Phylogeny of the subfamily Corydoradinae Hoedeman, 1952 (Siluriformes: Callichthyidae), with a definition of its genera

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ABSTRACT—A phylogenetic hypothesis of relationships within the callichthyid subfamily Corydoradinae is proposed based on 83 characters. The monophyly of the subfamily is well supported, as are those of two included genera, *Aspidoras* and *Brochis*. However, the monophyly of *Corydoras*, as traditionally defined, is not corroborated, with some of currently included species being more closely related to *Aspidoras* or *Brochis* than to nominal congeners. These conclusions contrast with a previous hypothesis, which considered *Brochis* and *Corydoras* as forming a monophyletic assemblage, with *Aspidoras* as its sister-group. A clade composed of *Aspidoras* and the species currently assigned to *Corydoras*, *C. barbatus*, *C. macropterus*, *C. prionotus* and *Corydoras* sp. A, is herein recognized based on the following characters: possession of anterior portion of frontal bone long, hypobranchial 2 well ossified, free margin of opercle angulated, epiphyseal branch of the supraorbital canal long, and ossified portion of pectoral spine reduced. The remaining corydoradines are grouped in a monophyletic assemblage with complex vertebra compact, posterior expansion of ceratobranchial 3 notched, presence of triangular dorsal lamina on anguloarticular, and medial expansion of coracoid exposed. A new classification is proposed to accommodate the monophyletic groups defined in the present study. Discussions about subgroups within each major clade are provided.

RESUMO—Uma hipótese sobre as relações filogenéticas da subfamília de Callichthyidae, Corydoradinae, é proposta com base em 83 caracteres. O monofiletismo da subfamília é corroborado, assim como o de dois gêneros nela incluídos, *Aspidoras* e *Brochis*. Entretanto, o monofiletismo de *Corydoras*, como tradicionalmente definido, não é corroborado, com algumas de suas espécies atuais sendo mais proximamente relacionadas a *Aspidoras* ou *Brochis* do que aos seus congêneres nominais. Estas conclusões contrastam com uma hipótese prévia que considera *Brochis* e *Corydoras* formando um agrupamento monofilético, com *Aspidoras* como seu grupo-irmão. Um clado composto por *Aspidoras* e as espécies assinaladas a *Corydoras*, *C. barbatus*, *C. macropterus*, *C. prionotus* e *Corydoras* sp. A, é diagnosticado pelos seguintes caracteres: porção anterior do osso frontal alongado, hipobranquial 2 bem ossificado, margem livre do opérculo angulada, ramo epifiseal do canal supra-orbital alongado, e porção ossificada do espinho peitoral reduzida. Os demais coridoradíneos são reunidos em um grupo monofilético definido pela vértebra complexa compacta, expansão posterior do ceratobranquial 3 com um entalhe, presença de lâmina dorsal triangular no ângulo-articular e expansão medial do coracóide exposta. Uma nova classificação é proposta para acomodar os grupos monofiléticos definidos no presente estudo. Discussões sobre subgrupos de cada um dos principais clados são fornecidas.

INTRODUCTION

The subfamily Corydoradinae includes about 90% of the species in the Neotropical catfish family Callichthyidae and is one of the most diverse siluriform assemblages in the Neotropics, with approximately 170 valid species (Nelson, 1994; Reis, 1998a). Species of the Corydoradinae are of small size (maximum about 90 mm in standard length) and are easily distinguished from other callichthyids by their deep bodies and short maxillary barbels. The Corydoradinae is currently composed of the genera *Corydoras* Lacépède, *Brochis* Cope, and *Aspidoras* Ihering (Reis, 1998a). The subfamily has a predominantly cis-Andean distribution north of the Rio de La Plata system, in Argentina, with only one trans-Andean species, *Corydoras melanotaenia* Regan,

from the Rio Magdalena basin (however, this could be a mislocation; see Nijssen and Isbrücker, 1983). Representatives of the Corydoradinae are found in several freshwater environments, ranging from fast-flowing piedmont streams with sandy or rocky bottom to lowland pools with muddy bottom. They are well known among fishkeepers worldwide, with *Corydoras* species being particularly popular.

Most of the studies dealing with Corydoradinae focused on species descriptions and taxonomic revisions (*e.g.* Ihering, 1907; Knaack, 1961; Nijssen, 1970; Nijssen and Isbrücker, 1976, 1983, 1986a; Burgess, 1993), and very little is known about the phylogenetic relationships of its genera, largely due to the scarcity of data on internal anatomy. Nijssen (1970) and Nijssen and Isbrücker (1980) arranged the species of *Corydoras* in several groups on the

basis of color pattern, morphometric and meristic data, however those groupings were not intended to reflect phylogenetic relationships (Nijssen and Isbrücker, 1986a). Only two attempts have been made to elucidate the interrelationships among Callichthyidae genera: Gosline (1940) and Reis (1998a), with only the latter study carried out under the cladistic paradigm. Although the recognition of the monophyly of *Aspidoras* and *Brochis*, Reis (1998a) recognized the genus *Corydoras* tentatively on the basis of absence of synapomorphies defining the other two Corydoradinae genera.

In the present study a phylogenetic analysis of the subfamily Corydoradinae is conducted, using as a framework recent phylogenetic hypotheses involving the Callichthyidae (Reis, 1997, 1998a), which demonstrated overwhelmingly the monophyly of Corydoradinae. The present analysis focused on species-level relationships in all three currently recognized genera of the Corydoradinae with the objective of testing the monophyly of each genus and determining the interrelationships within *Corydoras*, the most species-rich catfish genus. A new classification is proposed for the subfamily in order to reflect the monophyletic groups defined herein.

HISTORICAL BACKGROUND OF THE CORYDORADINAE

Various changes occurred in the classification of the Callichthyidae between the time of the original description of *Silurus callichthys* (= *Callichthys callichthys*) by Linnaeus (1758), and Hoedeman's (1952) original proposal of the subfamilies Callichthyinae and Corydoradinae. The history of what is now termed the Corydoradinae begins with the description of *Cataphractus punctatus* Bloch (now *Corydoras punctatus*).

Lacépède (1803) later described the genus *Corydoras*, including a new species *C. geoffroy* (the type-species of the genus, by monotypy). The name *Cordorinus* proposed by Rafinesque (1815) is an unjustified emendation of *Corydoras* (Follett, 1952; Nijssen and Isbrücker, 1980).

Callichthyid catfishes were first recognized as a group (named the "Callichthini") within the family Siluridae by Bonaparte (1838). In that same year, Swainson described *Hoplisoma* (subsequently emended to *Hoplosoma* by Agassiz in 1846) and designated *Cataphractus punctatus* as its type-species, since *Cataphractus* was already preoccupied (*Cataphractus* Catesby, 1771, belonging to the family Doradidae; although the names proposed in Catesby did not follow Linnaean nomenclature, they became available with the corrections to a Linnaean nomenclature in Edward's Appendix [in Catesby, 1771];

see ICZN, 1925: opinion 89, 1954: opinion 259, 1985; Eschmeyer, 1990).

Valenciennes (*in* Cuvier and Valenciennes, 1840) suggested the identity of *Corydoras geoffroy* with *Cataphractus punctatus* and added more morphological data on the former. Later, the two species were synonymized by Bleeker (1858), who proposed the new combination *Corydoras punctatus*. As a consequence, *Hoplosoma* became a junior synonym of *Corydoras* (see Nijssen, 1970). Recently, Isbrücker (1999a,b) pointed out that *Corydoras geoffroy* and *Cataphractus punctatus* are distinct species, with the former being a valid species. Isbrücker (1999b) considered *Corydoras octocirrus* Nijssen, 1970 as a junior synonym of *Corydoras geoffroy*.

Günther (1864) united callichthyid and loricariid catfishes in a subgroup, the "Loricarina", of the more inclusive group "Hypostomatina", of his subfamily "Siluridae Proteropodes". Furthermore, that author proposed the inclusion of all callichthyid species in a single genus, *Callichthys* Scopoli, divided into three subgenera: *Scleromystax* (described in that work and including only *Callichthys barbatus* Quoy and Gaimard), *Corydoras* (including species belonging to *Corydoras*) and *Callichthys* (containing all the remaining callichthyid species). Historically, Günther's (1864) study was the first to suggest distinct groups within *Corydoras*, with the placement of *Callichthys barbatus* (= *Corydoras barbatus*) in a subgenus apart from other *Corydoras* species. This distinction was proposed on the basis of "bristles" (odontodes) present on the sides of the head in *Callichthys barbatus* (Günther, 1864: 225).

In 1871, Cope provided brief comments on some catfish genera from the Amazon and proposed the genera *Brochis* and *Dianema*. A year later, in his study on fishes from the Ambyiacu river, Peru, Cope (1872) presented new formal descriptions of these two genera, apparently ignoring his previous study. In this latter study, Cope raised *Corydoras* to generic status and arranged its included species in four groups according to modifications of the lower lip. Gill (1872) removed callichthyids from Günther's "Hypostomatina" and placed them in a distinct family, the Callichthyidae, with only one genus, *Callichthys*, and considered the remaining nominal callichthyid genera as junior synonyms. Cope (1878) described two new callichthyid genera, *Chaenothorax* and *Gastrodermus*, from the Peruvian Amazon.

Subsequent to Gill (1872), the first systematic revision of the Callichthyidae was that of Eigenmann and Eigenmann (1890), who defined the family on the basis of characters from the gas bladder, osteology and external morphology. They proposed a new classification of the family, synonymized *Gastrodermus* with *Corydoras*, and *Chaenothorax* with

Brochis, and recognized *Callichthys*, *Decapogon* Eigenmann and Eigenmann, *Dianema*, *Hoplosternum* Gill, and *Scleromystax* as valid, with the latter previously raised to genus by Eigenmann and Eigenmann (1888). In the 1890's study, the authors arranged the genera of the Callichthyidae in two major groups based on association between the supraoccipital process and the nuchal plate. The group in which these elements were in contact to each other was composed of *Corydoras* and *Brochis*, and the other group, lacking this contact, included the remaining genera. The latter group was further subdivided into two assemblages according to the degree of exposure of the coracoids. The coracoids are covered by a thick layer of skin and were not externally visible in *Callichthys* and *Scleromystax*, whereas in *Dianema*, *Decapogon* and *Hoplosternum* they were covered by a thin layer of skin and visible externally. According to those authors, the latter condition was also observed in *Corydoras* and more so in *Brochis*.

At the end of the 19th century, Cope (1894) described a new genus, *Osteogaster*, encompassing species of *Corydoras* with the ventral region covered by the coracoids. That author noted that this condition also occurred in *Brochis*. Some years later, Ihering (1907) described the genus *Aspidoras*.

Eigenmann (1910) considered the valid genera in the Callichthyidae to be the same proposed by Eigenmann and Eigenmann (1890) plus *Aspidoras*, *Osteogaster* and *Chaenothorax*. A year later, Ribeiro (1911) suggested that *Corydoras eques* and *C. splendens* (= *Brochis splendens*) were more closely related to each other than to other *Corydoras* species, based on the degree of exposure of the coracoids. In 1913, Ellis revised the family, recognized as valid the same genera in Eigenmann (1910) and described a new one, *Cascadura*.

