual dimorphism. Rapp Py-Daniel & Oliveira (2001) put *Cteniloricaria* in the synonymy of *Harttia*. Ferraris (2003) maintained the validity of *Cteniloricaria*, put in synonymy all the genera described by Isbrücker and Isbrücker & Michels (in Isbrücker *et al.* 2001) and listed 197 species of Loricariinae distributed in 31 genera: *Apistoloricaria* (4 species), *Aposturisoma* (1 species), *Brochiloricaria* (2 species), *Crossoloricaria* (5 species), *Cteniloricaria* (3 species), *Dasylicaria* (5 species), *Dentectus* (1 species), *Farlowella* (25 species), *Furcodontichthys* (1 species), *Harttia* (18 species), *Harttiella* (1 species), *Hemiodontichthys* (1 species), *Ixinandria* (2 species), *Lamontichthys* (4 species), *Limatulichthys* (1 species), *Loricaria* (11 species), *Loricariichthys* (17 species), *Metaloricaria* (2 species), *Paraloricaria* (3 species), *Planiloricaria* (1 species), *Pseudohemiodon* (7 species), *Pseudoloricaria* (1 species), *Pterosturisoma* (1 species), *Pyxiloricaria* (1 species), *Reganella* (1 species), *Rhadinoloricaria* (1 species), *Ricola* (1 species), *Rineloricaria* (47 species), *Spatuloricaria* (11 species), *Sturisoma* (14 species), and *Sturisomatichthys* (4 species). Among all these genera, 13 are monotypic and very few of the most speciose have been revised. *Loricaria* was revised by Isbrücker (1981b), *Metaloricaria* by Isbrücker & Nijssen (1982), *Apistoloricaria* by Nijssen & Isbrücker (1988), and *Farlowella* by Retzer & Page (1997).

In light of all these works, which are sometimes contradictory, a taxonomic synthesis of Loricariinae is needed to provide a foundation for more detailed studies of its members. Furthermore, despite the large number of studies conducted on this group, a complete key to the genera of the subfamily Loricariinae is presently unavailable; partial keys are available in Isbrücker & Nijssen (1974a; 1986b), Isbrücker (1981b), Rapp Py-Daniel (1981), and Burgess (1989). To rectify this situation, a key to all the genera of the subfamily is proposed herein on the basis of external morphological data, and a synopsis is given for each genus. Multivariate and hierarchical analyses were conducted to classify and organize the information used to construct the key. Our study follows the classification of Ferraris (2003), except for maintaining *Cteniloricaria* in synonymy with *Harttia* (Rapp Py-Daniel & Oliveira 2001). As a result, we recognize herein 30 genera of Loricariinae.

## Material and methods

**Examined material.** A total of 1691 specimens, representing about 115 species in 26 of the 30 genera were examined. All material examined was deposited in the Museum of Natural History, Geneva (MHNG). Data were taken from publications of original descriptions of the four genera unavailable from MHNG. After evaluating for the homogeneity of the different genera and species samples, that is to say to verify that all the specimens of each batch share the same features, and that all these features were in agreement with those of the literature, a part of this material was used in multivariate analyses. The abbreviations of the institutions follow Leviton *et al.* (1985).

**Analyzed material.** Data of a single specimen representing each genus were subjected to multivariate analyses. The selected specimens exhibited all the characteristics of their respective genera given in the literature. Data extracted from the literature were those from the holotype of the type species. Material included in the analyses is as follows: *Aposturisoma*: *A. myriodon*:—MHNG 2087.1–2, 153.9 mm of SL, paratype, Peru, Ucayali Department, Province Coronel Portillo, Rio Aguaytia drainage, Rio Huacamayo (09°00'S, 75°29'W),

near the road from Pucallpa to Tingo Maria, around 8 km N.W. from the village of Aguaytia, de Rham *et al.*, 24 August 1981. **Brochiloricaria**: *B. macrodon*:—MHNG 2583.93, 305.4 mm of SL, Paraguay, Rio Pirapo, Caazapa, zoological expedition of the Museum of Geneva, camp 7, 28–31 March 1985. **Crossoloricaria**: *C. rhami*:—MHNG 2108.16, 69.8 mm of SL, paratype, Peru, Ucayali Department, Province Coronel Portillo, Rio Aguaytia drainage, Rio Huacamayo (09°00'S, 75°29'W), near the road from Pucallpa to Tingo Maria, around 8 km N.W. from the village of Aguaytia, de Rham *et al.*, 18 September 1981. **Dasylicaria**: *D. cf. filamentosa*:—MHNG 2674.052, 275.8 mm of SL, Panama, Panama Department, Rio Ipeti, de Rham, 11 March 2000. **Farlowella**: *F. platoryncha*:—MHNG 2588.93 (72), 185.3 mm of SL, Peru, Ucayali Department, Yarinacocha, Isla del Amor in the vicinity of Pucallpa, de Rham *et al.*, 29 May 1996. **Harttia**: *H. guianensis*:—MHNG 2621.97, 167.0 mm of SL, French Guiana, Approuague drainage, saut Mapaou, Weber *et al.*, 5 November 2001. **Hartiella**: *H. crassicauda*:—MHNG 2674.051 (MUS 221), 39.4 mm of SL, Suriname, Nassau mountains, Ijskreek, Mol, 2 November 2005. **Hemiodontichthys**: *H. acipenserinus*:—MHNG 2550.28, 129.8 mm of SL, Brazil, State of Pará, Rio Guamá at 12 km below Ourem, Stawikowski, 24 September 1990. **Ixinandria**: *I. montebelloi*:—MHNG 2676.31, 59.1 mm of SL, Bolivia, Province Tarija at Narvaez, Vaucher, 9 November 1993. **Lamontichthys**: *L. filamentosus*:—MHNG 2639.30, 127.8 mm of SL, Peru, aquarist import, donation Goldblatt, 29 October 2002. **Limatulichthys**: *L. griseus*:—MHNG 2090.25, Peru, Ucayali Department, Rio Neshuya at 60 km S.W. of Pucallpa, de Rham *et al.*, 21 August 1981. **Loricaria**: *L. sp.*:—MHNG 2583.85, 171.1 mm of SL, Paraguay, Rio Pirapo, Caazapa at 3 km E. of Yegros, zoological expedition of the Museum of Geneva, 28–31 March 1985. **Loricariichthys**: *L. platymetopon*:—MHNG 2583.100, 185.6 mm of SL, Paraguay, Arroyo Passo Ybucu at 35 km S.E. of Paraguari, zoological expedition of the Museum of Geneva, 24–26 March 1985. **Metaloricaria**: *M. paucidens*:—MHNG 2676.09, 220.8 mm of SL, French Guiana, Maroni drainage, Marouini River, surroundings of Antecume Pata, fishermen donation, 19 October 2000. **Paraloricaria**: *P. agastor*:—MHNG 2407.81, 279.2 mm of SL, Paraguay, Rio Alto Paraná, facing Cardelaria, Dlouhy, 25 September 1986. **Planiloricaria**: *P. cryptodon*:—MHNG 2625.86, 147.7 mm of SL, Peru, Loreto, Rio Amazonas, Mayoras, de Rham, 26 February 1998. **Pseudohemiodon**: *P. laticeps*:—MHNG 2584.58, 216.7 mm of SL, Paraguay, Rio Pirapo, Caazapa at 3 km E. of Yegros, zoological expedition of the Museum of Geneva, 31 March 1985. **Pseudoloricaria**: *P. laeviuscula*:—MHNG 2538.78, 205 mm of SL, Brazil, State of Pará, Rio Tapajos, temporary pond between Vila Nova and Urua, Stawikowski *et al.*, 26–28 September 1992. **Pterosturisoma**: *P. microps*:—MHNG 2574.13, 127.3 mm of SL, Peru, Rio Nanay, Caazapa, Bleher, 1993. **Reganella**: *R. depressa*:—MHNG 2676.05 (732068), 162.8 mm of SL, Brazil, Pará, Rio Trombetas, Lago Batata, Porto Trombetas locality, Oriximiná municipality (1° 25' to 1° 35' S, 56° 15' to 56° 25' W), D. A. Halboth, November 1991. **Rhadinoloricaria**: *R. macromystax*:—MHNG 2551.45, 2/5, (CMK 7514), 65.3 mm of SL, Brazil, Rio Tocantins facing São Felix, Stawikowski, 17 September 1990. **Ricola**: *R. macrops*:—MHNG PY 100025, 262.8 mm of SL, Paraguay, Rio Paraguay at Ita Enramada, Dlouhy, 24 July 1984. **Rineloricaria**: *R. steindachneri*:—MHNG 2583.65, 132.1 mm of SL, Brazil, Rio Paraiba do Sul W. of Sapucaia, Mazzoni *et al.*, 10 December 1990. **Spatuloricaria**: *S. sp.*:—MHNG 2676.10, 197.8 mm of SL, Brazil, Rio Tocantins, Serra da Mesa, Caramaschi *et al.*, October 1996. **Sturisoma**: *S. robustum*:—MHNG 2584.74, 244.5 mm of SL, Paraguay, Rio Pirapo, Caazapa at 3 km E. of Yegros, zoological expedition of the Museum of Geneva, 28 March 1985. **Sturisomatichthys**: *S. citurensis*:—MHNG 2676.04, 152.3 mm of SL, Panama, Darien, Rio Chucunaque near the village La Alba, de Rham, 13 March 1997.

The data extracted from the literature are: **Apistoloricaria** (in Isbrücker & Nijssen 1986a): *A. condei*:—FMNH 94683, 126.2 mm of SL, holotype, Ecuador, Province Napo, Rio Napo drainage, mouth of Rio Tiputini in the Rio Napo at the confluence of the main tributary, in deep water (00° 48.9' S, 75° 32.5' W), Stewart *et al.*, 28 October 1981. **Dentectus** (in Martín Salazar, Isbrücker & Nijssen 1982): *D. barbarmatus*:—MBUCV-v-12780, 136.5 mm of SL, holotype, Venezuela, State of Cojedes, Rio Salinas, tributary of the Rio Pao Viejo N.E. of El Baul (9° 13'N, 68° 07' W), Fernandez Yépez, 25 February 1950. **Furcodontichthys** (in Rapp Py-Daniel 1981): *F. novaesi*:—INPA T. 79-014, 102 mm of SL, holotype, Brazil, State of Amazonas,

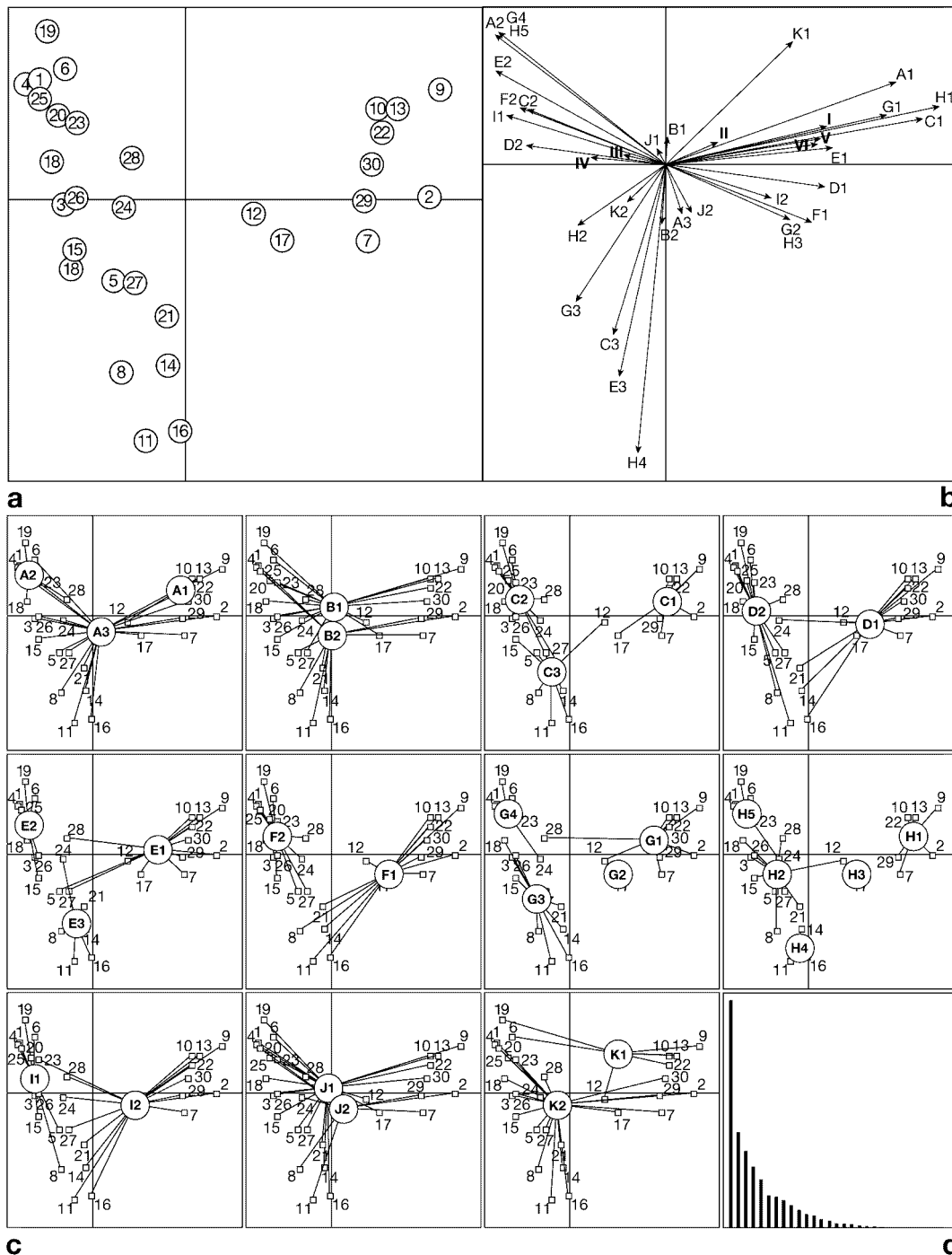
Rio Solimões, Lake Téfé at Caititu, Best *et al.*, 25 May 1979. *Pyxiloricaria* (in Isbrücker & Nijssen 1984): *P. menezesi*:—MZUSP 26800, 136 mm of SL, holotype, Brazil, State of Mato Grosso do Sul, in ponds located along the road Transpantaneira, at Miranda, Garavello *et al.*, 8–22 November 1981.

**Data analyses.** Six discrete quantitative variables, representing fin-ray and tooth counts, and eleven qualitative variables totalizing thirty character states, mainly representing the characteristics of abdominal cover, lips and dentition, were recorded from each specimen (for details, see Table 1). These variables were selected from the literature and on the basis of their diagnostic value at the genus level following examination of a large number of specimens. Data were first subjected to a Hill & Smith analysis (1976) which allows the mixing of quantitative and qualitative data in the same analysis. Quantitative data were first subjected to a Principal Components Analysis (PCA) using a correlation matrix. The normed PCA proceeds initially to the centering and reduction of the data (null mean and unitary variance) that permit the comparison of data expressed in different units. Invariable data such as the number of rays in the anal fin ( $n = i-4$ ) were excluded to allow this transformation. The weighting of the rows (individuals) is uniform (1/30) whereas that of the columns (variables) is unitary (1). A Multiple Correspondence Analysis (MCA) was used to analyse qualitative data. Each variable of the qualitative data set comprises a certain number of character states. Before the execution of the analysis, this first table was converted into a full disjunctive table where each column represents a character state. The sum of the weighting of the character states (frequencies) for each variable equals 1 and the weighting of each variable is uniform (1/11) in the analysis. The weighting of the rows is also uniform (1/30). In the Hill & Smith analysis, the two types of data are made compatible by reweighting the columns. A new statistical triplet [data table X with 30 rows and 36 columns, table Q containing row weights (30 rows and 1 column), and table D containing column weights (36 rows and 1 column)] was created by coupling the two tables of the two initial analyses. Uniform weighting of the rows in the two separate analyses (1/30) is maintained while one of the columns is modified. Weighting of the quantitative and qualitative variables becomes uniform, with each assigned a weight of 1 across the total number of variables (1/17). This gives the same value to each variable in the analysis, even though qualitative variables possess several character states (sum of frequencies of the different character states for each qualitative variable equals 1). Thus, PCA looks for axes that maximize square of correlations of the quantitative variables, MCA looks for axes that maximize the sum of ratios of correlations between modalities (character states) of the qualitative variables, and Hill & Smith analysis establishes a compromise between these two analyses by looking for axes that maximize the mean between the square of correlations (quantitative variables) and the ratios of correlations (qualitative variables). Secondly, this new statistical triplet was converted into a morphological distances matrix calculated from the coordinates of the individuals (rows) projected onto the factorial axes. This transformation allows a hierarchical sorting of the information represented in a dendrogram. Euclidian distances were measured and analyzed using the Unweighted Pair-Group Method using Arithmetic Averages algorithm (UPGMA) (Sneath & Sokal 1973). This analysis was used to classify the different genera based on morphological similarity calculated from shared characters and combination of characters. These analyses were conducted using the ADE-4 software (Thioulouse *et al.* 2001).