A new revision of the Callichthyidae was published by Gosline (1940). That author synonymized *Decapogon* with *Dianema*, *Chaenothorax* with *Brochis*, and *Osteogaster* and *Scleromystax* with *Corydoras*. He also recognized *Aspidoras*, *Callichthys*, *Cascadura*, *Cataphractops* Fowler and *Hoplosternum* as valid. Gosline also proposed a scheme of interrelationships among genera of the Callichthyidae based on ten morphological characters.

Hoedeman (1952), based on Gosline's (1940) phylogenetic arrangement, proposed a new classification of the Callichthyidae, dividing it into two subfamilies, the Corydoradinae (*Aspidoras*, *Brochis*, and *Corydoras*) and Callichthyinae (remaining genera). The Corydoradinae was subdivided into two tribes, Aspidoradidi (*Aspidoras*) and Corydoradidi (*Corydoras* and *Brochis*). The classification proposed by Hoedeman (1952) was later widely adopted (*e.g.,* Nelson, 1994), with the exception of *Cascadura*,

which was synonymized into *Hoplosternum* by Hoedeman (1960a).

The most recent studies on the taxonomy of the Corydoradinae (mainly the genus *Corydoras*) were carried out by Han Nijssen and Isaac Isbrücker. These authors described about 40% of the nearly 160 valid species of the Corydoradinae, and published extensive taxonomic revisions of all genera in the subfamily (Nijssen and Isbrücker, 1970 for *Brochis*; 1976 for *Aspidoras*; and 1980 for *Corydoras*; and also 1967, 1971, 1983). However, only on two occasions (Nijssen, 1970; Nijssen and Isbrücker, 1980) hypotheses of relationships were proposed.

In 1970, Nijssen arranged species of *Corydoras* into nine groups based on morphometric, meristic, and pigmentation data. However, four species were not assigned to any particular group. Nijssen and Isbrücker (1980) rearranged the species of *Corydoras* into five groups, which included those described subsequently to Nijssen's (1970) study, also based on morphometric, meristic and pigmentation characters. Subsequently, Nijssen and Isbrücker (1986a) stated that their proposed groups of *Corydoras* species did not reflect the phylogenetic relationships within that genus.

In 1985, Strauss conducted a statistical analysis based on the meristic and morphometric data of Nijssen and Isbrücker (1980) and demonstrated that the characters used by them to distinguish species groups were highly correlated with body size and were apparently continuous among members of distinct groups. That author concluded that as a consequence it was impossible to distinguish natural groups of *Corydoras* based on the characters proposed by Nijssen and Isbrücker (1980).

The phylogenetic relationships among genera of the Callichthyidae were recently investigated using cladistic methods by Reis (1993, 1997, 1998a,b). Based on 72 characters, Reis (1998a) corroborated the monophyly of Hoedeman's (1952) two subfamilies and the two corydoradine tribes Aspidoradini and Corydoradini. He also confirmed the monophyly of *Brochis* and suggested that *Corydoras* was paraphyletic. According to Reis (1993), some of Nijssen's (1970) groups actually agree with known patterns of endemism, such as the *Corydoras eques* group (upper rio Amazonas and rio Orinoco; Nijssen, 1970: fig. 34b), *C. caudimaculatus* (rio Madeira; Nijssen, 1970: fig. 35b) and *C. hastatus* (rios Madeira and Paraguay systems; Nijssen, 1970: fig 35a), which are corroborated by the distribution patterns of other fish taxa (see references in Reis, 1993), suggesting that future studies about phylogenetic relationships of these groups might reveal that they are monophyletic.

MATERIALS AND METHODS

Specimens were cleared and stained (cs) following Potthoff (1983), and Taylor and Van Dyke (1985). Vertebral counts were taken from cleared and stained individuals. The compound caudal centrum (preural 1 + ural 1; Fink and Fink, 1981) was counted as a single element. For vertebrae of the weberian apparatus see explanation on character 51. Osteological terminology follows Reis (1998a). Nomenclature of latero-sensory canals follows Arratia and Huaquin (1995). Homology of preopercular pores followed Schaefer (1988). Information about color pattern was taken from specimens preserved in ethanol, photographs of live specimens (*e.g.,* Burgess, 1989; Glaser et al., 1996), original descriptions, and, in some instances, from live individuals in aquarium or in the field. Drawings are from the left side of specimens, and were made with the aid of a *camera lucida*. In the illustrations, stippling indicates bone and small circles represent cartilage. Material examined is listed in Appendix 1.

Phylogenic Procedures

Hypotheses of relationship were erected according to the cladistic methodology (Hennig, 1966; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981; Wiley et al., 1991; Rieppel, 1988; Swofford and Olsen, 1990; Hall, 1994; Scotland et al., 1994; Harvey, 1996; Amorim, 1997; Kitching et al., 1998). Phylogenetic schemes proposed for Loricarioidea (Schaefer, 1990; de Pinna, 1992) and for Callichthyidae (Reis, 1997, 1998a,b) constituted the framework for outgroup comparisons (Maddison et al., 1984). Representatives of all Nijssen's (1970), and Nijssen and Isbrücker's (1980) *Corydoras* species groups, and all currently valid species of *Brochis* were sampled. Of the 143 currently valid species of *Corydoras* (Reis, 1993; Burgess and Finley, 1996), 82 were examined, and characters of 52 were coded in the data matrix (Table 1). Of the 17 currently valid species of *Aspidoras* (Britto, 1998), 12 were examined, and characters of eight were included in the matrix (Table 1). Differences in the number of species examined and those which had characters coded for are due to availability of cleared and stained material. Also, type-species of each Corydoradinae genera were examined. All terminals are single species, except *Corydoras barbatus*, dismembered in some of its populations (see explanation below). Outgroups included the subfamily Callichthyinae, and the loricarioid families Astroblepidae, Loricariidae, Nematogenyidae, Scoloplacidae, and Trichomycteridae.

Multistate characters were treated as "ordered" or "minimally connected" (Slowinski, 1993) according to a morphoclinal sequence of similarity among character-states, whenever possible. The outgroup condition provided the starting point of a series, with the other states ordered sequentially according to their divergence from this condition. Justification for ordering among character-states can be seen in Lipscomb (1992), Wilkinson (1992) and references therein. When determining a clear morphoclinal sequence was not possible, characters were treated as "unordered" or "maximally connected". The most parsimonious trees were obtained using the heuristic algorithm "mhennig*" associated with the command "bb*" ("branch-breaker") of Hennig86 software (Farris, 1988). As more than one fundamental cladogram was obtained, a strict consensus (Sokal and Rohlf, 1981) cladogram was generated using the command "nelsen" of Hennig86. Due to the relatively large size of the matrix (for morphological data), and the large number of homoplasies, Hennig86 saved a limited number of trees, with the message "overflow", indicating that there was not enough memory to search for more trees, which could affect the confidence of such consensus (Schuh, 2000), although it is useful as a predictive scheme.

Ambiguous characters were ACCTRAN optimized (Swofford and Maddison, 1987), where reversals are chosen over convergences, thus maximally preserving hypothesis of homology (de Pinna, 1991). Missing data are presented in three different forms (Table 1): as dashes ("-"), meaning non-comparable character-states ("neither 0 nor 1"), as variable ("v"), when more than one state (polymorphism) was present in the same terminal, or as question marks ("?") meaning that the character-states was not observed due to poor condition of the material. Although the three conditions above refer to logically different cases (*e.g.,* Nixon and Davis, 1991), Hennig86 interprets all in the same manner, that is, as "missing values". Therefore, in the matrix loaded in Hennig86, all missing entries were coded as a dash. The presentation of these conditions in Table 1 is only to allow better discrimination of the data. The largely polymorphic *Corydoras barbatus* was divided in two separate mostly monomorphic terminals: *Corydoras barbatus* I (populations from north of Baía da Guanabara, Rio de Janeiro, Brazil) and *Corydoras barbatus* II (populations from south of Baía da Guanabara) in order to minimize missing entries in the matrix. Furthermore, there are some doubts as to whether all populations assigned to *Corydoras barbatus*, in fact, represent a single species (Franciozi, 1989).

CHARACTER DESCRIPTION

In this section, characters used in the phylogenetic analysis are described and discussed. Character

numbers and character-state codes are the same as presented in the matrix (Table 1). Characters are grouped by anatomical units and for each character a summary of the conditions in the Corydoradinae and other Loricarioidea is provided. States observed in most basal loricarioids are coded as "0"; other conditions are coded as "1", "2",..., "n" followed by a list of taxa having the latter conditions.

Neurocranium

1. Anterior portion of mesethmoid: long (state 0; Fig. 1A); short (state 1; Fig. 1B). *Corydoras rabauti, C. eques, C. zygatus, C. aeneus, C. hastatus, C. pygmaeus, C. undulatus, C. gracilis, C. nanus, C. napoensis, C. elegans, C. panda, C. xinguensis, C. punctatus, C. reticulatus, C. bicolor, C. trilineatus, C. bondi, C. osteocarus, C. polystictus, C. ephippifer, C. julii, C. araguaiensis, C. maculifer, C. leucomelas, C. paleatus, C. flaveolus, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. ehrhardti, C. ambiacus, C. loretoensis,* and *C. guapore*.

Within the Loricarioidea, the Loricariidae and Astroblepidae possess a mesethmoid bone, which is rectangular-shaped in dorsal view. In the Nematogenyidae (de Pinna, 1989: fig. 16a) and Trichomycteridae the mesethmoid has two anterior lateral cornua that give it a T-shaped aspect in dorsal view. Species of the Scoloplacidae display a unique shape of the mesethmoid with a disc-like expansion situated anterior to the lateral ethmoid (Schaefer, 1990: fig. 6c). In the Callichthyidae this bone shows a somewhat triangular shape from a dorsal view. However, all loricarioids typically possess the anterior portion of the mesethmoid long, equal to or more than 50% of the overall bone length. In the corydoradine taxa listed above, this process is relatively short, being less than 50% of the bone length.

2. Posterior portion of mesethmoid: narrow (state 0; Fig. 1A); wide (state 1; Fig. 1B). All *Aspidoras, Corydoras rabauti, C. eques, C. zygatus, C. aeneus, C. hastatus, C. pygmaeus, C. macropterus, C. undulatus, C. gracilis, C. nanus, C. napoensis, C. elegans, C. panda, C. xinguensis, C. punctatus, C. bicolor, C. trilineatus, C. bondi, C. osteocarus, C. polystictus, C. ephippifer, C. julii, C. araguaiensis, C. maculifer, C. garbei, C. leucomelas, C. paleatus, C. flaveolus, C. arcuatus, C. baderi, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. ehrhardti, C. metae, C. atropersonatus, C. ambiacus, C. loretoensis,* and *C. guapore*.

In the Loricarioidea, the posterior portion of the mesethmoid is relatively narrow, its width smaller than its length (excluding the anterior process of the bone). In the Callichthyidae, the posterior portion of the mesethmoid has its profile detached from that of the anterior portion, giving to the bone a rough

inverted goblet-shape. Despite of the distinctive shape of the mesethmoid, the primitive condition described here is also found in several callichthyids. Nevertheless, in the above-cited corydoradines, the posterior half of mesethmoid is widened, its width being greater than its length.

3. Lateral cornua of mesethmoid: present (state 0; Fig. 2A); absent (state 1; Fig. 2B). All callichthyids, except *Brochis, Corydoras aeneus, C. hastatus, C. nanus, C. osteocarus, C. ephippifer, C. habrosus,* and *C. axelrodi*.

As noted by Schaefer (1990), the anterior tip of the mesethmoid with well-developed lateral cornua occurs in the families Trichomycteridae and Nematogenyidae. That author also observed this condition in the Scoloplacidae, Loricariidae and Astroblepidae, but in these families the cornua are poorly developed. Lateral cornua are absent in the Callichthyidae, except *Brochis* (Reis, 1998a) and in the *Corydoras* species listed above which have the same condition seen in the Loricariidae, Astroblepidae and Scoloplacidae.

4. Shape of lateral ethmoid: long (state 0); short (state 1). All callichthyines, all *Aspidoras, Corydoras rabauti, C. eques, C. zygatus, C. aeneus, C. hastatus, C. pygmaeus, C. undulatus, C. gracilis, C. nanus, C. napoensis, C. elegans, C. panda, C. xinguensis, C. punctatus, C. reticulatus, C. bicolor, C. trilineatus, C. bondi, C. osteocarus, C. polystictus, C. ephippifer, C. julii, C. araguaiensis, C. maculifer, C. difluviatilis, C. leucomelas, C. paleatus, C. flaveolus, C. arcuatus, C. baderi, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. ehrhardti, C. metae, C. atropersonatus, C. ambiacus, C. loretoensis,* and *C. guapore*.

In most Loricarioidea the lateral ethmoid is long in shape, with its width smaller than its length, and it also bears a small anterolateral process. The Callichthyinae and numerous corydoradines have a very small, or even absent, anterolateral process on the lateral ethmoid. Furthermore, the lateral ethmoid of these species is compact in shape, with its width greater than, or equal to, its length, a condition also seen in some members of the Trichomycteridae (de Pinna, 1992).

5. Anterior projection of frontal bone: short (state 0; Fig. 1A); long (state 1; Fig. 1B); long and widened (state 2). State 1: all *Aspidoras,* all *Brochis, Corydoras vittatus, C. undulatus, C. julii, C. difluviatilis, C. garbei, C. flaveolus, C. prionotos,* and *C. aurofrenatus*. State 2: *Corydoras gracilis*.

In the Loricarioidea, the anterior portion of the frontal, which adjoin the inner border of the lateral ethmoid, has a projection shorter than the length of nasal bone. In the taxa listed above the anterior projection is long, equal in size or surpassing the length of the nasal. An additional derived condition for this character is observed in *Corydoras gracilis* where the

Table 1. Data matrix of 83 characters used in the phylogenetic analysis of the subfamily Corydoradinae. Character ordered as in the text. Symbols as explained on "Phylogenetic procedures". A: Astroblepidae; L: Loricariidae; N: Nematogenyidae; T: Trichomycteridae; S: Scoloplacidae.

	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–83
N T	0000000000	0000000000	0000000000	000000-000	-00v000000	0000-00000	0000000000	-000000000	000
S L A	0000000?00	00-0000000	000000000v	00v0000000	-0000-0000	0010000000	0000000011	-000000000	000
Callichthyinae	00110000-0	0000011000	0000000100	00v0000000	0000000000	0000000000	0000000011	0000000000	000
Aspidoras fuscoguttatus	0111110101	0020211011	1001110112	0101100110	0100111111	0101000001	0000020111	0000000001	010
A. rochai	0111110101	0020211011	1101110112	0101100111	0110011111	0101000001	0000020111	0000000001	010
A. albater	0111110101	0020211011	1101110112	0101100111	0100111111	0101000001	0000020111	0000000001	010
A. aff. poecilus	0111110101	0020211011	1001110212	0101100110	0110111111	0101000001	0000020111	0000000001	010
A. poecilus	0111110101	0020211011	1101110112	0101100111	0110111111	0101000001	0000020111	0000000001	010
A. microgalaeus	0111110101	0020211011	1101110112	0111100100	0110110111	0101000001	0000020111	0000000001	010
A. belenos	0111110101	1020211011	1101110112	0101100110	0110110111	0101000001	0000020111	0000000001	010
A. virgulatus	0111110101	0020211011	1101101112	0101100111	0100101111	0101010001	0000120111	0001000001	110
Brochis splendens	0000110010	1021322111	1111101212	0101110120	0011100111	0101001111	1111000111	1000000001	010
B. multiradiatus	0000110010	1021322111	1111101212	0101110120	0011100111	0001001111	1111000111	1000000001	010
B. britskii	0000111010	1021322111	1101101212	0101010020	0011100111	0101001111	1111000111	1000000001	010
Corydoras rabauti	1110011010	1120321111	1111000212	0111110120	0011100111	1111000111	0111000111	1001000001	010
C. eques	1111010010	1120322111	1011000212	0101100120	0011100111	1111000111	0111000111	1001000001	010
C. zygatus	1111010010	1120321111	1111101211	0101000120	0010100111	1111000011	0111000111	1001000001	010
C. aeneus	1101v11000	1120321111	1111101212	0111100110	0110100111	v1v1000001	0101000111	1000000001	010
C. hastatus	1101010000	1120122221	110110011-	1111000110	0000100111	1101000001	0101000111	0000111001	011
C. pygmaeus	1111011000	0120122221	100110011-	1111100120	0001100111	1111000001	0100000111	0000111001	011
C. vittatus	0010121000	0020222111	0101100v12	01v1102121	1000111111	0111000011	1100010011	0000000011	010
C. acutus	0010010000	0020222111	1101100211	01v1102121	1000110111	0111000001	0101000111	0000000011	010
C. septentrionalis	0010011000	1020222111	1101101211	01?110212?	1000110111	1111000001	0101000111	0000000011	010
C. ellisae	0010010000	1020222111	1101100211	0101102121	0000110111	0101000001	0101000111	0000000011	010
C. stenocephalus	0010021000	1020222011	1001101211	0101102121	1000110111	0101010001	0100000111	0000000011	010
C. macropterus	0110010000	0020211011	1101100112	0111100111	1110110111	0101010001	0000110111	0000000011	110
C. barbatus I	0010v10000	0020211011	0101100112	0111001v1	1000110111	0101010001	0000110111	0100000011	110
C. barbatus II	0010010000	0020211011	0101100v12	0111100111	0000110111	0101010001	0000100111	0100000011	110
Corydoras sp. A	0010010000	1020211011	1101101212	0111100121	0000111111	0101010001	0000110111	0100000011	110
C. undulatus	1111110000	1000221111	1111110211	0111000120	0011100111	1111000011	0100000111	0000000011	010
C. gracilis	1111211000	1000221111	1101101111	0111000110	0011100111	0101000001	0100000111	0010000001	010
C. namus	1101010000	0120221111	1111100111	0111100110	0010100111	1111000001	0100000111	0000000001	010
C. napoensis	1111010000	1120221111	1111101111	0111100110	0010100111	1111000001	0101000111	0000000001	010
C. elegans	111101010?	1120211111	1111101211	0111100110	001010?111	1111000001	0101000111	0000000001	010

Table 1 (*continued*)

|	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–83
C. panda	1111010000	1100121011	1101100212	0101000120	0001100111	1101000001	0100000122	0000000101	010
C. xinguensis	1111010000	1110221011	1101101212	0101000120	0000100111	1101000001	0100000121	0000000001	010
C. punctatus	1111010000	1120221011	1111101212	0101100120	0000100111	1111000001	0100000122	0000000001	010
C. reticulatus	1011010000	1120222011	1101100212	0101101120	0000100111	0101100001	0100000111	1000000001	010
C. bicolor	1111010000	1120222011	1101101211	0101000111	0000100111	1101100001	0100000122	0000000001	010
C. trilineatus	1111010000	1100222011	1101101211	0101000110	0001100111	1101000001	0100000122	0000000001	010
C. bondi	1111010000	1120222011	1111101212	0101100110	0000100111	v101000001	0100000121	0001100001	010
C. osteocarus	1101010000	1020220011	1111101211	0101100110	0100100111	1101000001	0100000121	0000000001	010
C. polystictus	1111010000	1120222011	1111100212	0101100120	0000100111	1101000001	0100000121	0000000001	010
C. ephippifer	1101011000	1120222011	1111101212	0101100110	0000100111	11v1000001	0100000122	0000000001	010
C. julii	1111111000	1120222011	1101101211	0101000110	0000100111	1101000001	0100000122	0000000001	010
C. haraldschultzi	1111010000	1120222011	1111101211	0101001120	0000100111	1101000001	0100000122	0000000001	010
C. maculifer	1111010000	1120222v11	1111101212	0101001v0	0000100111	0101000001	0100000121	1000000001	010
C. difluviatilis	0011111000	0120211111	0111100112	0101101120	0110100111	0101000011	0100000111	0010000001	010
C. garbei	0110110000	1000211111	1011100212	0101000120	0111100111	0001000001	0100002111	0000000001	010
C. leucomelas	0010010000	1120221011	1111101212	0111100110	0000100111	1101000111	0100000122	0000000001	010
C. ornatus	0010010000	1020220011	1111100212	0101101110	0001100111	0101000001	0100000111	1000000001	010
C. paleatus	1111010010	1020221011	1011111212	0101000120	0000100111	0101000001	0100000121	1000000001	010
C. flaveolus	1111121000	1100211011	1101110211	0101000110	0000100111	0101000001	0100000121	1000000001	010
C. arcuatus	0111011000	1100220011	1111101211	0101000110	0001100111	0101000011	0100000111	0010000001	010
C. baderi	0111011000	1100222011	1111101211	0101000110	0001100111	1101000001	0100000121	0000100000	010
C. habrosus	1101010000	1110222011	1101101211	0101000111	0000100111	1111000001	0100000121	1000000101	010
C. axelrodi	1101011000	1120222011	1111101212	0101100110	0000100111	1101000001	0100000121	0000000001	010
C. cochui	1111011000	1120222011	1111101211	0101100110	0000100111	1101000001	0100000122	0000000001	010
C. nattereri	1111011000	1120221011	1111101212	0101000110	0010100111	1101000001	0100000121	0001000001	010
C. ehrhardti	1111010000	1120221011	1111101212	0101001v0	v010100111	0101000001	0100000121	0000000001	010
C. prionotos	0010110000	1020221011	1101101011	0101100111	0010110111	0101000001	0100010111	0000000001	110
C. aurofrenatus	0010111000	1120222111	1101100212	0101102121	1000100111	1101100001	0100010111	0000000011	010
C. metae	0111010000	1120220011	1101100211	0101100120	0000100111	1101100001	0100000122	0000000001	010
C. atropersonatus	0111010000	1120222011	1101101212	0101101110	0000100111	1101100001	0100000122	0000000001	010
C. agassizi	0010010000	1120222211	1011100212	0101100110	0000100111	0101000001	0100000111	0000000001	010
C. ambiacus	1111010000	1120222011	1111101212	0101100110	0001100111	1101000001	0100000122	0000000001	010
C. loretoensis	1111011000	1120222011	1111101212	0101100110	0101100111	0101100001	0100000122	0000000001	010
C. guapore	1111010010	1120222111	1111000212	0111100110	0000100111	0101000001	0100000111	0000000101	010
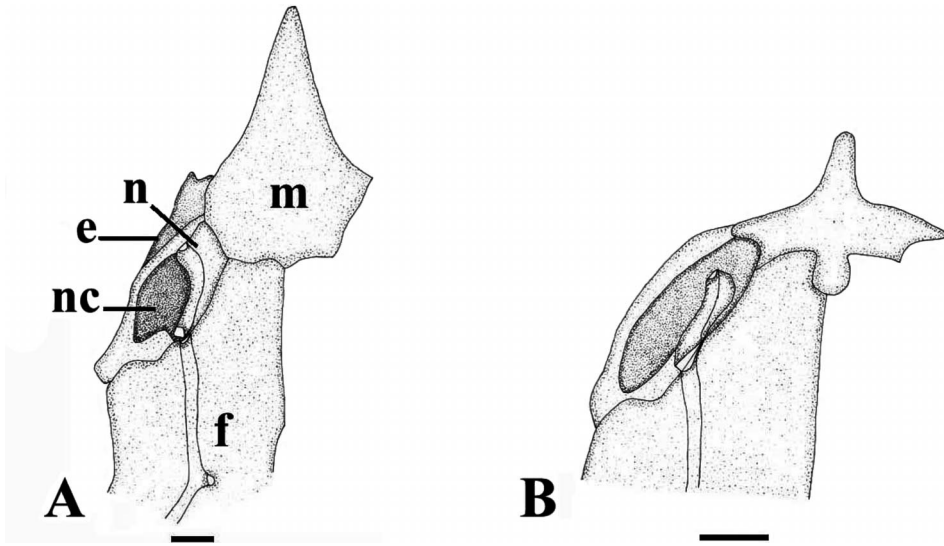
Fig. 1. Anterior portion of neurocranium, dorsal view (*e,* lateral ethmoid; *f,* frontal; *m,* mesethmoid; *n,* nasal; *nc,* nasal capsule). **A,** *Brochis splendens*, MCP 14261, 47.0 mm SL; **B,** *Corydoras undulatus*, MCP 13954, 35.0 mm SL. Scale bar = 1 mm.