## Results

Morphological data used in the analyses are given in Table 1. The Hill & Smith analysis revealed structuring of the data on the two first axes (Fig. 1c) that explained 52% of the total inertia of the scatter. The projection of the individuals onto the two first factorial axes (Fig. 1a) showed a partition of the 30 genera into two groups along the first axis. These two groups corresponded to the two tribes, Loricariini and Harttiini, the former comprising *Planiloricaria*, *Dentectus*, *Crossoloricaria*, *Apistoloricaria*, *Rhadinoloricaria*, *Pseudohemiodon*, *Pyxiloricaria*, *Spatuloricaria*, *Paraloricaria*, *Ricola*, *Brochiloricaria*, *Reganella*, *Loricaria*, *Dasylicaria*,

*Rineloricaria*, *Pseudoloricaria*, *Limatulichthys*, *Furcodontichthys*, *Loricariichthys*, and *Hemiodontichthys*, and the latter comprising *Harttia*, *Harttiella*, *Lamontichthys*, *Pterosturisoma*, *Sturisomatichthys*, *Aposturisoma*, and *Sturisoma*. *Metaloricaria* and *Ixinandria* appeared intermediate between these two groups. The second axis organized the genera at an infra-tribal level according to their morphological resemblance. For example, *Planiloricaria*, *Dentectus*, *Crossoloricaria*, *Apistoloricaria*, *Rhadinoloricaria*, *Pseudohemiodon*, and *Pyxiloricaria* appeared morphologically more closely related to each other than to *Pseudoloricaria*, *Limatulichthys*, *Furcodontichthys*, *Loricariichthys*, and *Hemiodontichthys*. The projection onto the first factorial plane of the variables (Fig. 1b) defined the primary morphological tendencies of each tribe along the first axis. The Harttiini were characterized by numerous and pedunculated teeth, a caudal fin with more branched rays, the absence of postorbital notches and predorsal keels, a rounded mouth, papillose lips weakly or not fringed, and short maxillary barbels. The Loricariini were characterized by a more important variation in lips and teeth shape, the frequent presence of postorbital notches and predorsal keels, longer maxillary barbels, and less numerous teeth and branched rays in the caudal fin. The second axis defined morphological groups in each tribe mainly on the basis of dentition and lip structure. Among the Loricariini, *Planiloricaria*, *Dentectus*, *Crossoloricaria*, *Apistoloricaria*, *Rhadinoloricaria*, *Pseudohemiodon*, and *Pyxiloricaria* shared filamentous lips, a trapezoidal mouth opening, and teeth often spoon-shaped and smaller. *Pseudoloricaria*, *Limatulichthys*, *Furcodontichthys*, *Loricariichthys*, and *Hemiodontichthys* shared bilobate lips and bicuspid teeth often reduced in size. Among the Harttiini, *Metaloricaria* showed a horse-shoe like mouth shape and smaller pedunculated teeth. Other genera were difficult to characterize and another approach was clearly necessary. A cluster analysis (Fig. 2) grouped genera based on their degree of morphological resemblance. *Metaloricaria* and *Farlowella* were the most divergent genera and formed the base of the tree. Two groups were then partitioned that corresponded to the two tribes, Harttiini and Loricariini. The Harttiini was comprised of *Aposturisoma*, the most morphologically divergent, followed by *Lamontichthys*, and then *Ixinandria*. This tribe was then divided into two other groups, one formed by *Harttia* and *Harttiella*, and another by *Sturisoma* joined with *Pterosturisoma* and *Sturisomatichthys*. The Loricariini divided into two principal groups. The *Loricariichthys* group was formed by *Furcodontichthys*, *Loricariichthys*, *Hemiodontichthys*, *Pseudoloricaria*, and *Limatulichthys*. The second group was subdivided into three groups: the *Pseudohemiodon* group consisting of *Reganella*, *Pseudohemiodon*, *Pyxiloricaria*, *Planiloricaria*, *Dentectus*, *Rhadinoloricaria*, *Crossoloricaria*, and *Apistoloricaria*; the *Rineloricaria* group formed by *Spatuloricaria*, *Rineloricaria*, and *Dasylicaria*; and the *Loricaria* group formed by *Loricaria*, *Paraloricaria*, *Ricola*, and *Brochiloricaria*. Our analyses resulted in the placement of two taxa that was inconsistent with previous classifications: *Ixinandria* appeared among Harttiini although its dentition and presence of postorbital notches align it with Loricariini; and *Spatuloricaria* appeared at the base of the *Rineloricaria* and *Loricaria* groups. Because these genera share similar lip structures, we followed Isbrücker (1979) by assigning them to the *Rineloricaria* group of the Loricariini. *Metaloricaria* and *Farlowella*, located at the base of the tree because of their particular morphology, were assigned to the tribe Harttiini, following Isbrücker (1979) and Rapp Py-Daniel (1997). To extract the main characteristics of each genus, shared as well as unique, new Hill & Smith analyses were performed on the above named groups. The projection of the individuals and qualitative variables onto the first factorial plane (Fig. 1c) summarized all this information by connecting the individuals to the center of gravity of the different modalities of the different variables possessed. For example, *Metaloricaria* (species 17) possesses a complete abdominal cover (A3) without particular organization (B2), neither postorbital notches nor predorsal keels (C1, D1), papillose lips (E1), no fringed barbels (F1), a horse-shoe like mouth shape (G2, unique character), teeth pedunculated and reduced in size (H3, unique character), short maxillary barbels (I2), no rostrum (J2), and a pointed snout (K2). Some variables with modalities close to the axes and to the center appear weakly informative on the first plane, such as the presence or absence of secondary organization in the abdominal cover (B) or the presence or absence of a rostrum (J).

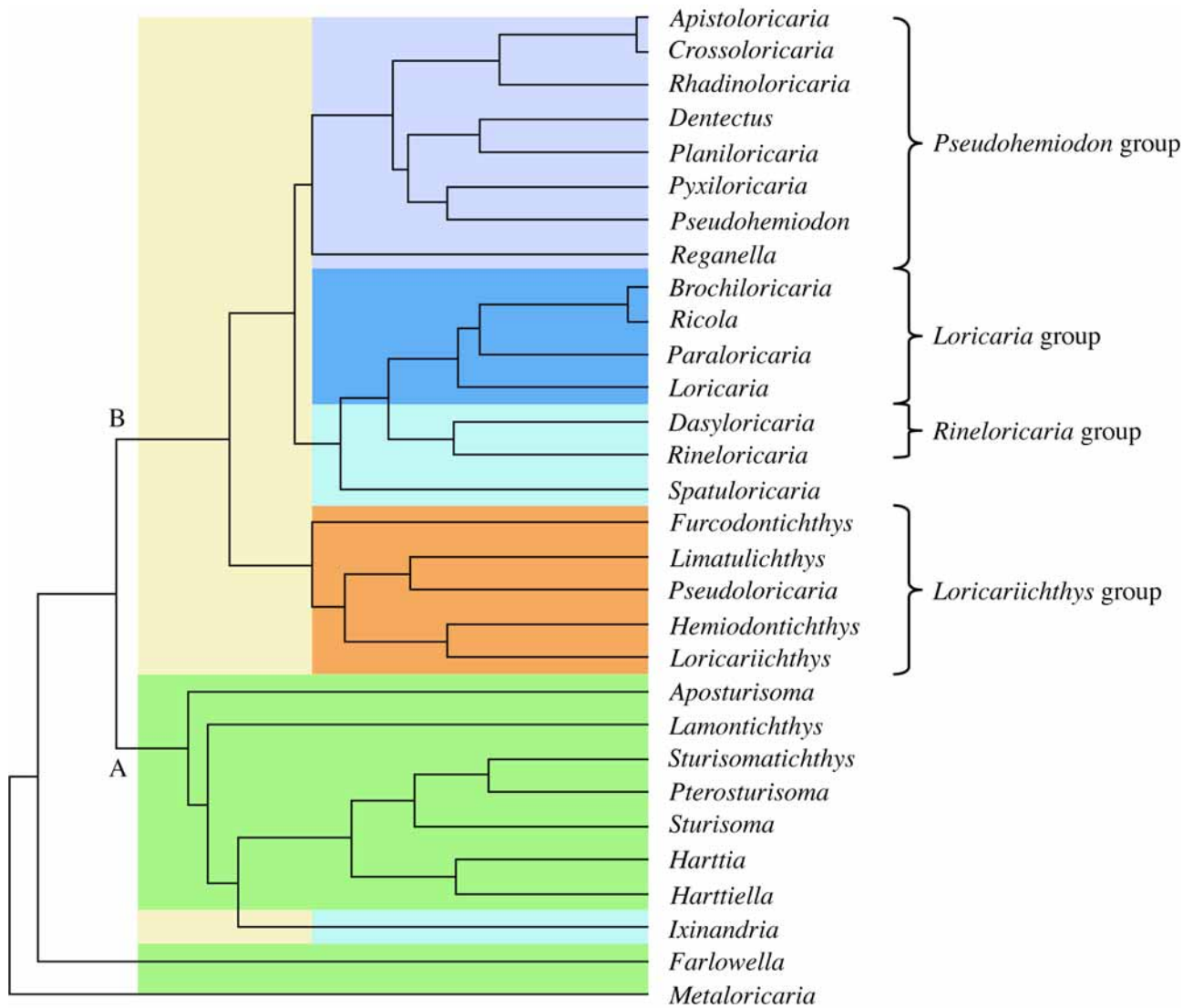


**FIGURE 1.** Hill & Smith analysis (1976) of the subfamily Loricariinae. **a:** projection of 30 individuals representing the 30 genera numbered as in Table 1 onto the first factorial plane of the Hill & Smith analysis (axis 1 horizontal and axis 2 vertical); **b:** projection of the 17 variables onto the first factorial plane of the Hill & Smith analysis (title and modalities in Table 1); **c:** projection of the individuals and of the qualitative variables onto the first factorial plane of the Hill & Smith analysis, one plane representing one qualitative variable (title and modalities in Table 1); **d:** eigenvalues.

**TABLE 1.** Main morphological data recorded on the selected specimen for each genus of the subfamily Loricariinae. A star (\*) indicates data taken from the literature. **I** to **VI**: Quantitative data. **I**: number of caudal-fin rays (including spines); **II**: number of pectoral-fin rays (including spine); **III**: number of pelvic-fin rays (including spine); **IV**: number of dorsal-fin rays (including spine); **V**: number of premaxillary teeth; **VI**: number of dentary teeth. **A** to **K**: qualitative data. **A**: abdominal cover with three modalities: 1 = absent, 2 = present incomplete, 3 = present complete; **B**: secondary organization in the abdominal cover with two modalities: 1 = absent, 2 = present; **C**: postorbital notches with three modalities: 1 = absent, 2 = present weak, 3 = present deep; **D**: predorsal keels with two modalities: 1 = absent, 2 = present; **E**: lips structure with three modalities: 1 = papillose, 2 = filamentous, 3 = rather smooth; **F**: fringed barbels with two modalities: 1 = absent, 2 = present; **G**: mouth shape with four modalities: 1 = elliptical, 2 = horse shoe like, 3 = bilobate, 4 = bilobate with trapezoidal opening; **H**: tooth shape with five modalities: 1 = pedunculated, 2 = straight bicuspid, 3 = pedunculated size reduced, 4 = straight bicuspid size reduced, 5 = spoon shaped size reduced; **I**: maxillary barbels with two modalities: 1 = conspicuous, 2 = inconspicuous; **J**: rostrum with two modalities: 1 = absent, 2 = present; **K**: snout shape with two modalities: 1 = rounded, 2 = pointed.

Genus	Species	I	II	III	IV	V	VI	A	B	C	D	E	F	G	H	I	J	K
<i>Apistoloricaria</i>	<i>A. condei</i> * [1]	12	7	6	7	4	7	2	2	2	2	2	2	4	5	1	1	2
<i>Aposturisoma</i>	<i>A. myriodon</i> [2]	13	7	6	6	85	85	3	2	1	1	1	1	1	1	2	2	2
<i>Brochiloricaria</i>	<i>B. macrodon</i> [3]	12	7	6	7	5	6	3	1	2	2	2	2	3	2	1	1	2
<i>Crossoloricaria</i>	<i>C. rhami</i> [4]	12	7	6	7	3	4	2	2	2	2	2	2	4	5	1	1	2
<i>Dasylicaria</i>	<i>D. cf. filamentosa</i> [5]	12	7	6	7	13	13	3	2	3	2	1	2	3	2	1	1	2
<i>Dentectus</i>	<i>D. barbarmatus</i> * [6]	12	7	6	7	3	3	3	1	2	2	2	2	4	5	1	1	1
<i>Farlowella</i>	<i>F. platoryncha</i> [7]	13	7	5	6	23	17	3	2	1	1	1	1	1	1	2	2	2
<i>Furcodontichthys</i>	<i>F. novaesi</i> * [8]	12	7	6	7	10	6	3	2	3	2	3	1	3	2	1	2	2
<i>Harttia</i>	<i>H. guianensis</i> [9]	14	7	6	7	85	68	1	1	1	1	1	1	1	1	2	1	1
<i>Harttiella</i>	<i>H. crassicauda</i> [10]	14	7	6	7	33	31	1	1	1	1	1	1	1	1	2	1	1
<i>Hemiodontichthys</i>	<i>H. acipenserinus</i> [11]	12	7	6	7	0	8	3	2	3	2	3	1	3	4	2	2	2
<i>Ixinandria</i>	<i>I. montebelloi</i> [12]	12	7	6	7	10	8	1	1	3	1	1	1	1	2	2	1	1
<i>Lamontichthys</i>	<i>L. filamentosus</i> [13]	14	8	6	7	38	36	3	1	1	1	1	1	1	1	2	1	1
<i>Limatulichthys</i>	<i>L. griseus</i> [14]	12	7	6	7	7	10	3	1	2	1	3	1	3	4	2	1	2
<i>Loricaria</i>	<i>L. sp.</i> [15]	12	7	6	7	3	6	3	1	3	2	2	2	3	2	1	1	2
<i>Loricariichthys</i>	<i>L. platymetopon</i> [16]	12	7	6	7	8	15	3	2	3	1	3	1	3	4	2	1	2
<i>Metaloricaria</i>	<i>M. paucidens</i> [17]	13	7	6	7	11	13	3	1	1	1	1	1	2	3	2	1	2
<i>Paraloricaria</i>	<i>P. agastor</i> [18]	12	7	6	7	4	7	2	1	2	2	2	2	3	2	1	1	2
<i>Planiloricaria</i>	<i>P. cryptodon</i> [19]	12	7	6	7	0	3	2	1	2	2	2	2	4	5	1	1	1
<i>Pseudohemiodon</i>	<i>P. laticeps</i> [20]	12	7	6	7	5	7	3	1	2	2	2	2	4	5	1	2	2
<i>Pseudoloricaria</i>	<i>P. laeviuscula</i> [21]	12	7	6	7	10	12	3	1	2	1	3	1	3	2	2	1	2
<i>Pterosturisoma</i>	<i>P. microps</i> [22]	14	7	6	7	46*	46*	3	1	1	1	1	1	1	1	2	1	1
<i>Pyxiloricaria</i>	<i>P. menezesi</i> * [23]	12	7	6	7	3	3	3	1	2	2	2	2	4	5	2	1	2
<i>Reganella</i>	<i>R. depressa</i> [24]	12	7	6	7	0	15	3	1	2	1	3	2	4	5	2	2	2
<i>Rhadinoloricaria</i>	<i>R. macromystax</i> [25]	12	7	6	7	4	8	2	2	2	2	2	2	4	5	1	2	2
<i>Ricola</i>	<i>R. macrops</i> [26]	12	7	6	7	10	10	3	1	2	2	2	2	3	2	1	1	2
<i>Rineloricaria</i>	<i>R. steindachneri</i> [27]	12	7	6	7	7	9	3	1	3	2	1	2	3	2	2	1	2
<i>Spatuloricaria</i>	<i>S. sp.</i> [28]	12	7	6	7	3	4	2	1	2	2	1	2	1	2	2	1	2
<i>Sturisoma</i>	<i>S. robustum</i> [29]	14	7	6	7	45	38	3	2	1	1	1	1	1	1	2	2	2
<i>Sturisomatichthys</i>	<i>S. citurensis</i> [30]	14	7	6	7	56	46	3	1	1	1	1	1	1	1	2	1	2





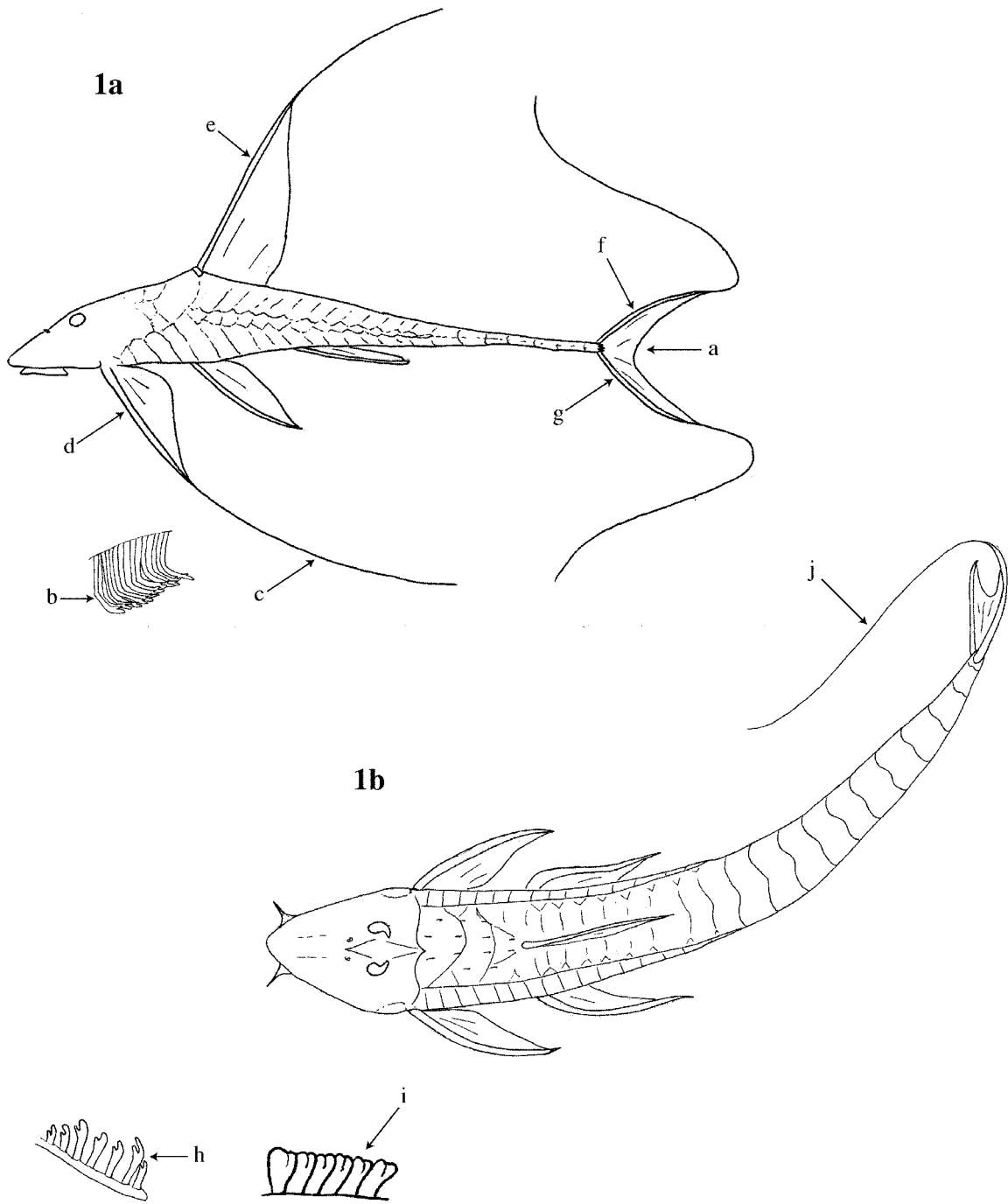
**FIGURE 2.** Cluster analysis of the subfamily Loricariinae. Dendrogram based on morphological distances matrix using UPGMA. **A:** Harttiini tribe; **B:** Loricariini tribe. Colors represent the different ranks established: : Harttiini tribe; : Loricariini tribe; : Loricariichthys group; : Rineloricaria group; : Loricaria group; : Pseudohemiodon group. Braces indicate the genera confirmed inside their own group.