projection is expanded. In this condition, the width of the projection is greater than or equal to 50% the width of the bone. In other members of the Loricarioidea the width is less than that of *Corydoras gracilis*. Character-states were treated as non-additive because an evident sequence among them was not clear. Specimens of *Corydoras aeneus* and *C. barbatus* I showed both short and long projections, and these taxa are coded as variable ("v").

6. Frontal bone width: wide (state 0); narrow (state 1); strongly narrow (state 2). State 1 all corydoradines except *Corydoras vittatus*, *C. stenocephalus*, and *C. flaveolus*, which have state 2.

The Nematogenyidae, Trichomycteridae, Scoloplacidae, Astroblepidae, Loricariidae and the subfamily Callichthyinae have wide frontal bone, its
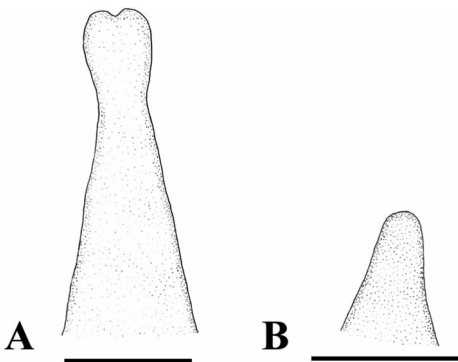

Fig. 2. Anterior tip of mesethmoid, dorsal view. **A,** *Brochis multiradiatus*, MCP 16302, 50.0 mm SL; **B,** *Corydoras undulatus*, MCP 13954, 35.0 mm SL. Scale bar = 1 mm.
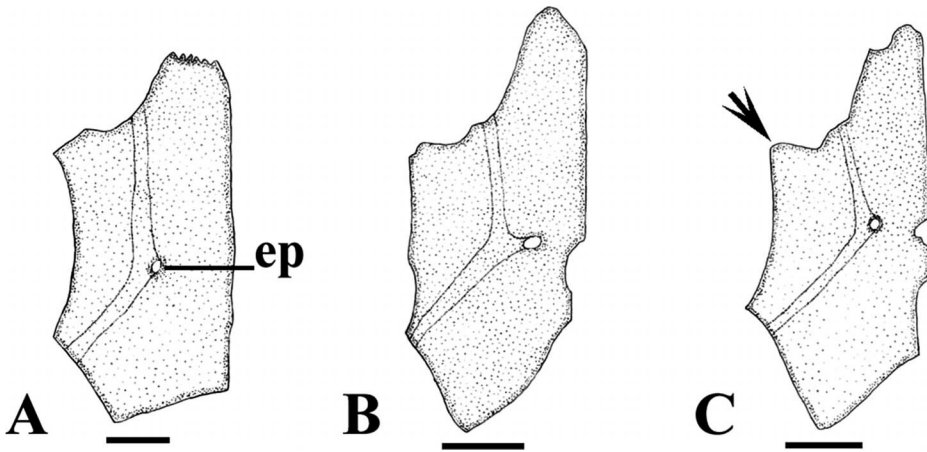
width equal to, or greater than, its length, giving the bone a roughly square shape (Reis, 1998: fig. 3). In the Corydoradinae, this bone is compressed transversely and its width is equal to or less than 50% of its length. Within this subfamily, *Corydoras vittatus*, *C. stenocephalus*, and *C. flaveolus* have this bone even narrower than in the remaining Corydoradinae. In these species the width of the bone is less than 30% of its length. The narrowing of the frontal bones is also possibly reflected in the interorbital width.

7. Process on anterolateral margin of frontal bone: absent (state 0; Fig. 3A,B); present (state 1; Fig. 3C: arrow). *Brochis britskii, Corydoras rabauti, C. aeneus, C. pygmaeus, C. vittatus, C. septentrionalis, C. stenocephalus, C. gracilis, C. ephippifer, C. julii, C. difluviatilis, C. flaveolus, C. arcuatus, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. aurofrenatus*, and *C. loretoensis*.

In the Siluriformes the frontals typically have a somewhat square or rectangular shape. In some catfish families there is a small process on the anterolateral border of the bone (*e.g.,* some bagrids; Mo, 1991: fig. 27). However, within the superfamily Loricarioidea, the presence of this process is exclusively shared by the taxa listed above. A process on the anterior lateral margin of the frontals is consequently considered a derived feature within the Loricarioidea, despite its presence in other distantly related siluriforms.

8. Frontal fontanel size: large (state 0); small (state 1). All *Aspidoras*. Discussed in Reis (1998a).

9. Contact between nasal and mesethmoid: ab-

Fig. 3. Frontal (*ep,* epiphyseal pore; *arrow,* process of frontal bone). **A,** *Corydoras leucomelas,* MCP 14249, 27.0 mm SL; **B,** *Aspidoras rochai,* MCP 19402, 40.0 mm SL; **C,** *Corydoras difluviatilis,,* UFRJ 4656, 32.3 mm SL. Odontodes not depicted. Scale bar = 1 mm.

sent (state 0; Fig. 1B); present (state 1; Fig. 1A). All *Brochis, Corydoras rabauti, C. eques, C. zygatus, C. paleatus,* and *C. guapore.*

In the Trichomycteridae, Astroblepidae (Howes, 1983: fig. 13), Scoloplacidae, and the majority of the Corydoradinae the nasal bone is located in a capsule delimited by the frontal, lateral ethmoid and mesethmoid. Despite some variation in the degree
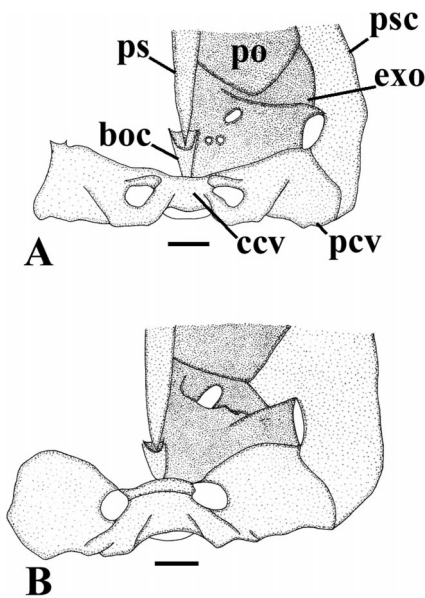

Fig. 4. Posterior portion of neurocranium, ventral view (*boc,* basioccipital; *ccv,* centrum of the complex vertebra; *exo,* exoccipital; *pcv,* parapophysis of the complex vertebra; *po,* prootic; *ps,* paresphenoid; *psc,* pterotic-supracleithrum). **A,** *Corydoras garbei,* MCP 16994, 34.0 mm SL; **B,** *Corydoras rabauti,* MCP 14258, 39.0 mm SL. Scale bar = 1 mm.

of participation of the mesethmoid, there is always contact between that bone and the nasal by means of connective tissue. In the taxa listed above, there is a greater participation of the mesethmoid in delimiting the nasal capsule and the nasal bone contacts the mesethmoid directly by means of bone sutures. In the Callichthyinae (Reis, 1993: fig. 4) and Loricariidae the nasal capsule is exclusively delimited by a concavity on the lateral ethmoid resulting in a non-homologous position of the nasal bone when compared with that in the remaining Loricarioidea. These character-states were coded as non-comparable ("-") for the Callichthyinae. This character was not seen in *Corydoras elegans* and was coded as missing ("?") in Table 1.

10. Supraoccipital fontanel: absent (state 0); present (state 1). All *Aspidoras.* Discussed in Reis (1998a).

11. Contact between the supraoccipital and the nuchal plate: absent (state 0); present (state 1). *Aspidoras belenos,* all *Brochis,* and *Corydoras,* except *C. pygmaeus, C. vittatus, C. acutus, C. macropterus, C. barbatus* I, *C. nanus,* and *C. difluviatilis.*

Reis (1998a) stated that the absence of contact between the supraoccipital and the nuchal plate occurs in the majority of members of the Loricarioidea. Furthermore, that author proposed that state 1 above is exclusive for a clade composed of *Brochis* plus *Corydoras.* However, contact between the supraoccipital and nuchal plate also occurs in one species of *Aspidoras* (Britto, 1998). In addition, some species of *Corydoras* (listed above) display no contact between these two structures. Character-states are variable ("v") in *Corydoras barbatus* II.

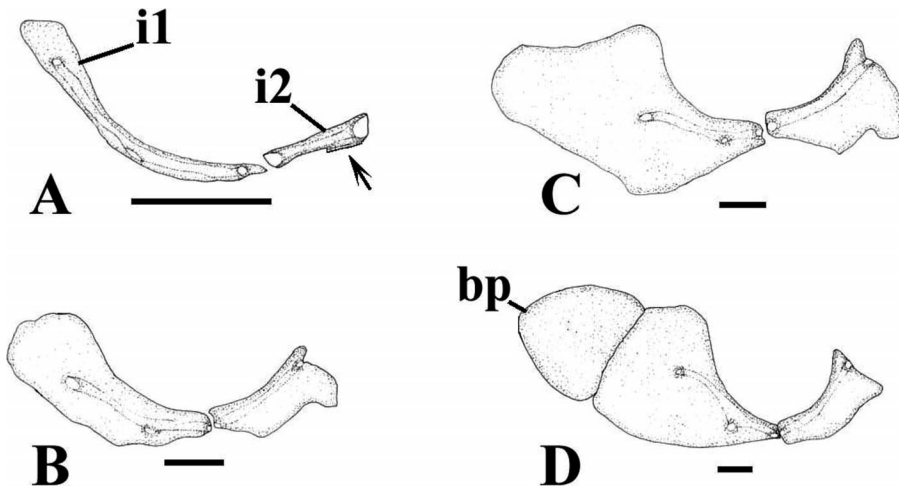**12. Shape of complex vertebra:** slender (state 0; Fig. 4A); compact (state 1; Fig. 4B). All *Corydoras,*

Fig. 5. Infraorbitals, lateral view (*bp,* bony plate; *i1–2,* infraorbitals 1–2; *arrow,* rectangular expansion on infraorbital 2). **A,** *Corydoras hastatus,* UFRJ 384, 21.0 mm SL; **B,** *Corydoras septentrionalis,* MZUSP 27953, 36.0 mm SL; **C,** *Corydoras aeneus,* MNRJ 5756, 46.0 mm SL; **D,** *Brochis splendens,* MCP 14261, 47.0 mm SL. Odontodes not depicted. Scale bar = 1 mm.

except *C. vittatus, C. acutus, C. ellisae, C. stenocephalus, C. macropterus, C. barbatus* I and II, *Corydoras* sp. A, *C. undulatus, C. gracilis, C. osteocarus, C. garbei, C. ornatus, C. paleatus,* and *C. prionotos.*

In the Loricarioidea the centrum of the complex vertebra and its parapophysis constitute a structure with a slender shape. In the majority of *Corydoras,* this structure is compressed, giving the complex vertebra a more compact shape, with its width nearly the same size as its length.

Infraorbitals

13. Odontodes on infraorbitals: absent (state 0); restricted to infraorbital 1 (state 1); on infraorbitals 1 and 2 (state 2). State 1: *Corydoras xinguensis* and *C. habrosus.* State 2: all corydoradines except *Corydoras undulatus, C. gracilis, C. panda, C. trilineatus, C. garbei, C. flaveolus, C. arcuatus,* and *C. baderi,* which exhibit state 0.

Odontodes on the body and/or fins are present only in the superfamily Loricarioidea among catfishes (Peyer, 1922; Bhatti, 1938; Baskin, 1973; Howes, 1983; Schaefer, 1990). The arrangement and disposition of odontodes vary markedly within the superfamily (for a complete discussion about odontode distribution on each Loricarioidea family, see Baskin, 1973, and Schaefer, 1990). Nonetheless, odontodes on bones of the head in the Callichthyidae are restricted to the mesethmoid, frontals and supraoccipital. Within the Loricarioidea odontodes on infraorbitals are found in the Loricariidae, but are absent in the Nematogenyidae, Trichomycteridae, Astroblepidae, and some representatives of the Callichthyidae. Nevertheless, two species of

Corydoras, C. xinguensis, and *C. habrosus,* have odontodes on infraorbital 1. The great majority of the Corydoradinae display a more extreme condition of this character, bearing odontodes on both infrabitals (in callichthyid catfishes, the infraorbital series is restricted to two bones; Reis, 1998a). For Scoloplacidae, Astroblepidae and Loricariidae, character-states were assigned as uncomparable ("-"; Table 1) due to the lack of infraorbitals in Scoloplacidae (Schaefer, 1990) and the presence of both conditions in Loricariidae and Astroblepidae (see discussion above).

14. Plate located anterior to infraorbital 1: absent (state 0; Fig. 5A, B, C); present (state 1; Fig. 5D). All *Brochis* species.

In the species of *Brochis* the first infraorbital is sutured with a well-developed bony plate devoid of sensory-canal pores. In conjunction with the anterior expansion of the first infraorbital (see character 15) this plate entirely covers the lateral region of snout. In juveniles, this plate is small and often does not contact infraorbital 1.

15. Anterior expansion of infraorbital 1: absent (state 0; Reis, 1998a: fig. 12a-e); small (state 1; Fig. 5A); large (state 2; Fig. 5B); very large (state 3; Fig. 5C, D). State 1: *Corydoras hastatus, C. pygmaeus,* and *C. panda.* State 2: all *Aspidoras* and all other *Corydoras* except by those, which have states 1 and 3. State 3: all *Brochis, Corydoras rabauti, C. eques, C. zygatus,* and *C. aeneus.*

The Loricariidae and Callichthyidae have a connection between the infraorbital series and lateral ethmoid. In the remaining members of the Loricarioidea there is no connection between these elements. *Corydoras hastatus, C. pygmaeus,* and *C. pan-*
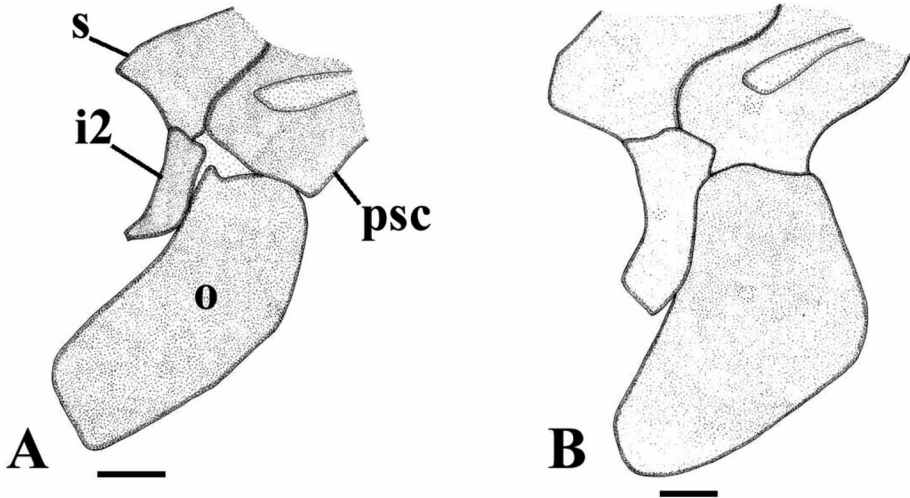
Fig. 6. Sphenotic (*s*), pterotic-supracleithrum (*psc*), opercle (*o*) and second infraorbital (*i2*), lateral view. **A,** *Corydoras melanistius*, UFRJ 3780, 26.0 mm SL; **B,** *Corydoras napoensis*, USNM 301949, 34.0 mm SL. Scale bar = 1 mm.

da have a small, sometimes difficult to detect, anteriorly situated expansion on infraorbital 1 that increases the contact area with the lateral ethmoid. In *Aspidoras* and the majority of *Corydoras* species, this expansion is more developed, larger, conspicuous, and somewhat triangular in shape. *Corydoras rabauti*, *C. eques*, *C. zygatus*, *C. aeneus*, and the species of *Brochis* have the anterior expansion even larger than the remaining members of the Corydoradinae, covering almost all the lateral surface of snout. Reis (1998a) indicated that an anterior expansion of first infraorbital was a synapomorphy for the Corydoradinae. This character is herein subdivided in three states (see "Discussion" section).

16. Inner expansion on infraorbital 1: absent (state 0); large (state 1); reduced (state 2). State 1: all callichthyines, all *Aspidoras*, *Corydoras macropterus*, *C. barbatus* I and II, *Corydoras* sp. A, *C. difluviatilis*, *C. garbei*, and *C. flaveolus*. State 2: all *Brochis* and remaining species of *Corydoras*.

Reis (1998a) indicated that a large inner expansion of the first infraorbital was an autapomorphy for the Callichthyidae. Furthermore that author identified a second state (a strong reduction in this inner expansion) as a synapomorphy for *Brochis* plus *Corydoras*. In the present study, a well-developed inner expansion was also observed in some species of *Corydoras* (listed above). The ordering of the character-states presented in this study was based on the fact that the sister-group of Corydoradinae, the subfamily Callichthyinae, also possesses a large inner expansion on the first infraorbital. This ordering is a working hypothesis that may be tested against relevant ontogenetic sequences when they are available. Accordingly, it was hypothesized the acquisition of a large inner expansion on the first infraorbital in

the ancestor of the whole family with a subsequent reduction of this structure in a less inclusive clade of Callichthyidae.

17. Inner expansion on infraorbital 2: absent (state 0); large (state 1); reduced (state 2). State 1: all callichthyines, except in *Callichthys*, all *Aspidoras*, *Corydoras rabauti*, *C. zygatus*, *C. aeneus*, *C. macropterus*, *C. barbatus* I and II, *Corydoras* sp. A, *C. undulatus*, *C. gracilis*, *C. nanus*, *C. napoensis*, *C. elegans*, *C. panda*, *C. xinguensis*, *C. punctatus*, *C. difluviatilis*, *C. garbei*, *C. leucomelas*, *C. ornatus*, *C. paleatus*, *C. flaveolus*, *C. nattereri*, *C. ehrhardti*, and *C. prionotos*. State 2: all *Brochis* and the remaining species of *Corydoras*.

According to Reis (1998a), a large inner expansion on the second infraorbital is exclusive for the Callichthyidae (but absent in *Callichthys*). In addition, Reis (1998a) indicated that the species of *Brochis* show a great reduction in this expansion. As found herein, the majority of Corydoras species also displays a reduction of the inner expansion on infraorbital 2. Justification for the present ordering of the states of this character is the same provided for character 6.