## Key to the genera

The methodology used in this study enabled us to sort the valuable information (grouping of individuals according to combinations of variables) into a hierarchy and create morphologically coherent groups by summarizing the characteristics of each genus. These results are intended to rectify problems with the identification of taxa and should not be interpreted as a phylogeny. We do not use the subtribal rank defined by Isbrücker (1979, 1981a) because the divisions are not well-defined. The results of our analyses support the recognition of two tribes, Harttiini and Loricariini, the latter of which contains four morphological groups. Characters that are underlined in the key couplets are also illustrated on the same page and identified by letters between brackets [a, b, c... aq, ar]. These letters are presented in alphabetical order in the couplets and in the illustrations, with two exceptions: character [ab] (first proposed in lead 13a, is illustrated in Figure 20b), and character [af] (first proposed in lead 15b, is illustrated in Figure 23a). Arrows indicate the most important characters for identification purposes. The numbers of the figures correspond to the numbers of the key couplet. Additional features are given at the level of identification to confirm this identification, certain specimens being sometimes poorly preserved or poorly characterized like juveniles, and certain genera being relatively variable.

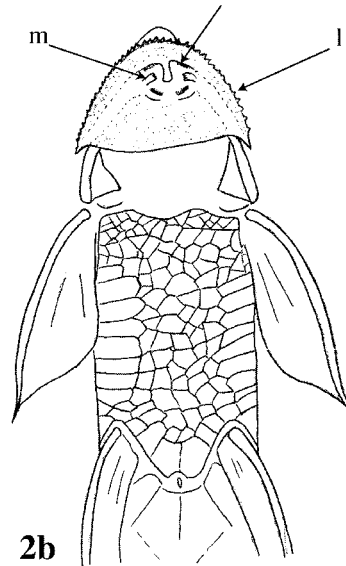
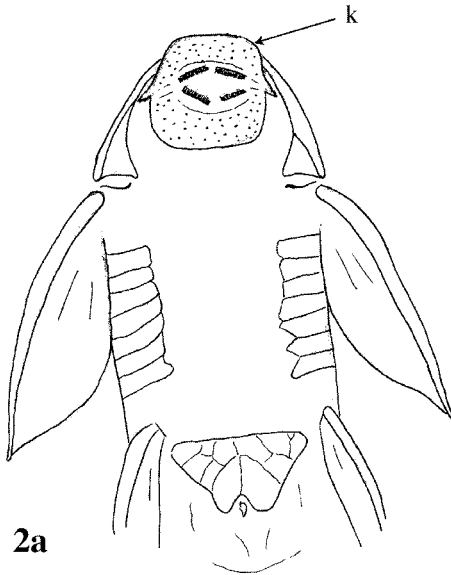
**1a.** – Caudal fin [a] with **i-12-i** or **i-11-i** rays; teeth pedunculated [b], bicuspid, numerous ( $\geq 10$  per premaxillae), organized in comb and weakly differentiated; sometimes with filamentous extensions [c] on pectoral [d], dorsal [e], upper [f] and/or lower caudal [g] spines: **Harttiini**.....**2**

**1b.** – Caudal fin [a] with **i-10-i** rays; teeth straight [h] bicuspid, spoon-shaped [i], not numerous ( $\leq 20$  per premaxillae), strongly differentiated, sometimes reduced in size or absent; often with a more or less strong whip [j] on upper caudal spine [f]: **Loricariini**.....**10**



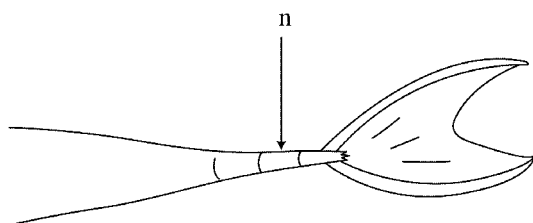
**2a.** – Mouth shape elliptical [k] ..... **3**

**2b.** – Mouth shape horseshoe like [l]; with three buccal papillae [m], lateral ones trilobate; teeth small and not numerous ( $\approx 10$  per premaxillae): ..... *Metaloricaria*

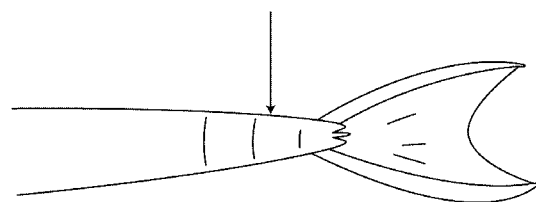


**3a.** – Caudal peduncle [n] strongly depressed, elliptical in transverse section (in average, the minimal depth of the caudal peduncle represents 1 to 3 % of the SL) ..... **4**

**3b.** – Caudal peduncle [n] weakly depressed, more or less circular in transverse section (in average, the minimal depth of the caudal peduncle represents 5 % of the SL); abdomen naked; body covered by numerous, short and dense odontodes giving a velvety aspect; species of small size ( $\approx 50$  mm): ..... *Harttiella*

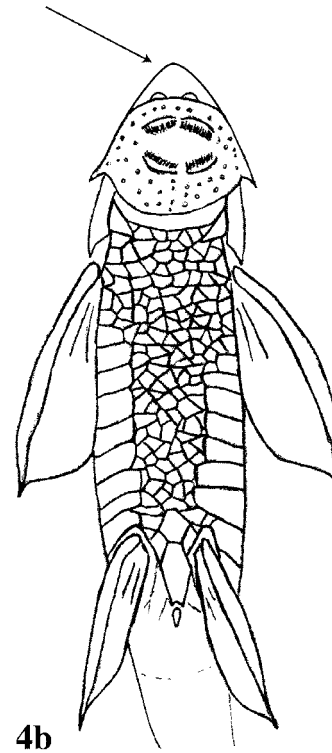
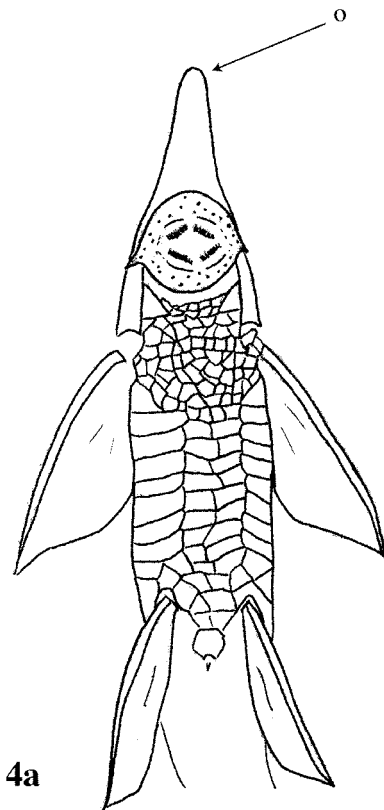


**3a**



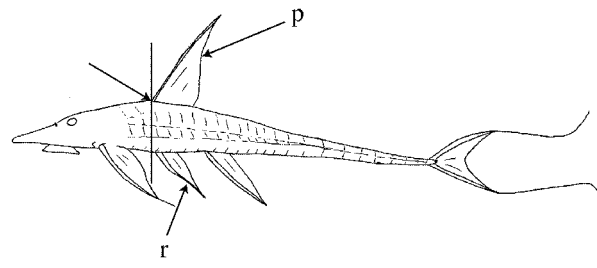
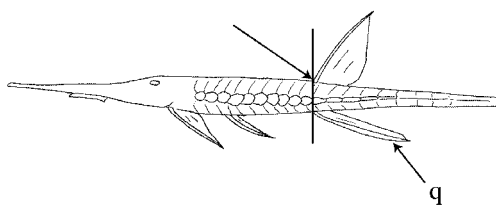
**3b**

- 4a. – Rostrum [o] present ..... 5
- 4b. – Rostrum [o] absent ..... 7



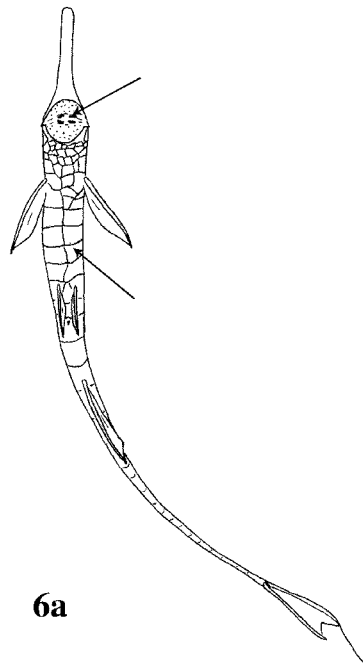
- 5a. – Dorsal fin [p] originating more or less in front of the anal-fin [q] origin .....6

- 5b. – Dorsal fin [p] originating more or less in front of the pelvic-fin [r] origin; abdominal cover complete and weakly structured in two to three rows: ...*Sturisoma*

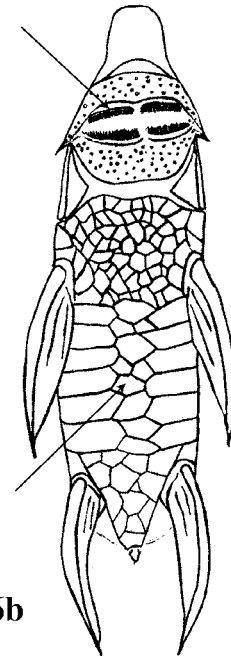


**6a.** – Teeth not numerous ( $\approx 20$  per premaxillae); two to three rows of abdominal plates; general aspect slender, reminiscent of a stick: .....*Farlowella*

**6b.** – Teeth numerous ( $\approx 100$  per premaxillae); three rows of abdominal plates: .....*Aposturisoma*



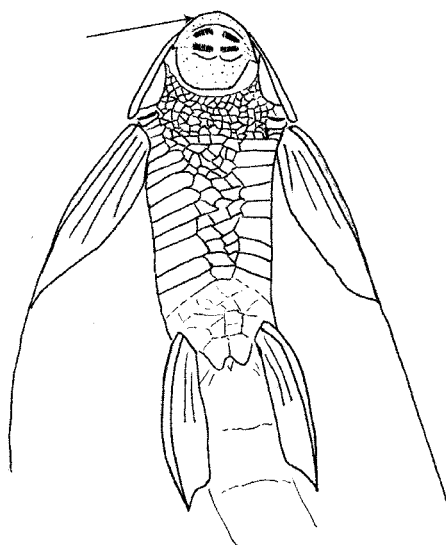
**6a**



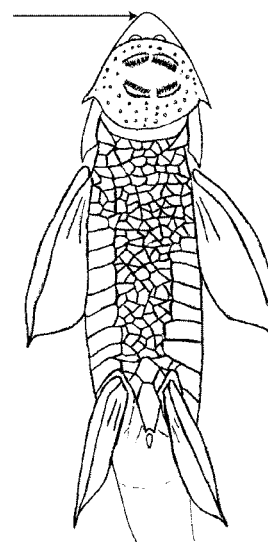
**6b**

**7a.** – Snout rounded ..... **8**

**7b.** – Snout pointed; abdominal cover complete without particular organization, or weakly structured in two to three rows .....*Sturisomatichthys*

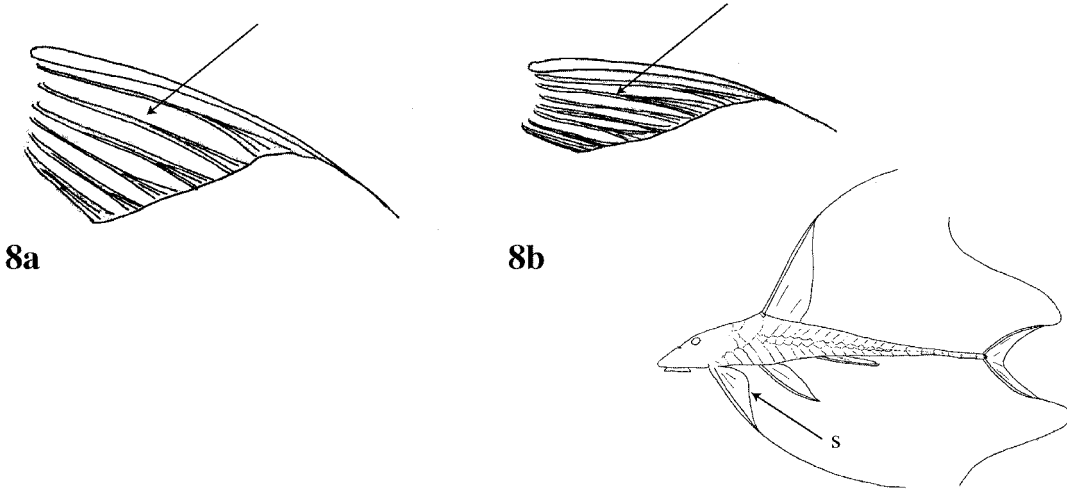


**7a**

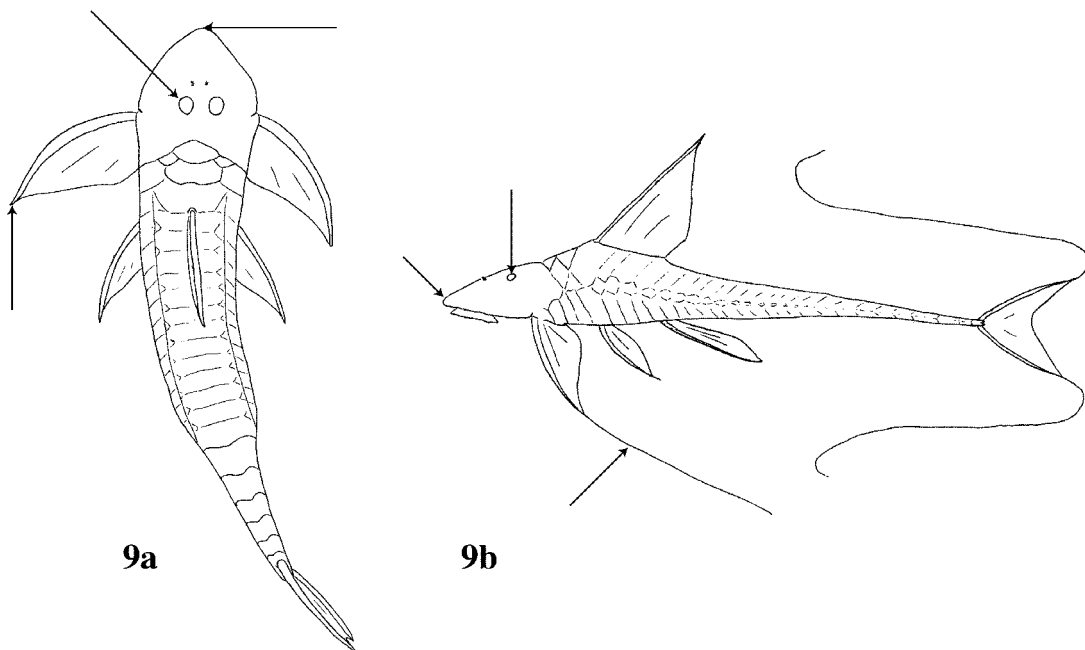


**7b**

- 8a.** – Pectoral fins [s] with **i-6** rays .....**9**  
**8b.** – Pectoral fins [s] with **i-7** rays; pectoral spine [d] sometimes with filamentous extensions [c]: ..... *Lamontichthys*

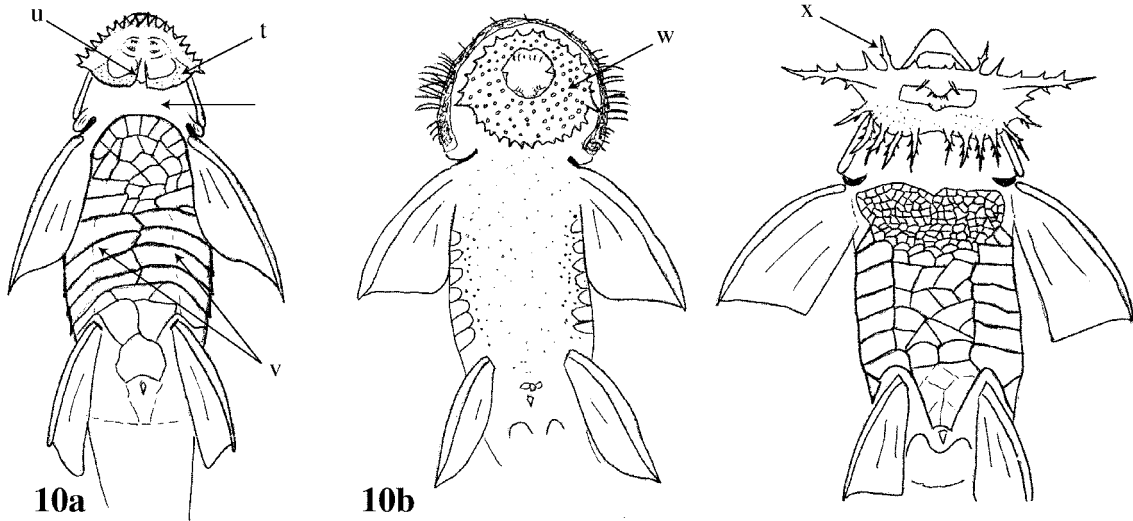


- 9a.** – Eye diameter large (on average  $\approx 20\%$  of head length); tip of snout naked; without filamentous extensions [c] on pectoral [d], upper [f] and lower caudal [g] spines: .....*Harttia*  
**9b.** – Eye diameter small (on average  $\approx 10\%$  of head length); tip of snout covered by plates; with filamentous extensions [c] on pectoral [d], upper [f] and lower caudal [g] spines: .....*Pterosturisoma*



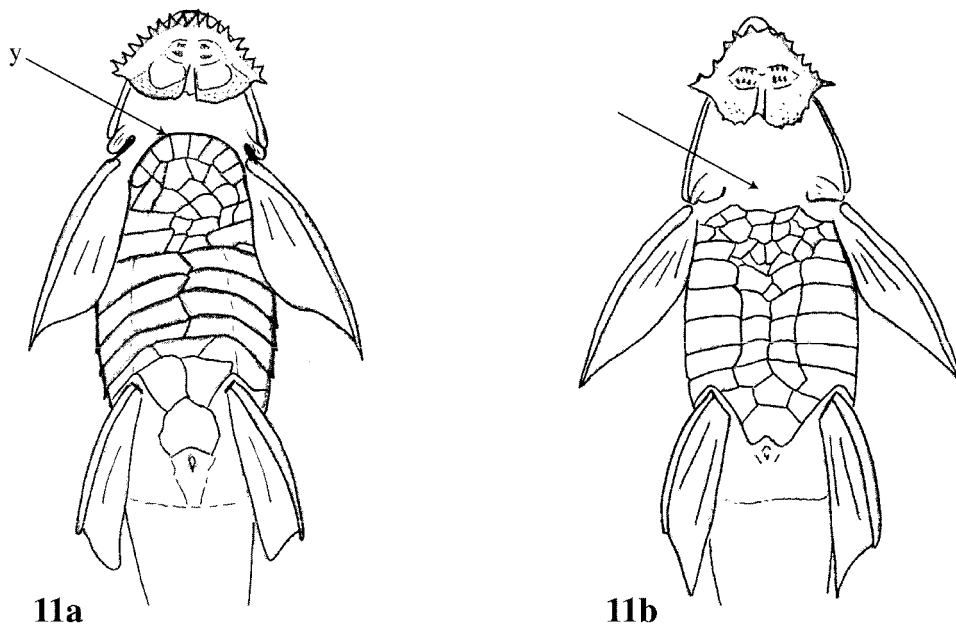
**10a.** – Lower lip bilobate [t] with a median furrow [u]; surface of this lip more or less smooth or weakly papillose; presence of a double abdominal keel [v]; throat never covered; whip [j] on upper caudal spine [f] weak or absent: *Loricariichthys* group .....11

**10b.** – Absence of such a combination of characters; lower lip more often strongly papillose [w] or filamentous [x].....15



**11a.** – Presence of a secondary structure in the organization of the abdominal cover forming a perfect elliptical area [y] at the level of the pectoral girdle: .....*Loricariichthys*

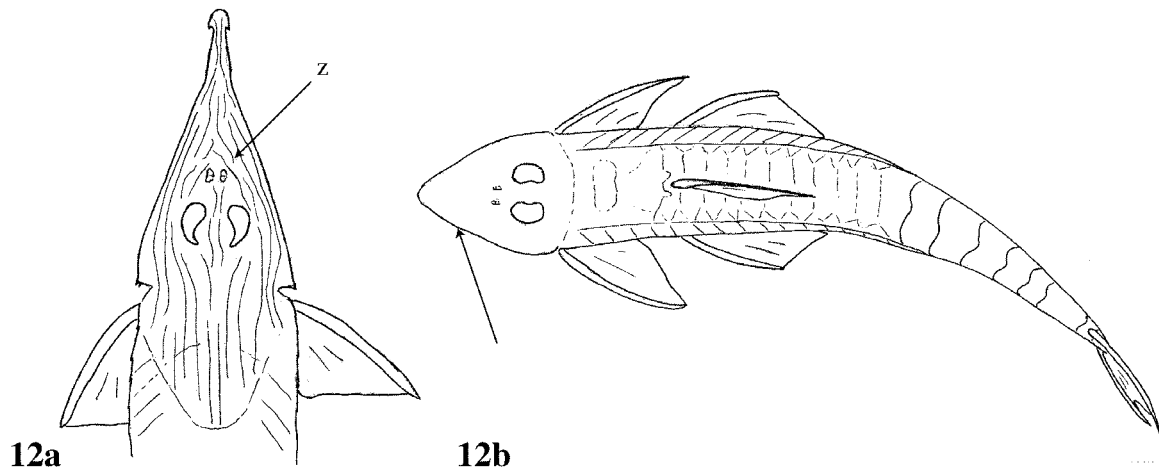
**11b.** – Without such structure .....12





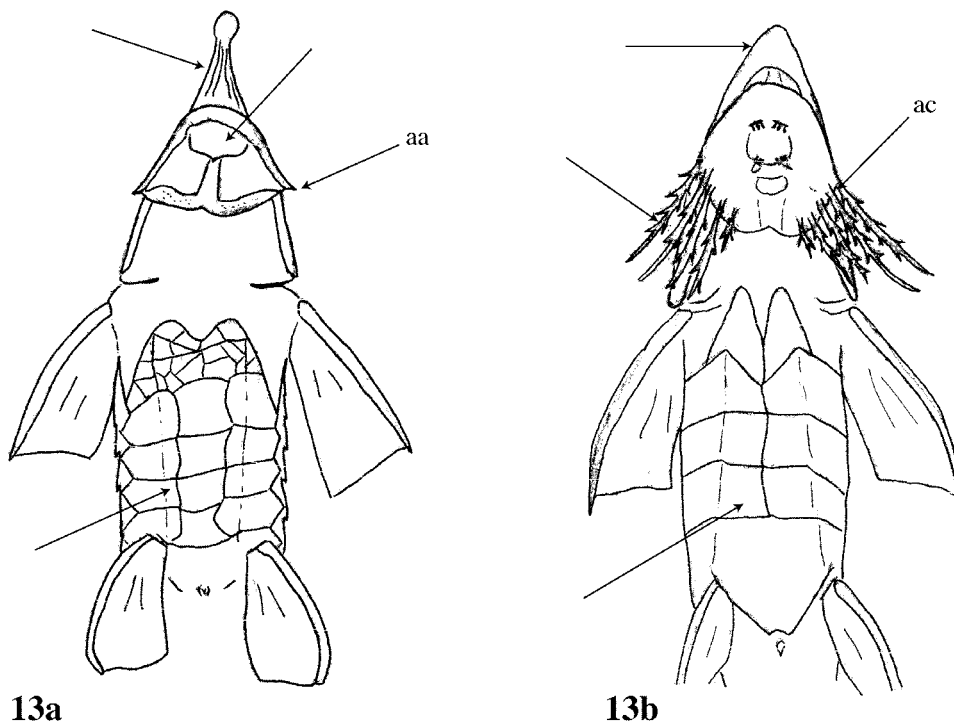
12a. – With conspicuous lines of odontodes [z] on head and snout .....13

12b. – Without lines of odontodes [z] on head and snout .....14



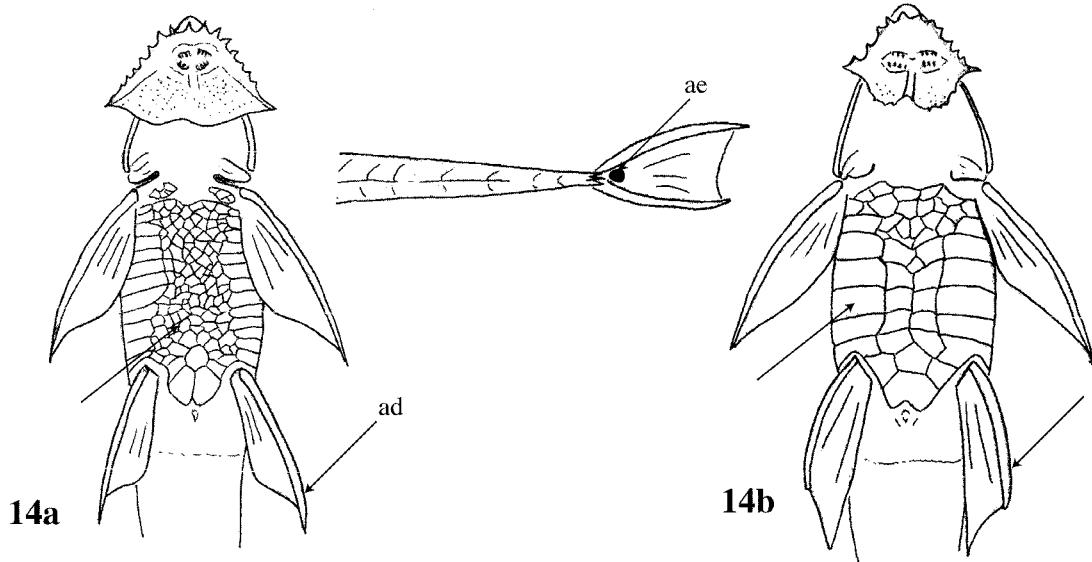
13a. – Rostrum [o] strongly pronounced; maxillary barbels [aa] short; premaxillary teeth [ab] absent; abdomen covered by large rectangular plates organized in three rows: .....*Hemiodontichthys*

13b. – Rostrum [o] weakly pronounced; maxillary [aa] and fringed [ac] barbels conspicuous and gathered in series at the lip corners; premaxillary teeth [ab] present; abdomen covered by large plates organized in two rows: .....*Furcodontichthys*



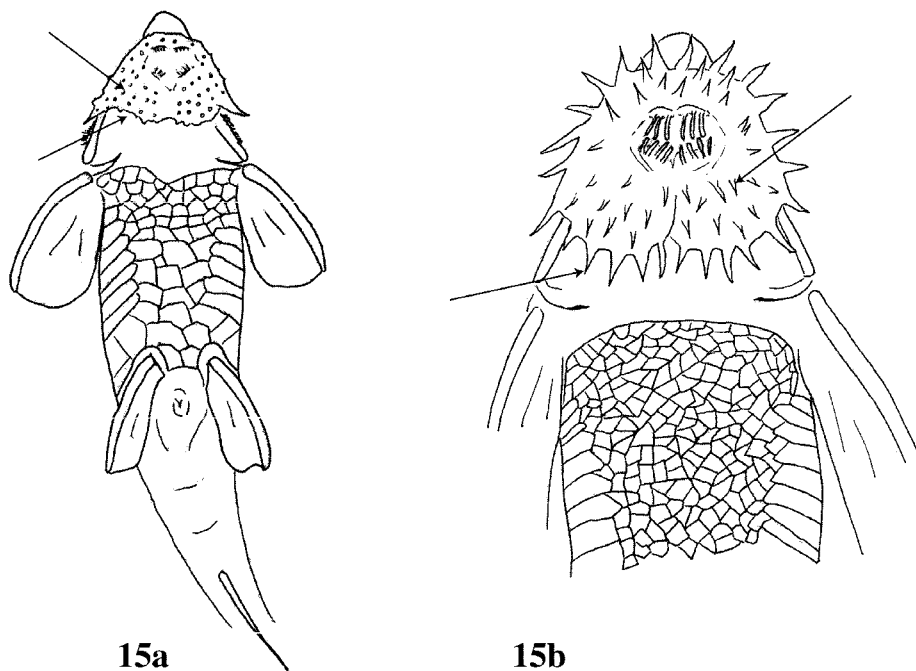
**14a.** – Abdomen covered by small plates without particular organization; in adults pelvic-fin spine [ad] longer than last pelvic-fin [r] ray; in juveniles presence of a conspicuous basicaudal spot [ae]: .....*Pseudoloricaria*

**14b.** – Abdomen covered by medium-sized plates weakly structured in two to three rows; in adults last pelvic-fin [r] ray longer than pelvic-fin spine [ad]; in juveniles absence of a conspicuous basicaudal spot [ae]: .....*Limatulichthys*



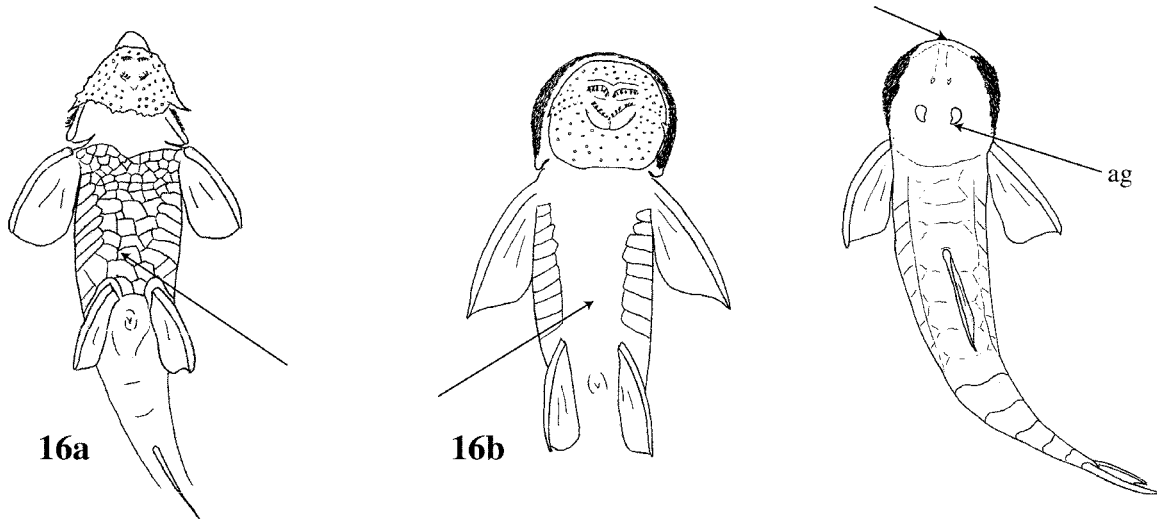
**15a.** – Lips papillose [w]; fringed barbels [ac] of lower lip absent or inconspicuous: *Rineloricaria* group .....16

**15b.** – Lips generally filamentous [x] or smooth [af]; fringed barbels [ac] of lower lip generally conspicuous .....19



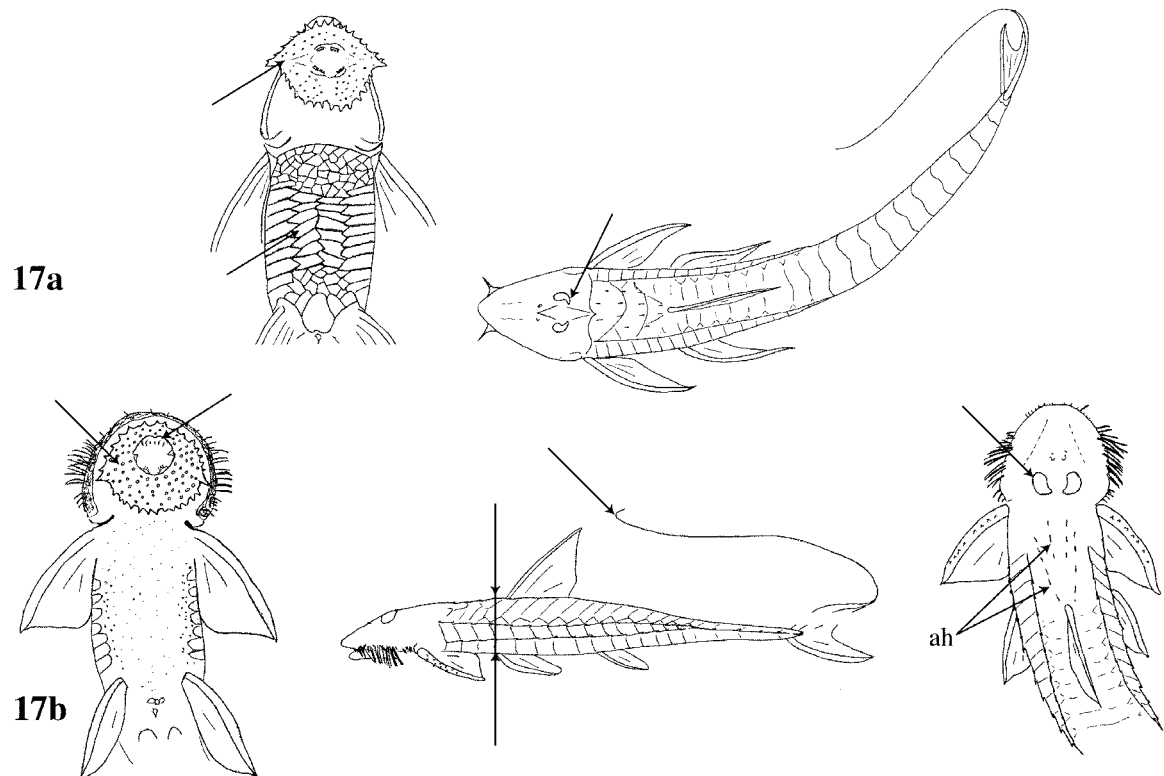
**16a.** – Abdomen partially to completely covered by plates .....17

**16b.** – Abdomen naked; snout rounded; mouth circular; postorbital notches [ag] deep; strongly depressed body covered by numerous, short, and dense odontodes giving a velvety aspect; species of small size ( $\approx 90$  mm): .....*Ixinandria*



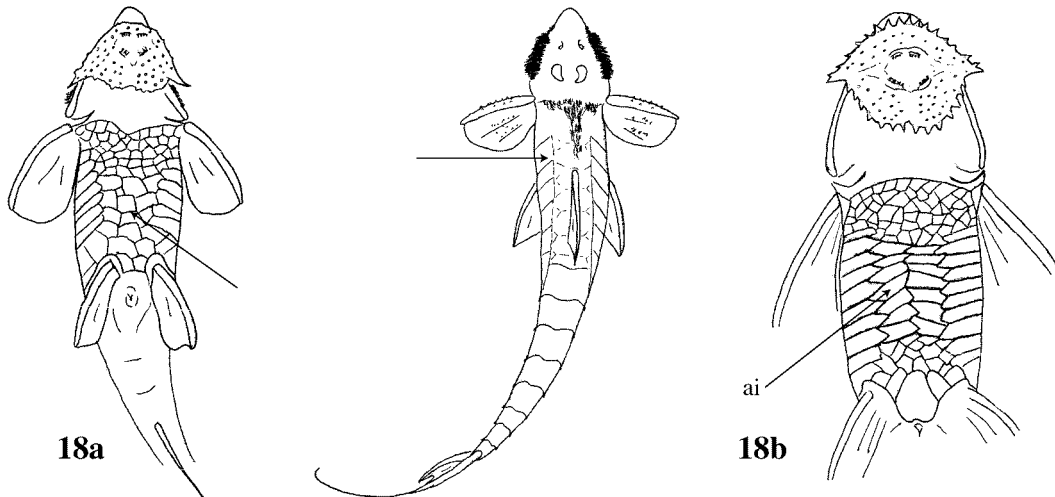
**17a.** – Abdomen partially to completely covered by medium-sized plates; mouth not circular; postorbital notches [ag] deep .....18

**17b.** – Abdomen covered by very small plates not contiguous; mouth circular and thick; postorbital notches [ag] weak; teeth few ( $\approx 4$  per premaxillae); body depth strong ( $\approx 12\%$  of SL); presence of a long whip [j] on upper caudal spine [f]; predorsal keels [ah] strong; .....*Spatuloricaria*