18. Contact between infraorbital 2 and pterotic-supracleithrum: absent (state 0; Fig. 6A); by means of a triangular expansion of the infraorbital (state 1; Fig. 6B); by a rectangular expansion of the infraorbital (state 2; Fig. 5A, arrow). State 1: all *Brochis*, *Corydoras rabauti*, *C. eques*, *C. zygatus*, *C. aeneus*, *C. vittatus*, *C. acutus*, *C. septentrionalis*, *C. ellisae*, *C. undulatus*, *C. gracilis*, *C. nanus*, *C. napoensis*, *C. elegans*, *C. difluviatilis*, *C. garbei*, *C. aurofrenatus*, and *C. guapore*. State 2: *Corydoras hastatus*, *C. pygmaeus*, *C. ornatus*, and *C. agassizi*.
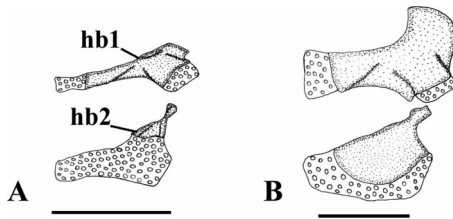
Reis (1998a) pointed out that a contact between

Fig. 7. First (*hb1*) and second (*hb2*) hypobranchials, dorsal view. **A,** *Callichthys callichthys*, UFRJ 3168, 50.0 mm SL; **B,** *Corydoras eques*, USNM 37921, 35.0 mm SL. Scale bar = 1 mm.

Fig. 8. Ceratobranchials (*cb*) 1–4, dorsal view. *Arrow 1* indicates anterior process on first ceratobranchial; *arrow 2* indicates the notch on the posterior expansion on third ceratobranchial. **A,** *Aspidoras fuscoguttatus*, MCP 19401, 34.0 mm SL; **B,** *Brochis multiradiatus*, MCP 16302, 50.0 mm SL. Scale bar = 1 mm.

the second infraorbital and pterotic-supracleithrum is a condition present in *Hoplosternum* and *Brochis*. That author also observed this condition in some species of *Corydoras*. In the present study, two forms of contact between these bones were observed within Corydoradinae. In the first, the contact between both bones occurs by means of a triangular expansion of infraorbital 2. This type of contact is seen in *Brochis*, several species of *Corydoras* (see above) and *Hoplosternum*. The second type of contact is made through a rectangular expansion of the second infraorbital and occurs only in a few species of *Corydoras*. In no other member of the Loricarioidea there is contact between the infraorbital series and pterotic-supracleithrum. The present character-states were treated as non-additive since it was not possible to depict an evident sequence from a less to a more extreme condition, and, no ontogenetic information concerning this character is available. The character-states are variable ("v") in *Corydoras maculifer*, which shows the three conditions.

Hyoid and Branchial Arches

19. Dorsal hypohyal: absent (state 0); present (state 1). All corydoradines. Discussed in Reis (1998a).

20. Shape of hypobranchial 1: slender (state 0; Fig. 7A); deep (state 1; Fig. 7B). All corydoradines.

In the subfamily Callichthyinae the first pair of hypobranchials has a laminar shape, with an elongate lateral process extending towards the basibranchials. The Trichomycteridae (de Pinna, 1992: fig. 6) and Nematogenyidae have an elongate hypobranchial with a small expansion on its tip closer to the first ceratobranchial. In the Loricariidae and Astroblepidae the shape of the hypobranchials is similar to that observed in the Trichomycteridae but without any expansion on the tips of any hypobranchial. In all these cases, hypobranchial 1 displays a slender shape. The overall shape of this bone in the Corydoradinae is like that in the Callichthyinae. However, in the former the lateral process is quite reduced, with the bone being deeper. This structure
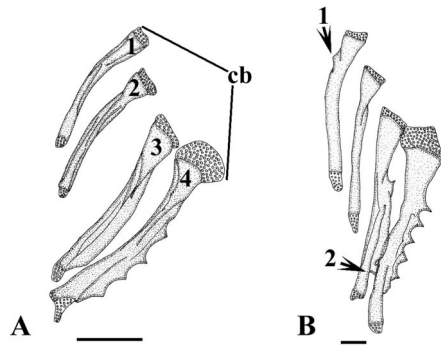
is not comparable in the Scoloplacidae due to the absence of separate hypobranchials in that family (Schaefer, 1990).

21. Degree of ossification of hypobranchial 2: absent or poorly developed (state 0; Fig. 7A); well developed (state 1; Fig. 7B). All corydoradines, except *Corydoras barbatus* I and II, and *C. difluviatilis*.

The second hypobranchial in loricarioids is either wholly cartilaginous or has a highly reduced bony portion, smaller than the cartilaginous area. The first condition is observed in the Loricariidae, Astroblepidae and some members of the Trichomycteridae (*e.g., Trichogenes* Britski and Ortega, 1983). The latter condition can be seen in the Callichthyinae, Nematogenyidae and *Copionodon* de Pinna, 1992. As cited in character 20 this structure is not comparable to that in the Scoloplacidae. In the Corydoradinae, the hypobranchial 2 is a well-developed ossification, greater than the cartilaginous portion, which is reduced and located posteriorly.

22. Anterior process of ceratobranchial 1: absent (state 0; Fig. 8A); present (state 1; Fig. 8B: arrow 1). All corydoradines, except *Aspidoras fuscoguttatus*, *A.* aff. *poecilus*, *Corydoras eques*, *C. pygmaeus*, *C. vittatus*, *C. stenocephalus*, *C. garbei*, *C. paleatus*, and *C. agassizi*.

In representatives of the Loricarioidea the first ceratobranchial is a slender bone, somewhat cylindrical or rectangular in shape. Almost all families of the Loricarioidea lack processes on this bone. In the Loricariidae there is an anterior strongly developed process in the first ceratobranchial, nearly the same size as the bone, with its tip close to the hypobranchials. According to Schaefer (1987), this well-developed process constitutes an exclusive derived feature of the Loricariidae. However, species of *Brochis* and almost all species of *Aspidoras* and *Corydoras* also

Fig. 9. Fifth ceratobranchials, ventral view. *Arrow* indicates the elongate process on the tip of the bone. **A,** *Callichthys callichthys*, UFRJ 3168, 50.0 mm SL; **B,** *Corydoras rabauti*, MCP 14258, 39.0 mm SL. Teeth not depicted. Scale bar = 1 mm.

display such a process, albeit highly reduced, on the anterior surface of ceratobranchial 1.

23. Posterior expansion of ceratobranchial 3: continuous (state 0; Fig. 8A); with a notch (state 1; Fig. 8B). All *Brochis* (except *B. britskii*), *Corydoras rabauti*, *C. eques*, *C. zygatus*, *C. aeneus*, *C. undulatus*, *C. nanus*, *C. napoensis*, *C. elegans*, *C. punctatus*, *C. bondi*, *C. osteocarus*, *C. polystictus*, *C. ephippifer*, *C. araguaiensis*, *C. maculifer*, *C. difluviatilis*, *C. garbei*,

Fig. 10. Epibranchials (*eb*) 1–4, pharyngobranchials (*pb*) 3–4 and upper tooth plate (*up*), ventral view. *Arrow 1* indicates the process on the posterior expansion of epibranchial 2; *arrow 2* indicats the lateral process on the posterior expansion of epibranchial 3; *arrow 3* indicates the posterior expansion of pharyngobranchial 3. **A,** *Brochis multiradiatus*, MCP 16302, 50.0 mm SL; **B,** *Aspidoras rochai*, MCP 19402, 40.0 mm SL. Teeth not depicted. Scale bar = 1 mm.

C. leucomelas, *C. ornatus*, *C. paleatus*, *C. arcuatus*, *C. baderi*, *C. axelrodi*, *C. cochui*, *C. nattereri*, *C. ehrhardti*, *C. agassizi*, *C. ambiacus*, *C. loretoensis*, and *C. guapore*.

Within the Loricarioidea, the third ceratobranchial is a slender, rectangular bone, and has a laminar expansion along its entire posterior border. In the majority of the members of the Loricarioidea there is no gap in this expansion. However, some members of the Corydoradinae (listed above) have a notch on the posterior expansion of the ceratobranchial near its tip proximate to the corresponding epibranchial (Fig. 8B, arrow 2).

24. Anterior tip of ceratobranchial 5: short (state 0; Fig. 9A); long (state 1; Fig. 9B, arrow). All corydoradines.

Among Siluriformes (de Pinna, 1996), the fifth ceratobranchial displays a laminar shape with an extension towards the basibranchials. Typically this extension is short. However, representatives of the Corydoradinae show a well-developed extension of the ceratobranchial that gives to the bone a more slender shape.

25. Anterior projection on epibranchial 1: absent (state 0); present (state 1). All corydoradines, except by *Corydoras guapore*, which shows the primitive condition. Discussed in Reis (1998a).

26. Posterior expansion of epibranchial 2: with a process (state 0; Fig. 10A, arrow 1); without a process (state 1; Fig. 10B). All *Aspidoras* (except *A. microgalaeus* and *A. virgulatus*), *Corydoras undulatus*, *C. paleatus*, and *C. flaveolus*.

Members of the Loricarioidea have a second epibranchial with a laminar expansion on its posterior facet. In the Trichomycteridae and most Callichthyidae this expansion on the second epibranchial has a small lateral process that runs parallel to the epibranchial towards the pharyngobranchials. In the Loricariidae, Astroblepidae and Scoloplacidae this small process is reduced to a more strongly ossified area of the posterior expansion. Almost all *Aspidoras* species and a few *Corydoras* species lack a process on the posterior expansion of epibranchial 2. This condition also occurs in the Nematogenyidae.
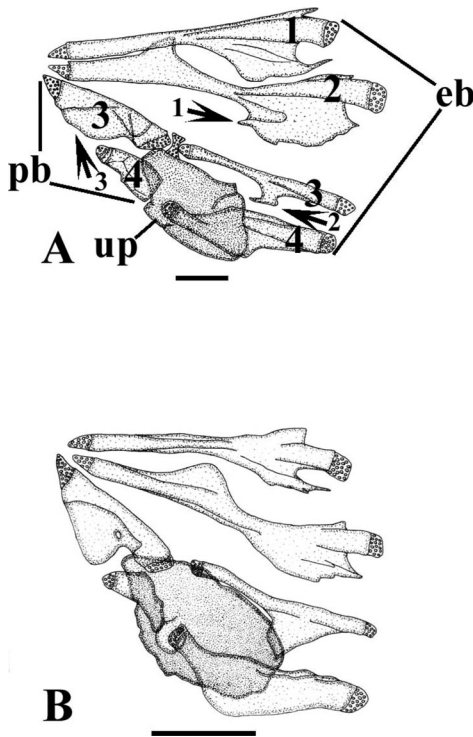
27. Uncinate process of epibranchial 3: triangular (state 0; Fig. 10B); curved mesially (state 1; Fig. 10A). *Aspidoras virgulatus*, all *Brochis*, *Corydoras zygatus*, *C. aeneus*, *C. septentrionalis*, *C. stenocephalus*, *Corydoras* sp.A, *C. gracilis*, *C. napoensis*, *C. elegans*, *C. xinguensis*, *C. punctatus*, *C. bicolor*, *C. trilineatus*, *C. bondi*, *C. osteocarus*, *C. ephippifer*, *C. julii*, *C. araguaiensis*, *C. maculifer*, *C. leucomelas*, *C. paleatus*, *C. arcuatus*, *C. baderi*, *C. habrosus*, *C. axelrodi*, *C. cochui*, *C. nattereri*, *C. ehrhardti*, *C. atropersonatus*, *C. ambiacus*, and *C. loretoensis*.