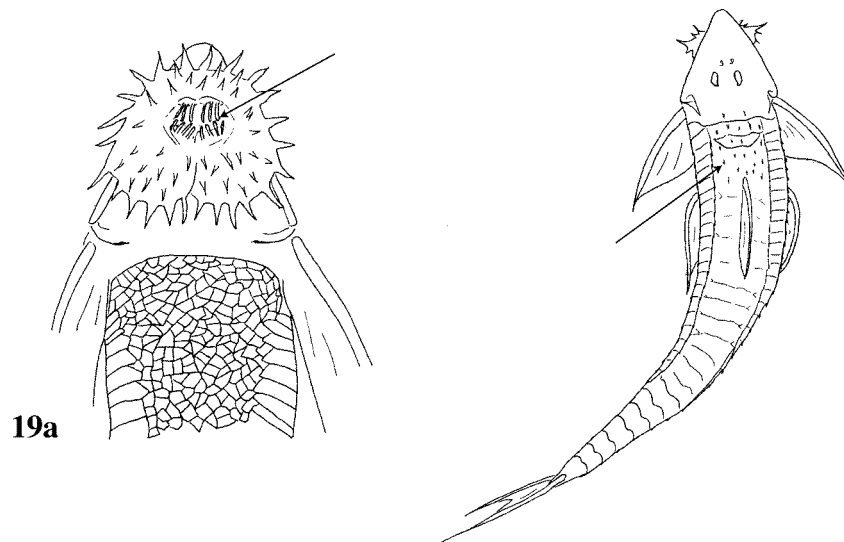
**18a.** – Without a secondary structure in abdominal cover; abdominal cover weakly organized in rows; predorsal keels [ah] more or less pronounced; species of medium size (generally  $\leq 20$  cm): .....*Rineloricaria*

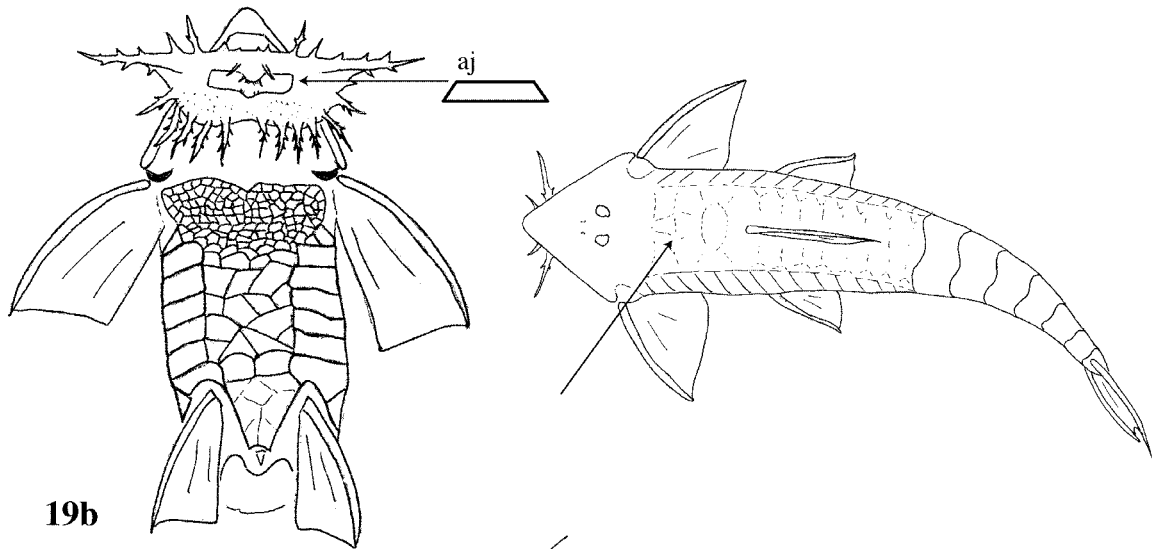
**18b.** – With a secondary structure on abdominal cover consisting in double median row of plates organized in chevrons [ai]; predorsal keels [ah] strong; species of large size (generally  $\geq 25$  cm): .....*Dasyloricaria*



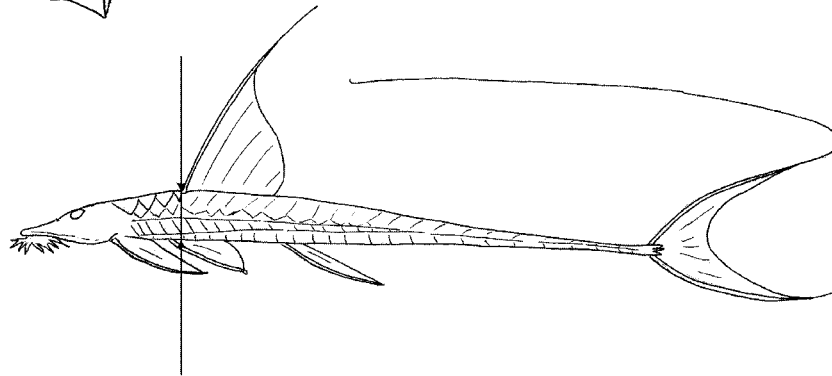
**19a.** – Mouth opening without particular shape; the most often predorsal keels [ah] strong; body generally weakly depressed: ***Loricaria* group** .....**20**

**19b.** – Mouth opening trapezoidal [aj]; predorsal keels [ah] weak; body strongly depressed: ***Pseudohemiodon* group** .....**23**



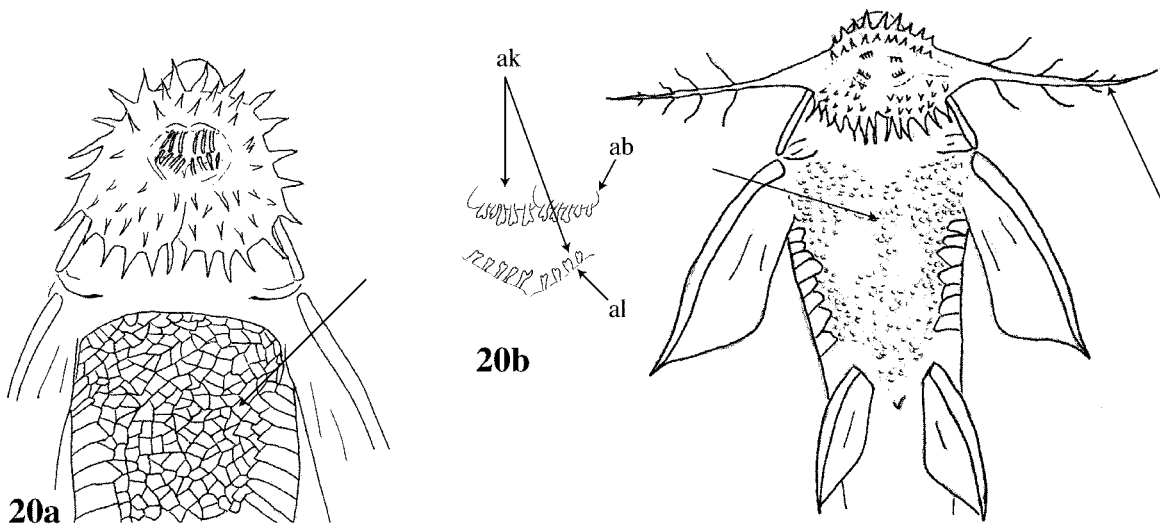


19b



20a. – Abdominal cover the most often complete made of medium to small plates .....21

20b. – Abdominal cover incomplete, made of very small plates not contiguous; equal size [ak] of dentary [al] and premaxillary teeth [ab]; tooth size-reduced; maxillary barbels [aa] long, branched and reaching pectoral-fin [s] origin: .....*Paraloricaria*

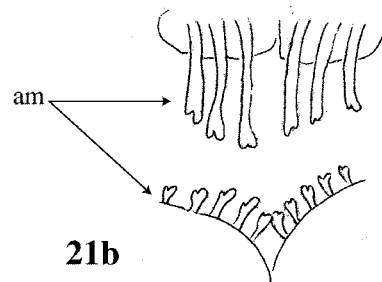
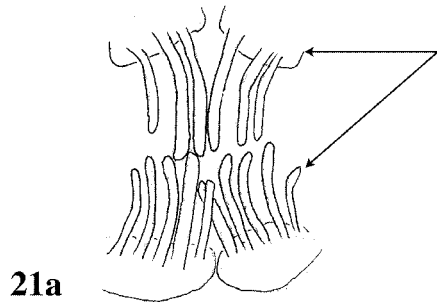


20a

20b

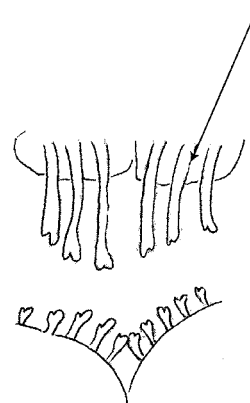
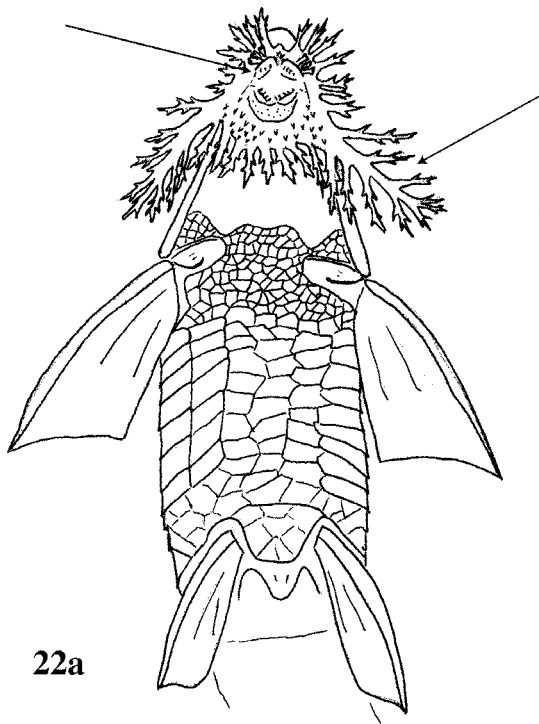
**21a.** – Equal size [ak] of dentary [al] and premaxillary teeth [ab]; tooth very long:  
 .....*Brochiloricaria*

**21b.** – Different size [am] of dentary [al] and premaxillary teeth [ab], the latter almost two times longer than the former .....**22**



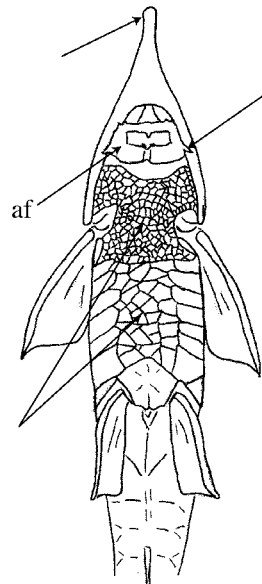
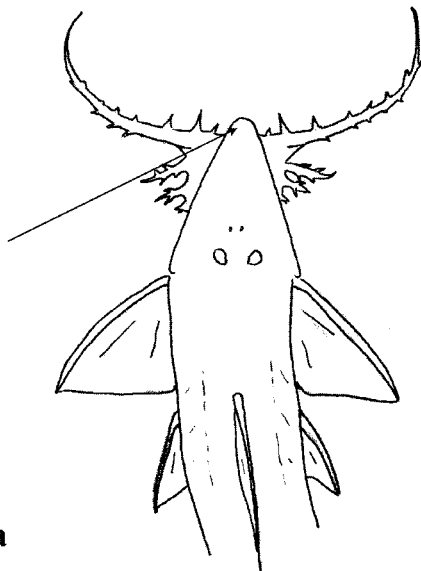
**22a.** – 10 to 15 premaxillary teeth [ab]; lips extremely filamentous [x]; maxillary barbels [aa] long, strongly branched, and reaching pectoral-fin [s] origin:  
 .....*Ricola*

**22b.** – 3 to 5 premaxillary teeth [ab]; lips filamentous [x]; maxillary barbels [aa] not reaching pectoral-fin [s] origin: .....*Loricaria*



23a. – Rostrum [o] weakly pronounced or absent: .....24

23b. – Rostrum [o] strongly pronounced; premaxillary teeth [ab] absent; dentary teeth [al] numerous ( $\approx 15$  per dentary) and reduced in size; lips smooth [af]; maxillary barbels [aa] short; abdominal cover complete, made of little plates without particular organization; throat covered: .....*Reganella*

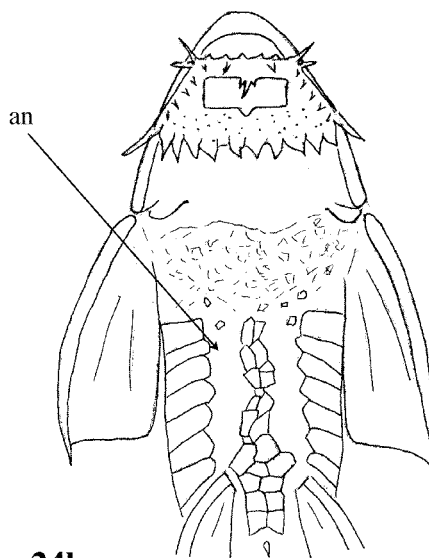
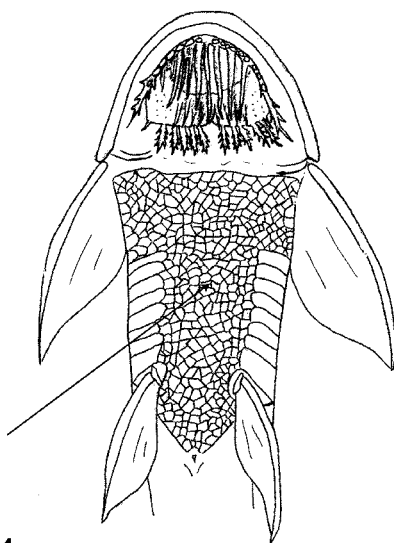


23a

23b

24a. – Abdominal cover complete: .....25

24b. – Abdominal cover incomplete, most often consisting in a double median row [an] of plates: .....27

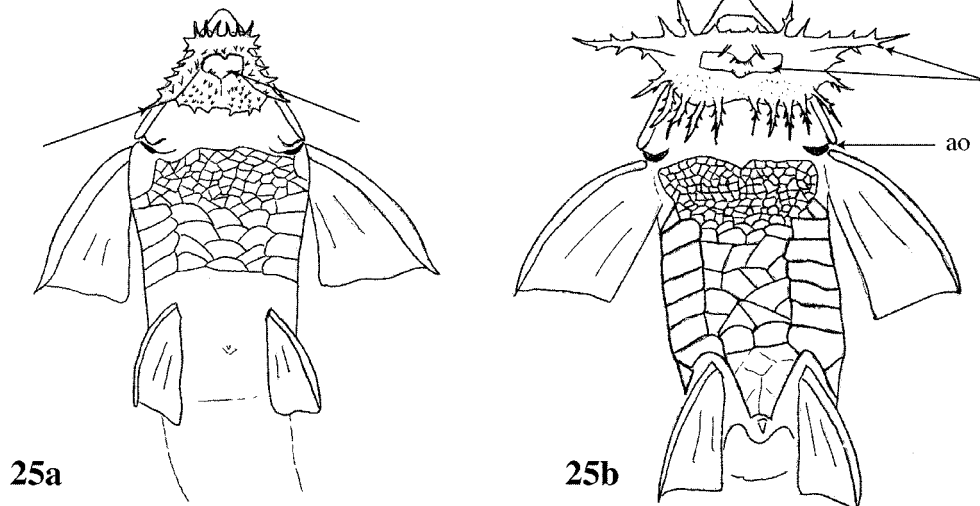


24a

24b

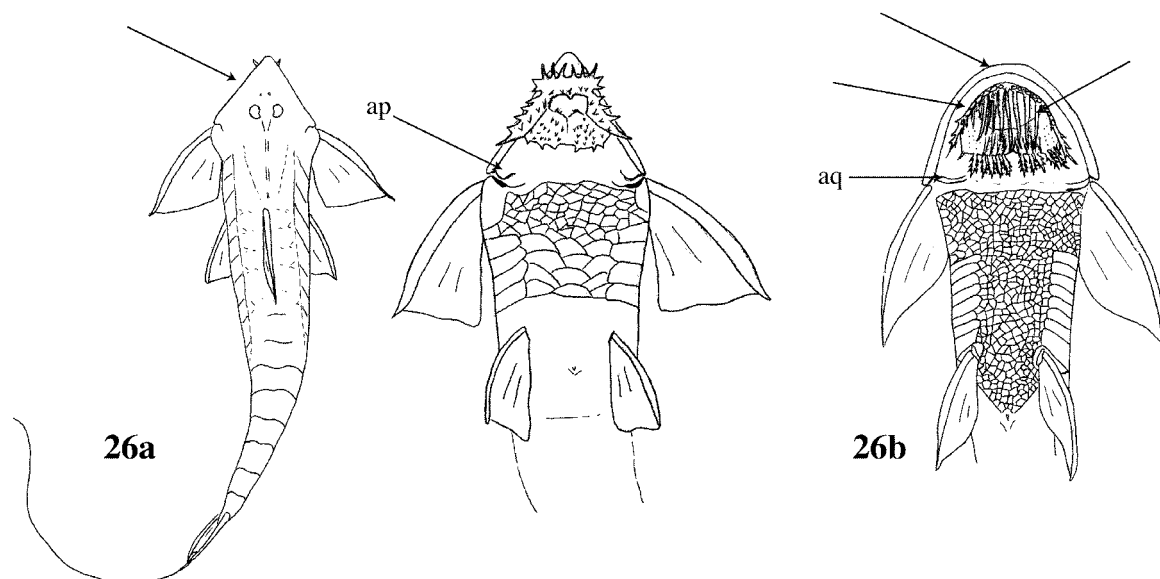
**25a.** – Maxillary barbels [aa] inconspicuous, not reaching gill opening [ao]; teeth very difficult to observe, invisible in normally preserved specimens .....**26**

**25b.** – Maxillary barbels [aa] conspicuous, reaching gill opening [ao]; teeth visible; head large; body strongly depressed: .....*Pseudohemiodon*



**26a.** – Head triangular and little; body large; trapezoidal in transverse section; with a fleshy flap [ap] partially covering the branchiostegal membrane [aq]: .....*Pyxiloricaria*

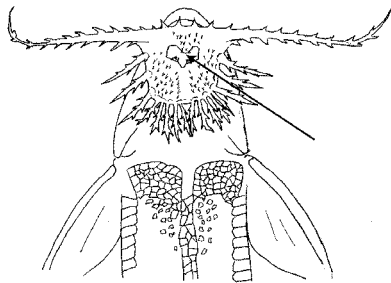
**26b.** – Head rounded; upper lip with numerous filaments reaching the lower lip margin; with plates on the external margin of the maxillary barbels [aa]: .....*Dentectus*