In the majority of the superfamily Loricarioidea the uncinate process is somewhat triangular in shape. In *Aspidoras virgulatus*, *Brochis* and several species of *Corydoras* the uncinate process has a peculiar funnel-like shape, curved mesially towards the pharyngobranchials. The character-states are variable ("v") in *Corydoras prionotos*.

28. Posterior expansion of pharyngobranchial 3: absent or narrow (state 0); triangular (state 1; Fig. 10B, arrow 3); concave or rounded (state 2; Fig. 10A, arrow 3). State 1: all callichthyines, all *Aspidoras* (except by *A.* aff. *poecilus*), *Corydoras hastatus*, *C. pygmaeus*, *C. macropterus*, *C. barbatus* I, *C. gracilis*, *C. nanus*, *C. napoensis*, *C. difluviatilis*, and *C. prionotos*. State 2: *Aspidoras* aff. *poecilus*, all *Brochis*, and remaining species of *Corydoras*.

The Nematogenyidae, Trichomycteridae, and Astroblepidae have a small, slender, somewhat cylindrical or rectangular third pharyngobranchial without any expansions. In the Loricariidae and Scoloplacidae this bone has a narrow posteriorly located expansion. The Callichthyinae, almost all species of *Aspidoras*, and a few *Corydoras* species have this expansion well developed, with a triangular shape. Another condition is observed in *Aspidoras* aff. *poecilus*, *Brochis*, and the majority of *Corydoras*, where the posterior expansion is also well-developed, but with a rounded or concave form. Because it was not possible to depict an evident ordering sequence among states, they were treated as non-additive. Character-states are variable ("v") in specimens of *Corydoras barbatus* II, which show narrow and triangular pharyngobranchials.

Suspensorium, Mandibular Arch and Palatine

29. Shape of hyomandibular: deep (state 0; Fig. 11A); slender (state 1; Fig. 11B,C; Fig. 12A,B). All corydoradines.

The hyomandibular in the Loricarioidea is a deep, somewhat quadrangular bone, with its length nearly equal to its depth. In the subfamily Corydoradinae the length of the hyomandibular is approximately one and a half times greater than its depth giving the bone an elongate, nearly rectangular shape.
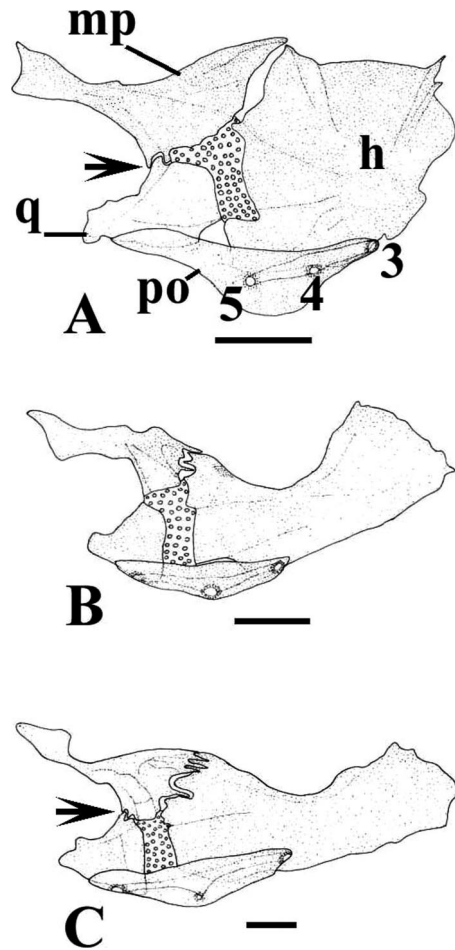
30. Junction between metapterygoid and hyo-

Fig. 11. Suspensorium, lateral view (*h*, hyomandibular; *mp*, metapterygoid; *po*, preopercle; *q*, quadrate; *3–5*, preopercular pores). *Arrows* indicate suture between metapterygoid and quadrate. **A,** *Callichthys callichthys*, UFRJ 3168, 50.0 mm SL; **B,** *Corydoras ehrhardti*, UFRJ 3662, 39.0 mm SL; **C,** *Corydoras barbatus* I, UFRJ 0167, 35.0 mm SL. Scale bar = 1 mm.

mandibular: synchondral (state 0; Fig. 11A); interdigitating suture along the upper half of posterior edge of metapterygoid (state 1; Fig. 12A); interdigitating along whole extension of posterior edge of metapterygoid (state 2; Fig. 11B,C). State 1: *Corydoras zygatus*, *C. acutus*, *C. ellisae*, *C. stenocephalus*, *C. undulatus*, *C. gracilis*, *C. nanus*, *C. napoensis*, *C. elegans*, *C. bicolor*, *C. trilineatus*, *C. osteocarus*, *C. julii*, *C. araguaiensis*, *C. flaveolus*, *C. arcuatus*, *C. baderi*, *C. habrosus*, *C. cochui*, *C. prionotos*, and *C. metae*. State 2: all *Aspidoras*, all *Brochis*, and remaining *Corydoras*.

Reis (1998a) indicated that an interdigitating suture between the metapterygoid and hyomandibular was a synapomorphy for *Aspidoras*, *Brochis*, and *Corydoras*. That author also pointed out that a
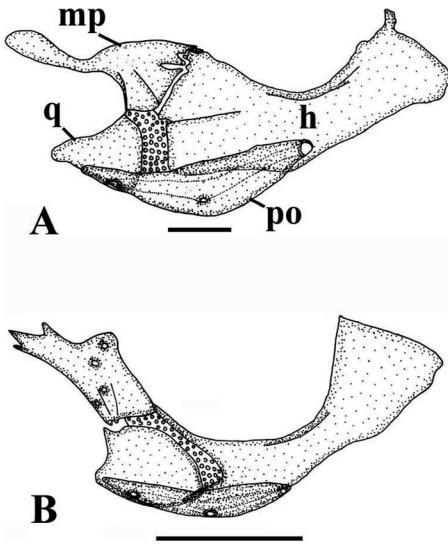
Fig. 12. Suspensorium, lateral view (*h,* hyomandibular; *mp,* metapterygoid; *po,* preopercle; *q,* quadrate). **A,** *Corydoras ellisae,* UMMZ 206339, 37.0 mm SL; **B,** *Corydoras hastatus,* UFRJ 0384, 21.0 mm SL. Scale bar = 1 mm.

synchondral suture is found in several other members of the Loricarioidea. According to the present study, the Corydoradinae shows two additional conditions for this character-state. In the first the interdigitating suture is restricted to the upper portion of the joint. This condition occurs in some species of *Corydoras* (listed above). In a second more extreme state, the interdigitations extend along the entire posterior edge of the metapterygoid, contributing to the joint seen in the majority of Corydoradinae. This last condition also occurs in the Loricariidae and Astroblepidae. In *Corydoras hastatus* and *C. pygmaeus* this character was coded as uncomparable ("-"; see next character).

31. Junction between metapterygoid and hyomandibular: wide (state 0; Figs. 11, 12A); reduced (state 1; Fig. 12B). *Corydoras hastatus* and *C. pygmaeus.*

Regardless of the kind of suture between metapterygoid and hyomandibular (see character 30), the contact area in those conditions is well developed and occupies the entire extension of the joint. In *Corydoras hastatus* and *C. pygmaeus* the suture area between these two bones is highly reduced and restricted to a small anterodorsal region of the hyomandibular.

32. Articulation between infraorbitals and hyomandibular: absent (state 0); present (state 1). All corydoradines. Discussed in Reis (1998a).

33. Interdigitation between quadrate and metapterygoid: absent (state 0; Fig. 11B; Fig. 12A); present (state 1; Fig. 11A,C; Fig. 12B). *Aspidoras microgalaeus, Corydoras rabauti, C. eques, C. aeneus,*

C. hastatus, C. pygmaeus, C. macropterus, C. barbatus I and II, *Corydoras* sp. A, *C. undulatus, C. gracilis, C. nanus, C. napoensis, C. elegans, C. leucomelas,* and *C. guapore.*

In the Trichomycteridae, Nematogenyidae, and Scoloplacidae, the contact between the quadrate and metapterygoid is via cartilage only. The Loricariidae (Schaefer, 1987) and Astroblepidae have the quadrate strongly sutured with the metapterygoid. Within the subfamily Callichthyinae, *Dianema* has a well-developed interdigitating suture between these two bones (Reis, 1998a: fig. 28). *Callichthys* and *Hoplosternum littorale* display a small anterior interdigitating suture between the bones. This last condition also occurs in *Aspidoras microgalaeus* and several species of *Corydoras.* The character-states were coded as variable ("v") for the Callichthyinae, *Corydoras vittatus,* and *C. acutus.* This character was not examined in *Corydoras septentrionalis* due to the bad conditions of the cleared-and-stained material, and was coded as a question mark ("?") in Table 1.

34. Preopercle: covered by skin (state 0); exposed (state 1). All corydoradines. Discussed in Reis (1998a).

35. Odontodes on preopercle: absent (state 0); present (state 1). Almost all corydoradines, except *Brochis britskii, Corydoras zygatus, C. hastatus, C. undulatus, C. gracilis, C. panda, C. xinguensis, C. bicolor, C. trilineatus, C. julii, C. garbei, C. paleatus, C. flaveolus, C. arcuatus, C. baderi, C. habrosus,* and *C. nattereri.*

Within the Loricarioidea, odontodes directly attached to the preopercular bone occur only in some representatives of the Corydoradinae. In the remaining families preopercular odontodes are absent. Nevertheless, several taxa in the Loricariidae have odontodes on the preopercular region, but these are attached to small bony plates overlapping the preopercle. Furthermore, sexually dimorphic odontodes occur on the preopercular region in males of some species in the Loricariidae and Corydoradinae (see character 81).