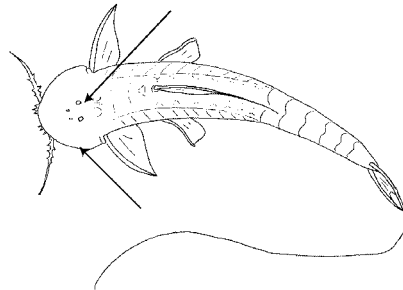


27a. – Premaxillary teeth [ab] present .....28

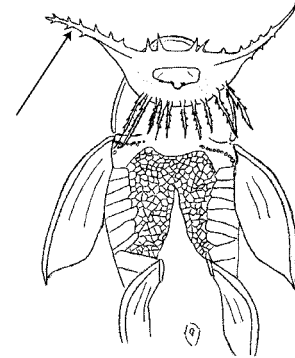
27b. – Premaxillary teeth [ab] absent; head rounded; eyes small; maxillary barbels [ac] conspicuous, reaching beyond pectoral-fin [s] origin: .....*Planiloricaria*



27a



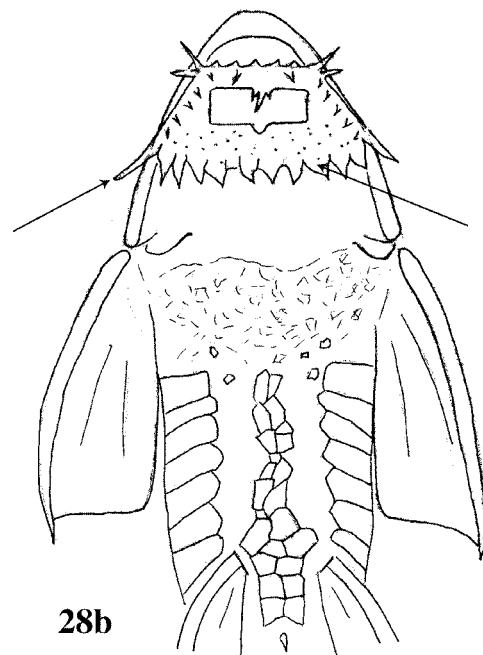
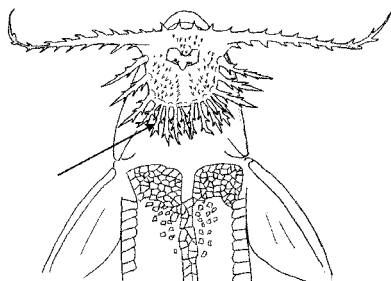
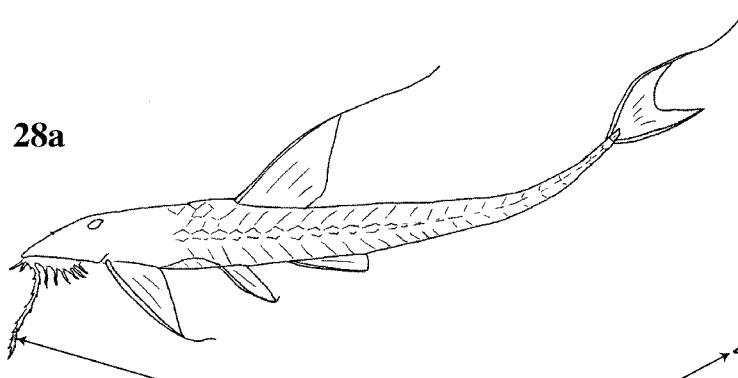
27b



28a. – maxillary barbels [aa] conspicuous, reaching beyond pectoral-fin [s] origin; lips strongly filamentous [x] .....29

28b. – maxillary barbels [aa] reaching gill opening [ao]; lips fairly filamentous [x] .....*Crossoloricaria*

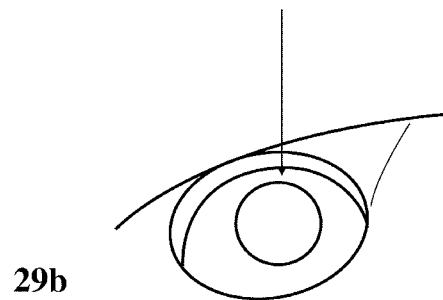
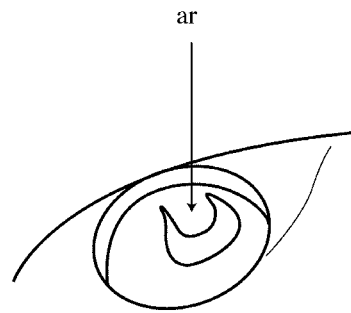
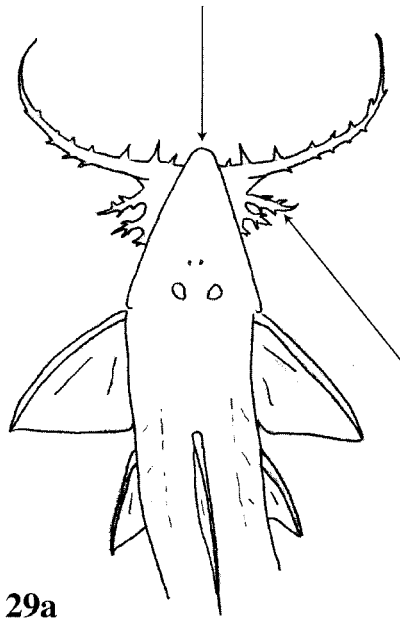
28a



28b

**29a.** – Rostrum [o] pointed; 12 fringed barbels [ac]; iris operculum [ar] generally present: .....*Rhadinoloricaria*

**29b.** – Rostrum [o] generally rounded; 14 fringed barbels [ac]; iris operculum [ar] absent or vestigial: .....*Apistoloricaria*



### Synopsis of the genera

*Apistoloricaria* Isbrücker & Nijssen, 1986. Type species: *Apistoloricaria condei* Isbrücker & Nijssen, 1986. Holotype: FMNH 94683, Ecuador, Rio Napo drainage, mouth of Rio Tiputini. Gender: feminine. Representatives of this genus are distributed in the upper Amazon and Orinoco drainages, along the Atlantic slope of the Andes. They inhabit sand substrates and are morphologically adapted to this habitat. As with other representatives of the *Pseudohemiodon* group, their body is strongly depressed and the pelvic fins are used for locomotion, enabling these fish to appear to “walk” on the substrate. Sexual dimorphism is apparent through differentiated lip structure. The lip surfaces of the male are rather papillose while those of the female are filamentous (Nijssen & Isbrücker 1988). These taxa are abdomino-lip brooders. Eggs are laid in a single layered mass, and are attached to the surface of the lower lip and abdomen of the male. Isbrücker & Nijssen (1986a) described the biotope of *A. condei* according to D. J. Stewart’s field notes. This species was collected in turbid and dark waters, in moderately fast flowing streams, between 2 to 10 meters deep. No submerged vegetation was noted, and the bottom was made of sand, mud, dead leaves, twigs, branches, and trunks. *Apistoloricaria*

is not well diagnosed and upon further examination, may prove to be a synonym of *Rhadinoloricaria*. These two genera are distinguished primarily by the presence or absence of the iris operculum (absent or vestigial in *Apistoloricaria* versus present in *Rhadinoloricaria*), a more conspicuous rostrum in *Rhadinoloricaria*, and by the number of fringed barbels (14 in *Apistoloricaria* versus 12 in *Rhadinoloricaria*). Four valid species are recognized (Ferraris 2003) and a key to the species is available in Nijssen & Isbrücker (1988).

***Aposturisoma* Isbrücker, Britski, Nijssen & Ortega, 1983.** Type species: *Aposturisoma myriodon* Isbrücker, Britski, Nijssen & Ortega, 1983. Holotype: MZUSP 15328, Peru, Ucayali Department, Coronel Portillo Province, Rio Aguaytia drainage, Rio Huacamayo at Tingo Maria. Gender: neuter. This monotypic genus is only known from its type locality and few data are presently available. This is a rheophilic species that has been collected with representatives of the genus *Chaetostoma* (Isbrücker *et al.* 1983). Evers & Seidel (2005) described the habitat of *Aposturisoma myriodon* as clear, with swift current and shallow waters. They noticed that *Aposturisoma* frequents areas with rubble substrates in this biotope. Its morphology is similar to that of *Farlowella*, to which it is closely related because of the numerous predorsal plates and the origin of the dorsal fin in front of the origin of the anal fin. Nevertheless it has a larger mouth, a much deeper and wider body and a much thicker caudal peduncle which can be interpreted as an adaptation to stream habitat, as this kind of adaptations is also found in rheophilic fishes of the genus *Chaetostoma*, rather than an intermediary between *Farlowella* and *Sturisoma* as supposed by Isbrücker *et al.* (1983), these two genera not being particularly rheophilic.

***Brochiloricaria* Isbrücker & Nijssen, 1979.** Type species: *Brochiloricaria chauliodon* Isbrücker, 1979. Holotype: ZSM 23342, Argentina, Entre Rios Province, Isla El Dorado, Paraná, Guaza (locality not stated). Gender: feminine. The species of this genus are distributed in the Paraná system, including the Paraguay River. *Brochiloricaria* is an abdomino-lip brooder. The species reproduce like those of *Loricaria* (Evers & Seidel 2005). Kavalco *et al.* (2005) made a cytogenetic analysis of four species of Loricariidae and provided a synthesis of the karyotypic diversity of the family. These authors hypothesized that the diploid number of  $2n = 54$  chromosomes was a plesiomorphic character within Loricariidae. This number was found in all characterized species and populations of Neoplecostominae and Delturinae, and in twelve of the fourteen characterized species of Hypoptopomatinae. For this reason, they considered these three subfamilies basal. Considering Loricariinae, they argued that according to the sampling and to the great observed diversity in diploid numbers (from  $2n = 36$  to  $2n = 74$ ), evolutionary trends were difficult to establish. Nevertheless, they underlined that a dozen of species possessed  $2n = 54 \pm 2$  chromosomes as found in Hypoptopomatinae, Neoplecostominae and Delturinae. Kavalco *et al.* (2005) gave karyotypic characteristics of *B. macrodon*, with  $2n = 58$  chromosomes. *Brochiloricaria* is morphologically very similar to *Loricaria* and can be distinguished from the latter only by its teeth characteristics (teeth very long of equal size on both jaws *versus* premaxillary teeth almost two times longer than dentary ones). On the basis of molecular data and tooth shape of *Hypostomus fonchii* Montoya-Burgos *et al.* (2002) and Weber & Montoya-Burgos (2002) demonstrated that dentition is not always a reliable character to define a genus. The genus *Cochliodon*, placed in Hypostominae, was erected on the basis of its spoon-shaped dentition; it is now considered as a junior synonym of *Hypostomus*. Consequently, *Brochiloricaria* may be a synonym of *Loricaria*, but complementary studies based on molecular data need to be conducted. Two valid species are assigned to the genus (Ferraris 2003).

***Crossoloricaria* Isbrücker, 1979.** Type species: *Loricaria variegata* Steindachner, 1879. Holotype: NMW 45138, Panama, Rio Mamoni drainage at Chepo. Gender: feminine. The species of this genus are distributed in the northwestern part of the South-American continent along the Pacific slope (in Panama and Columbia), Lake Maracaibo region (Venezuela), and the upper Amazon system (Peru). Like other representatives of the *Pseudohemiodon* group, *Crossoloricaria* species occur over sandy substrates of larger rivers and their tributaries. Sexual dimorphism is unknown but males are abdomino-lip brooders. *Crossoloricaria* is poorly diagnosed and is in need of revision. Its only diagnostic character (incomplete abdominal cover consisting of a double median row of plates) is shared by two other representatives of the *Pseudohemiodon* group,

*Apistoloricaria* and *Rhadinoloricaria*. Rapp Py-Daniel (1997) suggested the synonymy of *Apistoloricaria* and *Crossoloricaria* with *Rhadinoloricaria*, but the structure of the lips and the length of the maxillary barbels tend to place *Crossoloricaria* closer to *Pseudohemiodon*. Moreover, *Crossoloricaria rhami*, described by Isbrücker & Nijssen (1983), like *Pseudohemiodon* possesses complete abdominal plate development, thus rendering the diagnostic feature of *Crossoloricaria* invalid. Five valid species are currently recognized in this genus (Ferraris 2003).

***Dasyloricaria* Isbrücker & Nijssen, 1979.** Type species: *Loricaria filamentosa* Steindachner, 1878. Holotype: NMW 44874, Colombia, Rio Magdalena drainage. Gender: feminine. Distribution includes the northwestern South America on the Pacific slope of Colombia and Panama. *Dasyloricaria* is poorly known and no ecological data are available. Sexual dimorphism is similar to that of *Rineloricaria*, including hypertrophied odontodes forming brushes on the lateral surfaces of the head in mature males. Steindachner (1878) reported hypertrophied development of the lower lip, a characteristic of representatives of the *Loricariichthys* group, suggesting that *Dasyloricaria* is also a lip brooder. This genus is unusual in several respects. Its distribution is restricted to the Pacific slope of the Andes, unique pattern of distribution within the subfamily, distinguishing it from the rest of the Loricariinae, although it shares morphological characteristics with representatives of other groups mainly distributed on the Atlantic slope. Along with other members of the *Rineloricaria* group, it shares papillose lips and hypertrophied odontodes along the sides of the head in breeding males. With some representatives of the *Loricariichthys* group, it shares deep postorbital notches, an abdominal cover strongly structured, and a similar mouth shape, including the hypertrophied lower lip of breeding males. Finally, with some representatives of the *Loricaria* group, it shares a triangular head, strong predorsal keels, and the upper caudal fin ray produced into a long whip. *Dasyloricaria* could represent a link between all other morphological groups. Based on sexually dimorphic characters and lip structure it is placed within the *Rineloricaria* group following Isbrücker (1979). Currently, five valid species are recognized (Ferraris 2003).

***Dentectus* Martín Salazar, Isbrücker & Nijssen, 1982.** Type species: *Dentectus barbarmatus* Martín Salazar, Isbrücker & Nijssen, 1982. Holotype: MBUCV V-12780, Venezuela, State of Cojedes, Rio Salinas drainage, tributary of the Rio Pao Viejo, northeast of El Baul. Gender: masculine. This monotypic genus occurs in the upper Orinoco drainage. Ecological and behavioral data are unavailable. Although it has been placed within the *Pseudohemiodon* group based on its strongly depressed body, its filamentous lips with long fringed barbels, and its spoon shaped and size reduced dentition, *Dentectus* also shows unique derived features such as the presence of plates along the outer margin of its maxillary barbels, and a unique mouth structure that distinguish it from all other genera.

***Farlowella* Eigenmann & Eigenmann, 1889.** Type species: *Acestra acus* Kner, 1853. Holotype: NMW 47795, Venezuela, Caracas. Gender: feminine. The genus *Farlowella* is broadly distributed in Amazon, Orinoco, Paraná, and coastal rivers of the Guyana Shield. Curiously, it seems to be absent from the Pacific slope of the Andes and from the coastal rivers of the Brazilian shield. *Farlowella* has a very unique body shape that resembles of a thin stick of wood. The body is slender and elongate, often with a pronounced rostrum and a brownish color with two lateral dark stripes beginning at the tip of the rostrum, passing over the eyes and ending at the tail, which are periodically interrupted on the caudal peduncle. Species inhabit areas of gently flowing water in submerged dead leaves and sticks, among which it blends remarkably (pers. obs.). Some specimens can sometimes be found in swift current over rocks and submerged wood. These species appear scarce (Le Bail *et al.* 2000, Evers & Seidel 2005) but their mimicry can explain in part this apparent scarcity (Le Bail *et al.* 2000). Sexual dimorphism includes hypertrophied odontodes along the sides of the rostrum or the head in species with a short rostrum. These species are open water brooders (pers. obs.). The eggs are laid on open vertical surfaces such as submerged vegetation or rocks, in a single layer and are guarded by the male. Morphological (Rapp Py-Daniel 1997) and molecular (Montoya-Burgos *et al.* 1998) phylogenetic studies have placed *Farlowella* as sister to *Sturisoma*. This relationship is supported by their sexual dimor-

phism and reproduction strategy, which are identical in all respects. For these reasons, the tribe Farlowellini described by Isbrücker (1979) herein is considered a synonym of Harttiini. The character used to define Farlowellini (i. e. the relative position of the dorsal and anal fins), is subjective and could be interpreted as a generic feature following the example of European cyprinids like *Scardinius erythrophthalmus* and *Rutilus rutilus* which are also distinguished by this criterion. A revision and a key to twenty five valid species of *Farlowella* were made available by Retzer & Page (1997), and an additional species from the Rio Beni drainage in Bolivia has been described recently by Retzer (2006).

***Furcodontichthys* Rapp Py-Daniel, 1981.** Type species: *Furcodontichthys novaesi* Rapp Py-Daniel, 1981. Holotype: INPA T.79–014, Brazil, State of Amazonas, Rio Solimões, Tefé Lake at Caititu. Gender: masculine. This monotypic genus is known from the middle Amazon at Lake Tefé and from the upper Jurua River drainage in the Solimões River basin. *Furcodontichthys* inhabits sandy substrates. Evers & Seidel (2005) captured *Furcodontichthys novaesi* at night, on a sand bank, in black waters of the Rio Tefé. As with representatives of the *Loricariichthys* group, males of *Furcodontichthys* show a hypertrophied development of the lips suggesting that this genus is a lip brooder. The presence of conspicuous fringed barbels at the lip corners is unique among the Loricariinae. These barbels have branching patterns comparable to those of the *Pseudohemiodon* group.

***Harttia* Steindachner, 1877.** Type species: *Harttia loricariformis* Steindachner, 1877. Lectotype: NMW 46346, Brazil, Rio Paraíba do Sul. Gender: feminine. Distribution primarily includes rivers draining the Guyana Shield, coastal rivers in northeastern Brazil, and the Amazon basin. These rheophilic fishes are found in the upper courses of rivers over rocky and sandy bottoms. Casatti & Castro (2006) characterized ecomorphological trends in fishes living in riffles of the Rio São Francisco. They split the fish communities into three groups comprising nektonic, nektobenthic, and benthic species. Among the latter, *Harttia* sp. is supposed to be able to exploit areas with the strongest current, because of its extremely depressed body and long caudal peduncle, comparing to other species. This fact was also empirically noted by Le Bail *et al.* (2000). Sexual dimorphism includes hypertrophied odontodes on the pectoral spines and along the margins of the snout in mature males. Representatives of this genus seem to be open brooders (Dotzer & Weidner 2003). Recent evidence has suggested that Harttiini could represent a paraphyletic assemblage. Using molecular data, Montoya-Burgos *et al.* (1998) demonstrated *Harttia* to be sister to two sister clades, one consisting of *Farlowella* and *Sturisoma*, two representatives of the Harttiini, and the second including the representatives of the Loricariini. Moreover, *Harttia* is in need of revision. For example, the synonymy of *Cteniloricaria* with *Harttia* (Rapp Py-Daniel & Oliveira 2001) is questionable (Covain *et al.* 2006) because it rests solely on the characteristics of *Harttia fowleri* (Pellegrin, 1908) without considering the type species of *Cteniloricaria*. Likewise, the genus *Quiritixys* Isbrücker, 2001, also placed in synonymy by Ferraris (2003) is possibly valid. The description of *Quiritixys* is based on the unusual sexual dimorphism of *Harttia leiopleura* Oyakawa, 1993. This feature alone is insufficient to define a genus because it only concerns mature males and is most of the time seasonal in Loricariinae. This means that the majority of individuals of the species (juveniles, females, and non breeding males) cannot be diagnosed by this single criterion because they do not possess this feature. Nevertheless, the addition of some other features by Oyakawa (1993), such as the absence of the subpreopercle, supports the validity of *Quiritixys*. Other species such as *H. novalimensis* could also belong to *Quiritixys* because this species also lacks the subpreopercle, but its sexual dimorphism is undescribed. Nevertheless, Langeani *et al.* (2001) noted well developed odontodes on the posterior body of this species. *Harttia* also exhibits considerable karyotypic diversity with chromosome numbers between  $2n = 52$  and  $2n = 58$  in the four species characterized (Kavalco *et al.* 2005, Centofante *et al.* 2006). Kavalco *et al.* (2005) also reported differences in karyotypic formula, symmetry, nucleolar organizing regions (NOR), and diploid number ( $2n = 52$  versus  $2n = 56$ ) between two different populations (respectively Grande Stream and Paraitinga River) of *H. loricariformis* from the Paraíba do Sul basin. These authors hypothesized the sedentary habits of some species to explain these differences. Centofante *et al.* (2006) characterized a heteromorphic XX/XY<sub>1</sub>Y<sub>2</sub> sex chromo-

some system in *H. carvalhoi*. Currently, *Harttia* comprises 22 species (Provenzano *et al.* 2005). Partial keys are available for species occurring in Atlantic coastal drainages (Oyakawa 1993, Langeani *et al.* 2001), Amazon and Guianas drainages (Rapp Py-Daniel & Oliveira 2001), and Guianas drainages (Covain *et al.* 2006).

**Harttiella Boeseman, 1971.** Type species: *Harttia crassicauda* Boeseman, 1953. Holotype: RMNH 19418, Surinam, in a creek of the Nassau Mountains, Marowijne River drainage. Gender: feminine. This monotypic genus is only known from its type locality. The single species was collected in a little forest creek over sandy and rocky bottoms (Boeseman 1971). Sexual dimorphism is similar to that of *Harttia*, in which mature males develop hypertrophied odontodes on the pectoral spines, along the margin of the snout, and on the entire body except for the abdominal region. The phylogenetic position of *Harttiella* remains uncertain. Boeseman (1971), and Isbrücker (1981a) gave it a rather basal position within Loricariinae but its geographic isolation in the Marowijne drainage could also correspond to a more derived state within Harttiini. The morphology of *Harttiella* suggests it is a dwarf form closely related to *Harttia*. Rapp Py-Daniel (1997) tentatively placed *Harttiella* within Harttiina because of its close resemblance with *Harttia*. Unfortunately, this question may remain unresolved as Mol & Ouboter (2004) mentioned the possible disappearance of this species because of mining activities in the Nassau Mountains. This species is also interesting because of its morphological convergence with *Ixinandria*, a genus within Loricariini found in the southwestern part of the continent. The morphological likeness between *Ixinandria* and *Harttiella* may have misled Boeseman (1971) when he moved *Canthopomus montebelloi* Fowler, 1940 into *Harttiella*.

**Hemiodontichthys Bleeker, 1862.** Type species: *Hemiodon acipenserinus* Kner, 1853. Lectotype: NMW 46139, Brazil, State of Mato Grosso, Rio Guaporé drainage. Gender: masculine. This monotypic genus is widely distributed in the Amazon basin and the Essequibo, Oyapock, and Paraguay River drainages. *Hemiodontichthys* is a sand dweller that lives partially buried in the substrate, its cryptic coloration providing efficient protection. As with other representatives of the *Loricariichthys* group, mature males develop hypertrophied lips for brooding eggs. Eggs are laid in a mass and held by the male in the fold made by its lips (pers. obs.). This taxon is often compared with morphologically similar *Reganella depressa* (Kner, 1853). Isbrücker & Nijssen (1974b) and Isbrücker (1979, 1981a) characterized these two genera without discussing any relationship between them or to other taxa. Isbrücker (1979) created the subtribes Reganellina and Hemiodontichthyina to accommodate these two genera. However a comparison is made in Isbrücker (1979) between Hemiodontichthyina and Loricariichthyina with reference to abdominal cover and sexual dimorphism, comparable in both subtribes. Rapp Py-Daniel (1997) considers *Hemiodontichthys* to be the sister genus of *Reganella* on the basis of osteological data. However, the similar external morphology of these two taxa could be interpreted as an evolutionary convergence, as they occupy the same ecological niche. Considering morphological data given in the key, particularly the mouth structure and abdominal cover, *Hemiodontichthys* is assigned herein to the *Loricariichthys* group. Molecular data (Montoya-Burgos *et al.* 1998) tend to support this relationship by placing *Hemiodontichthys* as sister to *Loricariichthys*. We assign *Reganella* to the *Pseudohemiodon* group on the basis of its mouth shape, the presence of vestigial fringed barbels, its strongly depressed body, and the characteristics of its abdominal cover made of little plates without particular organization and extending toward the lower lip margin. This kind of organization in the abdominal plating is never observed within the *Loricariichthys* group. Thus, the appearance of a rostrum and the loss of maxillary teeth could have evolved independently in different lineages subjected to similar environmental constraints. Given its broad geographic range and variation in morphometric features, *Hemiodontichthys acipenserinus* could comprise a species complex. Isbrücker & Nijssen (1974b) reported that populations from the Amazonian region tend to be more slender than those from the Paraguay and Guaporé Rivers.

**Ixinandria Isbrücker & Nijssen, 1979.** Type species: *Loricaria steinbachi* Regan, 1906. Lectotype: BMNH 1906.5.31: 37, Argentina, Rio Salado drainage at Salta. Gender: feminine. Distribution includes rivers of the Atlantic slope of the Andes in Bolivia and Argentina. According to Gladys Monasterio de Gonzo (pers. comm.), *Ixinandria steinbachi* occurs in Salta province in mountainous areas at high altitudes ranging from

around 1000 to 2900 meters above sea level. This rheophilic species lives in fast flowing and very oxygenated waters. Its color pattern reflects mimicry with stoned bottoms. Fertilized eggs have been found on the hidden surface of a stone, suggesting that *I. steinbachi* could be a cavity spawner. Sexual dimorphism includes hypertrophied odontodes around the head margin and on the pectoral spines of mature males. The phylogenetic position of *Ixinandria* within Loricariini remains uncertain. Reis & Cardoso (2001) suggested that *Ixinandria* could be synonym of *Rineloricaria*. This hypothesis seems plausible considering the weakness of the diagnostic feature given for *Ixinandria*, its naked belly, and several species of *Rineloricaria* from South-East Brasil or Argentina with the belly partly covered such as *R. maquinensis*, *R. aequalicuspis* or *R. misionera*. Nevertheless, the typology of *Rineloricaria lima* needs clarification prior to further investigations on the taxonomy of *Ixinandria*. Two valid species are currently recognized (Ferraris 2003).

***Lamontichthys* Miranda Ribeiro, 1939.** Type species: *Harttia filamentosa* La Monte, 1935. Holotype: AMNH 12616, Brazil, Rio Jurua drainage, Rio Embira. Gender: masculine. *Lamontichthys* is distributed in the northwestern part of South America in the upper Amazon and Orinoco River drainages, and in the Lake Maracaibo region. Species in this genus occupy the same ecological niche as those of *Harttia*. They mainly live in the mainstream of rivers, on rocky and sandy bottoms (Taphorn & Lilyestrom 1984). Sexual dimorphism includes hypertrophied odontodes on the pectoral spines in mature males. *Lamontichthys* is an open brooder. Eggs are laid on an open surface such as rocks, submerged wood or plants, and are generally exposed to the current. Females lay a few large-sized (1.4 to 1.8 mm in diameter) yellowish eggs during each spawning event (Taphorn & Lilyestrom 1984). These authors expressed doubts concerning the value of the character given by Isbrücker & Nijssen (1978) to diagnose *Lamontichthys* (i. e. the number of pectoral fin rays i–7 versus i–6 for all other Loricariinae). However, this feature is present in all species assigned to this genus, suggesting a common origin. Isbrücker & Nijssen (1976a) demonstrated that fin ray numbers, with few exceptions, were particularly conservative among members of Loricariinae. The phylogenetic position of *Lamontichthys* remains uncertain. Rapp Py-Daniel (1997) considers it to be sister to *Harttia*, whereas *Lamontichthys* shows much more similarities with *Pterosturisoma*, a monotypic genus which only differs from *Lamontichthys* by the number of pectoral fin rays. Nevertheless, Rapp Py-Daniel (1997) tentatively placed *Pterosturisoma* within Harttiina because of its similarity with *Lamontichthys*, but did not provide any hypotheses on the phylogenetic relationships between these genera. *Lamontichthys* includes four valid species, and a key to their identification is available in Taphorn & Lilyestrom (1984).

***Limatulichthys* Isbrücker & Nijssen, 1979.** Type species: *Loricaria punctata* Regan, 1904. Lectotype: BMNH 1893.4.24: 18, Brazil, Rio Negro at Manaus. Gender: masculine. This monotypic genus is widely distributed in the Amazon basin and in the Essequibo River drainage. *Limatulichthys* is a sand dweller. As suggested by the hypertrophied development of lower lip in males, *Limatulichthys* may be a lip brooder like many representatives of the *Loricariichthys* group. Isbrücker & Nijssen (1976b) revised *Pseudoloricaria* Bleeker, 1862, in which they assigned two species: *P. laeviuscula* (Valenciennes, 1840) and *P. punctata* (Regan, 1904), and designated a lectotype for the latter from BMNH 1893.4.24: 18, described by Regan (1904) as *Loricaria punctata*. Isbrücker & Nijssen (1976b) also put *Loricaria griseus* Eigenmann, 1909, *Rhineloricaria petleyi* Fowler, 1940, and *Loricariichthys parnahybae* Fowler, 1941 into the synonymy of *Pseudoloricaria punctata* (Regan, 1904). Isbrücker & Nijssen (1976b: p. 125) wrote: “Kner (1854b: 281) published a manuscript name “*Loricaria punctata* Natterer” in the synonymy of “*Ancistrus duodecimalis*?” (Valenciennes). Since this name fails to satisfy the provisions in article 11(d) of the International Code of Zoological Nomenclature (1964), therefore *Loricaria (Pseudoloricaria) punctata* Regan, 1904 is not subject to the Law of Homonymy”. According to Ferraris (2003) *Loricaria punctata* Regan, 1904 constitutes a primary homonymy of *Loricaria punctata* Kner (ex Natterer), 1854, a representative of the genus *Glyptoperichthys*. However, it appears that Kner (1854) does not refer to Natterer’s manuscript for a description of *Loricaria punctata*, but only to a specimen (number 87) recorded in Natterer’s field notes and identified as a representative of the genus *Ancistrus*. Consequently, according to articles 11.5, 11.6, and 12.3 of the International Code of Zoological Nomenclature

(ICZN, 1999), the name *Loricaria punctata* Kner is not made available. Later, Günther (1864) refers to Kner's work using the name *Loricaria punctata* as an available name in a new combination *Pterygoplichthys punctatus*. According to ICZN article 11.5.2, referring to an unavailable name does not make it available by its mere citation. Consequently, this species name is hereby new and has to be considered as *Pterygoplichthys punctatus* Günther, 1864. Steindachner (1881) used the name "*Chaetostomus punctatus* sp. Gthr." and redescribed the species without taking into account the name *Loricaria punctata*. Consequently, the new species described as *Loricaria punctata* by Regan (1904) is not a homonym of *Loricaria punctata* Kner (1854). Regan (1904) also confirmed the status of *Pterygoplichthys punctatus* Günther, 1864. Conversely, Isbrücker (1980) considered that Günther (1864) validated the name *Loricaria punctata* Natterer, 1854 by authorship to Natterer. However, the name *Loricaria punctata* Natterer is not available as seen previously. Moreover, Günther (1864) published the description of *Pterygoplichthys punctatus* with *Loricaria punctata* Natterer listed as junior synonym. Considering ICZN article 11.6, the name *Loricaria punctata* Natterer is not available. Isbrücker *et al.* (2001) accepted the primary homonymy between *L. punctata* Natterer and *L. punctata* Regan, considered *Limatulichthys griseus* (Eigenmann, 1909) as a distinct species, and therefore established *Limatulichthys petleyi* (Fowler, 1940) as a substitution name for *Limatulichthys punctatus* (Regan, 1904). Ferraris (2003) considered *L. petleyi* to be a synonym of *L. griseus* and also established the latter as a substitution name for *L. punctata*. The nomenclatural status of *Limatulichthys* remains unclear and this case should be submitted to the International Commission on Zoological Nomenclature in order to rule on the validity of *Loricaria punctata* Regan, 1904.

***Loricaria* Linnaeus, 1758.** Type species: *Loricaria cataphracta* Linnaeus, 1758. Lectotype: NRM 33, In South America, also holotype of *Loricaria dura* Bleeker, 1862, Surinam. Gender: feminine. This genus is distributed east of the Andes on nearly the entire subcontinent. Species occur in a variety of habitats from the main flow of rivers on sandy and rocky bottoms to flooded areas and lakes over muddy and sandy bottoms. Sexual dimorphism includes hypertrophied development of the pectoral spines, blunt odontodes on the pelvic and anal fin spines, and tooth crowns becoming shortened and rounded in mature males (Isbrücker 1981b). Males are abdomino-lip brooders. *Loricaria* is the nominal genus of the family. Phylogenetic relationships within *Loricaria* and among other members of Loricariini remain uncertain. Its external morphology shows few shared derived characters, making comparison with other genera difficult. *Loricaria* has been hypothesized to occupy a basal position among members of the subtribe Loricariina, with the other genera possessing derived characters. Based on the characteristics of its mouth, *Loricaria* appears to maintain a close relationship with representatives of the *Pseudohemiodon* group. This hypothesis has been proposed in the studies of Rapp Py-Daniel (1997) and Montoya-Burgos *et al.* (1998), in which *Loricaria* maintained a sister relationship to the *Pseudohemiodon* group. However, these authors did not resolve relationships among species of the *Loricaria* group. Kavalco *et al.* (2005) reported karyotypic diversity ranging from  $2n = 62$  to  $2n = 68$  for the four species characterized. Under the impression that the original syntypes were lost, Isbrücker (1972) established a neotype for *L. cataphracta* (ZMA 109.616). Between 1972 and 1981, Isbrücker learned that the two syntypes did in fact exist and are currently housed at the Swedish Museum of Natural History in Stockholm. Based on a photograph of two syntypes, Isbrücker (1981b) designated one as the lectotype (NRM 33). The rediscovery of these syntypes invalidated the previous neotype according to the ICZN (1999), article 75.8. The disposition of the lectotype according to Eschmeyer (1998), which is based on Wheeler (1989), is Zoological Museum, University of Copenhagen (ZMUC 27). However, Wheeler (1989: pp. 214–215) confirmed Isbrücker's designation of the lectotype: "Two loricariid specimens from the collection of King Adolf Fredrik, one of which has been designated as the lectotype of *L. cataphracta* by Isbrücker (1981), are preserved in the Swedish Museum of Natural History, Stockholm. This specimen was certainly the specimen which Linnaeus used for the major source material of his description (Fernholm & Wheeler, 1983)". Moreover, concerning specimen ZMUC 27 deposited in Copenhagen, Wheeler (1989: p. 215) concluded: "It thus seems certain that this specimen is not one of those referred to by Linnaeus (1758) in his diagnosis of the species, or its variety



beta". *Loricaria* was revised by Isbrücker (1981b) who recognized eleven valid species. For lack of clear diagnostic features, *Proloricaria* Isbrücker, 2001 is herein considered a junior synonym of *Loricaria*. A twelfth species has been described from North-East of Argentina by Rodríguez & Miquelarena (2003).

***Loricariichthys* Bleeker, 1862.** Type species: *Loricaria maculata* Bloch, 1794. Lectotype: ZMB 3163, type locality restricted to Surinam (Isbrücker 1971). Gender: masculine. *Loricariichthys* is widely distributed in the Amazon basin, the Paraná system, and coastal rivers of the Guyana and Brazilian Shields. These species occur in a large diversity of habitat over sandy and muddy bottoms. Like other members of the *Loricariichthys* group, *Loricariichthys* species are lip brooders. Sexual dimorphism includes hypertrophied development of the lips, which are used by the male to incubate the eggs. During the spawning period, the first function of this organ (mainly adherence to the substrate) is reoriented toward a new reproductive function. Although this genus is well diagnosed, the species are very similar and difficult to identify. Moreover, missing holotypes and type localities has led to uncertain taxonomic status for several species which would benefit from a generic revision. *Loricariichthys* seems to be intermediate between *Limatulichthys* and *Pseudoloricaria* on one hand, and *Furcodontichthys* and *Hemiodontichthys* on the other. Concerning the karyotypic characteristics of *Loricariichthys*, Kavalco *et al.* (2005) reported a diploid number of  $2n = 56$  for the two species characterized. A ZZ/ZW sex chromosome system was also reported for *L. platymetopon* by Kavalco *et al.* (2005) and Centofante *et al.* (2006). Seventeen valid species are assigned to this genus (Ferraris 2003). A key to the southern species is available in Reis & Pereira (2000).

***Metaloricaria* Isbrücker, 1975.** Type species: *Metaloricaria paucidens* Isbrücker, 1975. Holotype: IRSNB 549, French Guiana, Maroni River drainage, Ouaiqui River upstream of Bali falls. Gender: feminine. *Metaloricaria* is only known from the Guyana Shield in French Guiana and Surinam where the species occupy an ecological niche similar to that of *Harttia*. The species are rarely found in their natural environment and inhabit primarily streams over rocky and sandy substrates (Le Bail *et al.* 2000). Sexual dimorphism includes hypertrophied development of odontodes arranged in brushes along the sides of the head and on the spine and rays of the pectoral fins in mature males. Females also possess such brushes along sides of the head, but do not seem to develop pectoral-fin enlarged odontodes (pers. obs. on an adult specimen collected in Crique Voltaire, Maroni drainage, that spontaneously laid large yellowish eggs after catching). *Metaloricaria* is a curious genus because of its geographic isolation and unique combination of morphological characteristics. The length of the maxillary barbels (longer than in all other Harttiini), low number of teeth and their reduced size, reduction of the number of caudal-fin rays (i-11-i), and sexual dimorphism reminiscent of that seen in the *Rineloricaria* group, tend to support a closer relationship of *Metaloricaria* with the Loricariini. This agrees with Rapp Py-Daniel (1997), who also suggested placement in Loricariini, but outside of any clade, because of an apparent lack of affinities to other Loricariini. The phylogenetic position of *Metaloricaria* remains uncertain. It was revised by Isbrücker & Nijssen (1982), in which a key to the two species is available.

***Paraloricaria* Isbrücker, 1979.** Type species: *Loricaria vetula* Valenciennes, 1836. Holotype: MNHN A.8996, no type locality, described by Valenciennes in Cuvier & Valenciennes (1840: 466) from the surroundings of Buenos-Aires. Gender: feminine. This genus is distributed in the southern part of the continent in the Paraguay, Uruguay, and La Plata River basins. Males *Paraloricaria* are abdomino-lip brooders (Reis & Pereira 2000). It is assigned to the *Loricaria* group but it shows characteristics that possibly represent close phylogenetic relationship with representatives of the *Pseudohemiodon* group (a group established on the basis of a filamentous structure of the lips as also found in the *Loricaria* group). In particular, it shows a strongly flattened body, weak postorbital notches, long and ramified maxillary barbels, and overall, conspicuous fringed barbels. Three valid species are assigned to this genus (Ferraris 2003).

***Planiloricaria* Isbrücker, 1971.** Type species: *Pseudohemiodon (Planiloricaria) cryptodon* Isbrücker, 1971. Holotype: ZFMK 1865, Peru, Rio Ucayali drainage near Pucallpa. Gender: feminine. This monotypic genus is distributed in the upper Amazon basin, including the Ucayali, Purus, and Mamoré River drainages.

*Planiloricaria* inhabits sandy substrates in the main streams of large rivers (Evers & Seidel 2005). Reproductive ecology is unknown but could be reminiscent of those of other representatives of the *Pseudohemiodon* group. Evers & Seidel (2005) characterized sexual dimorphism by the shape of the genital area. The genital area in males is elongate and narrow compared with the large and roundish area of females. *Planiloricaria* shows derived features such as a reduction in size and number of teeth, premaxillary teeth absent, a circular head shape, and eyes reduced in size without iris operculum.

***Pseudohemiodon* Bleeker, 1862.** Type species: *Hemiodon platycephalus* Kner, 1853. Holotype: lost (Isbrücker 1971), Brazil, Rio Cuiaba. Gender: masculine. *Pseudohemiodon* is distributed in the Amazon and Paraná River basins. This genus is also known from the Orinoco system. Like other members of the *Pseudohemiodon* group, *Pseudohemiodon* occurs primarily over sandy substrates. This ecological specialization is reflected by the dramatic dorsoventral compression of the body and pelvic fins that are used mainly for locomotion on sand. Sexual dimorphism is unknown, but like the other genera in this group, *Pseudohemiodon* species are abdomino-lip brooders (pers. obs.). The very large eggs are incubated by the male. Considering their ecological and morphological specialization, representatives of the *Pseudohemiodon* group may represent highly derived Loricariinae. This is in agreement with Rapp Py-Daniel (1997), who found *Planiloricaria* nested within Loricariini, as sister group of *Loricaria*. Seven species are currently recognized (Ferraris 2003). A partial key to the species is available in Isbrücker (1975).

***Pseudoloricaria* Bleeker, 1862.** Type species: *Loricaria laeviscula* Valenciennes, 1840. Holotype: MNHN B 365, no type locality. Gender: feminine. This monotypic genus is distributed in the middle and lower Amazon basin. *Pseudoloricaria laeviscula* was collected over sandy bottoms, in clear waters, in the main flow of rivers, and in neighboring temporary ponds (pers. obs.). Sexual dimorphism includes hypertrophied development of the lower lip suggesting that *Pseudoloricaria* is a lip brooder. The phylogenetic position of *Pseudoloricaria* is uncertain. This genus closely resembles *Limatulichthys* in external morphology. Isbrücker & Nijssen (in Isbrücker 1979) considered *Limatulichthys* to be the most primitive representative of the *Loricariichthys* group. Consequently, *Pseudoloricaria* could occupy a basal position among its group, as the sister genus of *Limatulichthys*. Rapp Py-Daniel (1997) found *Pseudoloricaria* and *Limatulichthys* as sister groups to the Hemiodontichthyina but didn't resolve the relationships between these two genera. A key to distinguish *Pseudoloricaria* (*P. laeviscula*) from *Limatulichthys* (*Pseudoloricaria punctata* in Isbrücker & Nijssen 1976b) is available in Isbrücker & Nijssen (1976b).

***Pterosturisoma* Isbrücker & Nijssen, 1978.** Type species: *Harttia microps* Eigenmann & Allen, 1942. Lectotype: CAS 28543, Peru, Iquitos. Gender: neutral. This monotypic genus is known only from the upper Amazon River basin. *Pterosturisoma* is a rheophilic species. Evers & Seidel (2005) described this species as an open brooder. Males do not possess hypertrophied odontodes neither on the sides of head, nor on pectoral-fin spines. Nevertheless, Evers & Seidel (2005) distinguished both sexes by the width of a naked trapezoidal area framed by four bony plates in the genital region. This area appeared broader in females, and longer and narrower in males. *Pterosturisoma* appears morphologically very similar to *Lamontichthys* from which it differs primarily in the number of pectoral fin rays (i–6 in the former versus i–7 in the latter). These two genera share features with *Sturisoma* such as similar body depth at dorsal-fin origin, presence of filamentous extensions on caudal-fin spines, and complete abdominal plate cover extending to the lower lip margin. These features are never observed in *Harttia*, suggesting these two genera share a closer relationship with *Sturisoma* than with *Harttia* as hypothesized by Rapp Py-Daniel (1997).

***Pyxiloricaria* Isbrücker & Nijssen, 1984.** Type species: *Pyxiloricaria menezesi* Isbrücker & Nijssen, 1984. Holotype: MZUSP 26800, Brazil, Mato Grosso do Sul, Miranda. Gender: feminine. This monotypic genus is only known from the Paraguay River drainage. *Pyxiloricaria menezesi* inhabits sandy substrates and is sympatric with representatives of the genus *Pseudohemiodon*. Sexual dimorphism and reproductive ecology are unknown. In the *Pseudohemiodon* group, *Pyxiloricaria* more closely resembles *Pseudohemiodon* than other representatives of the group. Moreover, with *Loricaria*, it shares filamentous lips, inconspicuous fringed

barbels on the lower lip, and shorter maxillary barbels. The phylogenetic position of *Pyxiloricaria* remains uncertain, and its presence in the *Pseudohemiodon* group could be artificial, given the characters shared with *Loricaria*. Herein, following Isbrücker & Nijssen (1984), it is maintained in the *Pseudohemiodon* group.

**Reganella Eigenmann, 1905.** Type species: *Hemiodon depressus* Kner, 1853. Lectotype: NMW 9438, Brazil, Rio Negro, Marabitanas. Gender: feminine. This monotypic genus is distributed in the middle Amazon River basin. Ecological and behavioral data are unavailable. The dorsoventrally flattened body suggests that *Reganella* inhabits flowing waters over sandy substrates. *Reganella depressa* is a poorly known species and uncommon in collections. Its phylogenetic position remains uncertain and relationship to other representatives of the *Pseudohemiodon* group is unclear.

**Rhadinoloricaria Isbrücker & Nijssen, 1974.** Type species: *Loricaria macromystax* Günther, 1869. Holotype: BMNH 1869.5.21.8, Peru, Amazon River. Gender: feminine. This monotypic genus is distributed in the upper Amazon and Orinoco River basins, Essequibo, and Tocantins drainages. Although poorly known and uncommon in collections, *Rhadinoloricaria* is known to occur over sandy substrates. Ecological and behavioral data are unavailable. Most studies of *Rhadinoloricaria* are based on the holotype, which is in a poor state of preservation (particularly its mouth, which is one of the most important features for the study of this group). The holotype is an adult with complete abdominal plate cover; smaller specimens have incomplete abdominal plate cover forming a double median row of platelets. This feature, which is also observed in *Apistoloricaria*, *Crossoloricaria*, and one species of *Dasylicaria*, could reflect a common developmental pattern of abdominal plates among these taxa. Consequently, its use as a diagnostic feature should be rejected (see *Crossoloricaria* above).

**Ricola Isbrücker & Nijssen, 1974.** Type species: *Loricaria macrops* Regan, 1904. Lectotype: BMNH 1868.9.16.1, Argentina, Rio de la Plata. Gender: feminine. This monotypic genus is known from the lower Paraná River basin. Ecological and behavioral data are unavailable. This genus is interesting in many respects. It shares features with representatives of different groups within Loricariini. For example, it possesses conspicuous fringed barbels on the lower lip, a feature shared by the representatives of the *Pseudohemiodon* group. It also bears numerous papillae on the inner surfaces of the lips and numerous straight bicuspid teeth (approx. 15 per premaxillae) that are characteristic of the *Rineloricaria* group.

**Rineloricaria Bleeker, 1862.** Type species: *Loricaria lima* Kner, 1853. Holotype: NMW probably lost (Isbrücker, 1979), from Brazil according to Natterer. Gender: feminine. This genus, by far the most speciose in Loricariinae, is widely distributed on nearly the entire subcontinent, from Costa Rica to Argentina, on both slopes of the Andes. The species inhabit an extremely diverse array of environments. Sexual dimorphism includes hypertrophied development of the odontodes along the sides of the head, on the pectoral spines and rays, and predorsal area of mature males. Several species also show hypertrophied development of the odontodes on the entire caudal peduncle. *Rineloricaria* are cavity brooders (pers. obs.). Numerous eggs (often more than 100) are laid attached to one another in single layer masses on the cavity floor, and are brooded by males. *Rineloricaria* exhibit high levels of karyotypic diversity with chromosome numbers ranging from  $2n = 36$  to  $2n = 70$  in the five species characterized (Kavalco *et al.* 2005). These authors also described, according to Giuliano-Cataneo (1998), a Robertsonian polymorphism between several populations of *R. latirostris*, with a variation of  $2n = 36$  to  $2n = 48$  chromosomes. If the loss of the holotype of *R. lima* is confirmed, a neotype must be designated in order to permit all the necessary clarifications for a detailed and much needed revision of this genus. The characters given by Kner (1853), although very detailed, are valid for almost all congeneric species. Without the type locality, it is presently impossible to decide which species represents *R. lima*. Isbrücker & Nijssen (1976a) and Isbrücker (1981a) proposed the revalidation of *Hemiloricaria* Bleeker, 1862 (type species: *Hemiloricaria caracasensis*), but they finally left it in the synonymy of *Rineloricaria* because of the lack of sufficient features to split these two genera. In 2001, Isbrücker *et al.* revalidated *Hemiloricaria* and created two new genera: *Fonchiichthys* (type species: *Loricaria uracantha*) and *Leliella* (type species: *Rineloricaria heteroptera*) on the basis of subtle differences in the sexual dimorphism. These

characters are expressed only during the spawning period and are outweighed by other shared characters used to diagnose *Rineloricaria*. Moreover, as specified by Isbrücker & Nijssen (1976a: pp. 110–111) in the description of *R. heteroptera*: “As in *Spatuloricaria* Schultz, 1944 it shows strong secondary sexual dimorphism: males develop ‘bristles’ along sides of snout, usually also on dorsum of pectoral fin spine and rays, and often dorsum of head, on post-occipital and predorsal scutes. There are specific differences in the development of male bristles”. Following this interpretation, the characters given to define *Leliella* and *Fonchiiichthys* can be regarded as species specific characters. Herein, *Hemiloricaria*, *Leliella*, and *Fonchiiichthys* are considered as synonyms of *Rineloricaria* for lack of sufficient diagnostic features. Forty nine valid species are assigned to this genus considering Ferraris (2003), Knaack (2003), and Rodríguez & Miquelarena (2005).

***Spatuloricaria* Schultz, 1944.** Type species: *Spatuloricaria phelpsi* Schultz, 1944. Holotype: USNM 121121, Venezuela, Rio Socuy. Gender: feminine. This genus is distributed in the northwestern part of the subcontinent, in drainages of the Pacific and Atlantic Slopes of the Andes. Several species occur also in the upper Amazon River basin, upper Paraguay, and São Francisco River basins. Ecological data are unavailable and reproductive biology is unknown. Sexual dimorphism includes hypertrophied development of claw-like odontodes along the sides of the head and on the pectoral spines in mature males. *Spatuloricaria* is in need of revision, as species boundaries and distributions are poorly known. The phylogenetic position of *Spatuloricaria* remains uncertain. Rapp Py-Daniel (1997) placed *Spatuloricaria* at the base of a clade including representatives of the *Loricaria* and *Pseudohemiodon* groups. Its dentition, with few teeth on the premaxillae, and its abdominal cover consisting of minute disjointed platelets resembles that of some representatives of the *Loricaria* group. Conversely, the papillose surface of the lips and sexually dimorphic features are more characteristic of the *Rineloricaria* group. Eleven valid species are currently recognized (Ferraris 2003).

***Sturisoma* Swainson, 1838.** Type species: *Loricaria rostrata* Spix & Agassiz, 1829. Brazilian rivers. Holotype: lost (Isbrücker 1979). Gender: neuter. The species of the genus *Sturisoma* are widely distributed on both slopes of the Andes, in Panama and Colombia, and in the Amazon, Orinoco, and Paraná River basins. *Sturisoma* inhabit gently to swiftly flowing white waters (Evers & Seidel 2005) where submerged wood is abundant in the main flow of rivers. Sexual dimorphism includes hypertrophied odontodes on the sides of the head of the male. As representatives of *Farlowella*, *Sturisoma* species are open brooders (pers. obs.). Kavalco *et al.* (2005) reported a diploid number of  $2n = 74$  chromosomes for the single species characterized: *S. cf. nigrirostrum*. A neotype has yet to be designated for *Sturisoma rostratum*, the type species, which was destroyed during World War II (Isbrücker 1979). Neotype designation is needed to fix the type locality, which is unspecified and may pertain to several of the currently recognized species. Ghazzi (2003) revised genus, but it remains unpublished and unavailable for the moment. *Sturisoma* has been shown to be sister to *Farlowella* according to Rapp Py-Daniel (1997) and Montoya-Burgos *et al.* (1998). Ghazzi (2005) confirms this relationship. Sexual dimorphism and reproductive strategy are comparable in both genera and tend to corroborate the molecular and morphological data. Fifteen valid species are currently recognized (Ferraris 2003, Ghazzi 2005). Ghazzi (2005) described a new species, *Sturisoma kneri*, replacing an unavailable name, *Loricaria kneri*, proposed by Tortonese (1940). She argued (p. 564) that “Tortonese’s (1940) intention was solely to publicize the large number of species housed in Museo di Torino; it was not his intention to validate De Filippi’s manuscript names.” However Tortonese (1940: p. 134–135) explained in his introduction: “*Infine, ho avuto anch’io la ventura di trovare nei nuclei di materiale da me studiato diversi Pesci che ho creduto dover attribuire a specie non ancora note.*” In this citation we can see the intention of Tortonese to publish the names of new species, in part from De Filippi’s manuscript. The name *Loricaria kneri* De Filippi in Tortonese, 1940 is here used as the valid name of this species, because the author refers to a holotype and because he gives a short diagnosis according to De Filippi’s manuscript. Thus, Tortonese made the name *Loricaria kneri* De Filippi available. Secondly, Tortonese proposes that *L. kneri* could be a representative of the genus *Sturisoma* as he specified in his introduction: “*Ciascuna specie è elencata secondo l’ordine sistematico, col nome dell’A. che per primo la descrisse: ad esso seguono, oltre le indicazioni bibliografiche, il nome cor-*

etto – se il primo è passato in sinonimia o vi è stato cambiamento di genere – il numero che il materiale porta nel Catalogo della collezione e i dati relativi alla provenienza, al raccoglitore o donatore e allo stato attuale di conservazione.” The statement on the validity of *Loricaria kneri* De Filippi in Tortonese, 1940 should be submitted to the International Commission on Zoological Nomenclature.

***Sturisomatichthys* Isbrücker & Nijssen, 1979.** Type species: *Oxyloricaria leightoni* Regan, 1912. Lectotype: BMNH 1909.7.23.45, Colombia, Honda. Gender: masculine. The genus *Sturisomatichthys* is distributed in the northwestern part of South America, on the Pacific and Atlantic slopes of the Andes. The species appear to occupy the same ecological niche as those in *Sturisoma*. Sexual dimorphism and reproductive biology of *Sturisomatichthys* are also similar to *Sturisoma*. *Sturisomatichthys* is distinguished from *Sturisoma* primarily by the absence of a rostrum. Only one species, *Sturisomatichthys citurensis*, from Panama, seems to be significantly different from all congeneric species in having an abdominal plate cover consisting of small platelets without any particular organization. Other species may represent a species complex with a short snout as in the genus *Farlowella* with reference to the representatives of the *F. curtirostra* group. The weakness of this diagnostic feature could lead to the synonymy of *Sturisomatichthys* with *Sturisoma*.

## Conclusions

This work attempts to provide a useful tool for the identification of representatives of the subfamily Loricariinae in the laboratory as well as in the field. As laboratory apparatus are rarely available in the field, an approach mainly based on the external morphology was preferred. It also provides a short summary of the present knowledge concerning this group. Major taxonomic problems are underlined and solutions are proposed. This study also tries to promote original statistical tools such as the Hill & Smith analysis (1976) and cluster analysis, still rarely used in morphology for solving complex problems of identification. Although the matrix analyzed here contains phylogenetic information, the methods used do not allow robust phylogenetic inferences. Thus, the tree proposed here must not be interpreted as a phylogeny, but as a representation of groups of individuals sharing common morphological characteristics. The results of this study reflect our present knowledge concerning the taxonomy of Loricariinae and encourage future research endeavors into the evolutionary history of this group.

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