36. Shape of anguloarticular: slender (state 0; Fig. 13A, B, C); deep (state 1; Fig. 13D). *Brochis* and *Corydoras rabauti.*

The Scoloplacidae, Loricariidae, and the subfamily Callichthyinae have a slender anguloarticular, which is elongate along its longitudinal axis, with a somewhat rectangular shape. In the Trichomycteridae and Astroblepidae this bone has a dorsal process adjacent to the coronoid process of the dentary, which gives the bone a triangular shape. In the species of *Brochis* and *Corydoras rabauti* the anguloarticular is more compact, with its depth approaching its length, resulting in a somewhat more squarish shape. Some species also seems to show a deep an-
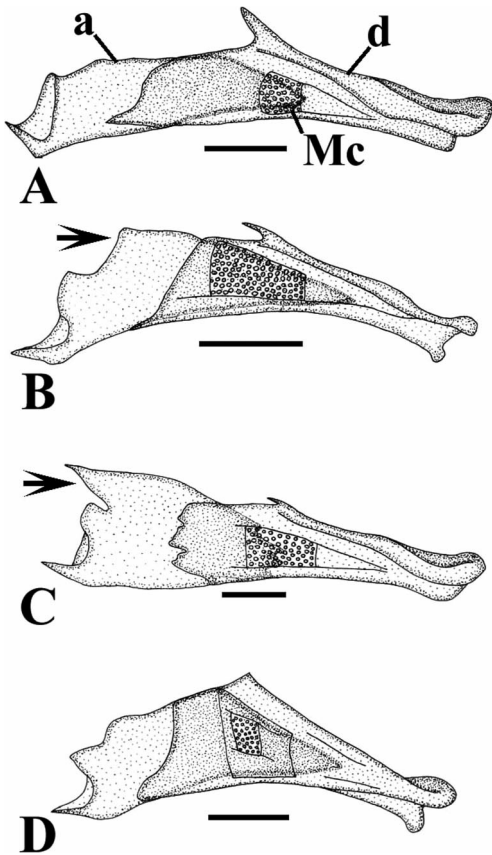
Fig. 14. Upper jaw, dorsal view (*mx,* maxilla; *pmx,* premaxilla; *arrow 1,* dorsal process of premaxilla; *arrow 2,* process for insertion of *retractor tentaculi* muscle). **A,** *Callichthys callichthys,* UFRJ 3168, 50.0 mm SL; **B,** *Corydoras macropterus,* UFRJ 0202, 47.0 mm SL; **C,** *Corydoras rabauti,* MCP 14258, 39.0 mm SL. Scale bar = 1 mm.

to a more extreme condition. Also, no ontogenetic information is available.

38. Dorsal process on premaxilla: absent (state 0; Fig. 14A); present (state 1; Fig. 14B, C, arrow 1). All corydoradines.

The Nematogenyidae, Trichomycteridae, Scoloplacidae, and Loricariidae have rectangular or round-shaped premaxilla when seen from a dorsal view. Despite the strong reduction of this bone within the Callichthyidae (Reis, 1998a), the overall shape presented by the majority of the Callichthyinae is the same as that in the remaining loricarioid taxa. In the Corydoradinae the premaxilla displays a distinct funnel-like shape with a conspicuous posterodorsal process. *Hoplosternum* and *Dianema* also have a dorsal process on the premaxilla, albeit not ably reduced in both genera. A well-developed dorsal process on the premaxilla also occurs in the Astroblepidae (Schaefer, 1990), however, its shape and position differ from that in *Aspidoras, Brochis,* and *Corydoras,* thus, it was treated as non-homologous.

39. Process for insertion of *retractor tentaculi* muscle on maxilla: absent (state 0; Fig. 14A); laminar (state 1; Fig. 14B, arrow 2); pointed (state 2; Fig. 14C, arrow 2). State 1: all *Aspidoras, Corydoras aeneus, C. hastatus, C. macropterus, C. barbatus* II, *C. gracilis, C. nanus, C. napoensis, C. elegans, C. bicolor, C. trilineatus, C. bondi, C. osteocarus, C. ephippifer, C. julii, C. leucomelas, C. ornatus, C. flaveolus, C. arcuatus, C. baderi, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. prionotos, C. atropersonatus, C. agassizi, C. ambiacus, C. loretoensis,* and *C. guapore.* State 2: all *Brochis, Corydoras rabauti, C. eques, C. zygatus, C. pygmaeus, C. vittatus, C. acutus, C. ellisae, C. stenocephalus, Corydoras* sp. A, *C. undulatus, C. panda, C. xinguensis, C. punctatus, C. reticulatus, C. polystictus, C. araguaiensis, C. difluviatilis, C. garbei, C. paleatus, C. aurofrenatus,* and *C. metae.*

According to Reis (1998a) the presence of a small process on posterolateral facet of the maxilla, which serves as an area for insertion of retractor tentaculi muscle, is a feature shared by *Aspidoras, Brochis,* and *Corydoras.* However, it is possible to distinguish two

Fig. 13. Lower jaws, mesial view (*a,* anguloarticular; *d,* dentary; *Mc,* Meckel's cartilage; *arrow,* dorsal lamina of anguloarticular). **A,** *Corydoras macropterus,* UFRJ 4442, 47.0 mm SL; **B,** *Corydoras ornatus,* MCP 14259, 39.0 mm SL; **C,** *Corydoras vittatus,* UFRJ 4438, 35.0 mm SL; **D,** *Corydoras rabauti,* MCP 14258, 39.0 mm SL. Scale bar = 1 mm.

gulo-articular, however, this is due to the presence of a lamina on the dorsal surface of the bone.

37. Dorsal lamina on anguloarticular: absent (state 0; Fig. 13A, D); triangular (state 1; Fig. 13B); falciform (state 2; Fig. 13C). State 1: *Corydoras reticulatus, C. difluviatilis, C. ornatus,* and *C. agassizi.* State 2: *Corydoras vittatus, C. acutus, C. septentrionalis, C. ellisae, C. stenocephalus,* and *C. aurofrenatus.*

In several members of the Loricarioidea, the anguloarticular never has any kind of process. *Corydoras reticulatus, Corydoras difluviatilis, C. ornatus,* and *C. agassizi* have a triangular lamina situated dorsally on the anguloarticular. Another condition is that found in *Corydoras vittatus, C. acutus, C. septentrionalis, C. ellisae, C. stenocephalus,* and *C. aurofrenatus,* in which the bone has a falciform dorsal lamina. Character-states were treated as non-additive since there is no evident sequence from a less
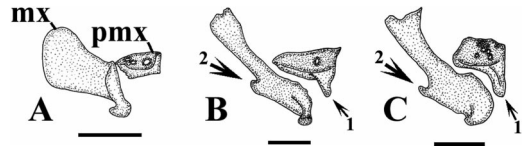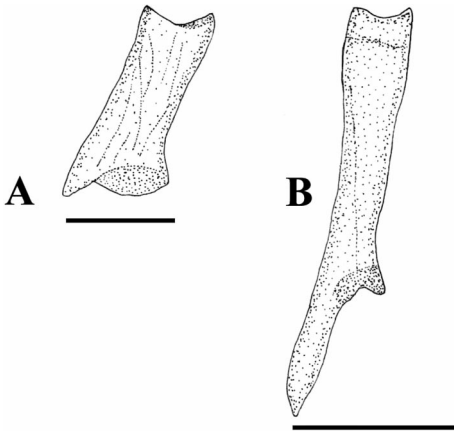
Fig. 15. Palatine, ventral view. **A,** *Callichthys callichthys*, UFRJ 3168, 50.0 mm SL; **B,** *Corydoras vittatus*, UFRJ 3781, 35.0 mm SL. Scale bar = 1 mm.

conditions within the family. In one of these, the process of the maxilla is a laminar expansion of the bone, which increases the area of muscle insertion. In the other state, the process is a small pointed structure with muscle insertion limited to a smaller area. It was not possible to assign an ordering succession among these character-states since no evident sequence from a less to a more extreme was perceived. Also, no ontogenetic information is available. Thus, character-states were treated as non-additive. Character-states are variable ("v") for *Corydoras barbatus* I, *C. maculifer*, and *C. ehrhardti*. Also, this character was not seen in *Corydoras septentrionalis* due to the bad conditions of the cleared-and-stained material, and was coded as a question mark ("?").

40. Shape of palatine: compact (state 0; Fig. 15A); slender (state 1; Fig. 15B). *Aspidoras rochai, A. albater, A. virgulatus, Corydoras vittatus, C. acutus, C. septentrionalis, C. ellisae, C. stenocephalus, C. macropterus, C. barbatus* I and II, *Corydoras* sp. A, *C. bicolor, C. habrosus, C. prionotos,* and *C. aurofrenatus.*

Primitively in the Loricarioidea the palatine is a short compact bone with a small posterolateral process. In the species listed above this bone is quite elongate, slender and with a well-developed posterolateral process. This derived condition is also seen in some members of the Trichomycteridae (W. Costa, pers. comm.).

Opercular Series

41. Odontodes on interopercle: absent (state 0); present (state 1). *Corydoras vittatus, C. acutus, C. septentrionalis, C. stenocephalus, C. macropterus, C. barbatus* I, and *C. aurofrenatus.*

Within the Loricarioidea, the Trichomycteridae has the autapomorphic presence of a ventral expansion of the interopercle, which bears odontodes on its distal tip (de Pinna, 1992). *Corydoras vittatus, C. acutus, C. septentrionalis, C. stenocephalus, C. macropterus, C. barbatus* I, and *C. aurofrenatus* have minute odontodes inserted on the interopercle, similar to the condition observed on the infraorbitals (character 13), preopercle (character 35) and opercle (character 44). The odontodes of these corydoradines differ from those in the interopercle of the Trichomycteridae in not being restricted to a given area of the bone, but being rather scattered over its whole surface. The remaining members of the Loricarioidea do not have odontodes on the interopercle. Character-states are variable ("v") in specimens of *Corydoras ehrhardti.*

42. Shape of opercle: long (state 0; Fig. 16A); compact (state 1; Fig. 16B, C). All *Aspidoras, Corydoras aeneus, C. macropterus, C. osteocarus, C. difluviatilis, C. garbei,* and *C. loretoensis.*

In the majority of the Loricarioidea, the opercle is an elongate bone with its length nearly twice its greater depth, and having an ellipsoid shape. In *Aspidoras* and some species of *Corydoras* the opercle is deeper, its depth somewhat smaller than its length and has a more rounded form.

43. Free margin of opercle: smooth (state 0; Fig. 6A; Fig. 16A); angulated (state 1; Fig. 6B; Fig. 16B, C). *Aspidoras* aff. *poecilus, A. poecilus, A. microgalaeus, A. belenos, A. rochai, Brochis britskii, Corydoras rabauti, C. eques, C. zygatus, C. aeneus, C. macropterus, C. undulatus, C. gracilis, C. nanus, C. napoensis, C. elegans, C. difluviatilis, C. garbei, C. nattereri, C. ehrhardti,* and *C. prionotos.*

Among representatives of the Loricarioidea, the posteroventral region of the opercle is smooth. However, in the species listed above, the free margin of opercle is angulated, forming nearly a ventral and a posterior borders.

44. Odontodes on opercle: present (state 0); absent (state 1). All *Brochis, Corydoras rabauti, C. eques, C. pygmaeus, C. undulatus, C. gracilis, C. panda, C. trilineatus, C. garbei, C. ornatus, C. arcuatus,* and *C. baderi.*

Opercular odontodes are found in the families Trichomycteridae, Loricariidae, Scoloplacidae and the majority of species in the Corydoradinae. In the Nematogenyidae, Astroblepidae and some members of the Corydoradinae, odontodes are absent from the opercle. Although the presence of odontodes is a derived condition among Siluriformes, their presence on the opercle is plesiomorphic within the Loricarioidea.

45. Orientation of keel for *levator operculi* muscle insertion on opercle: upwards (state 0);
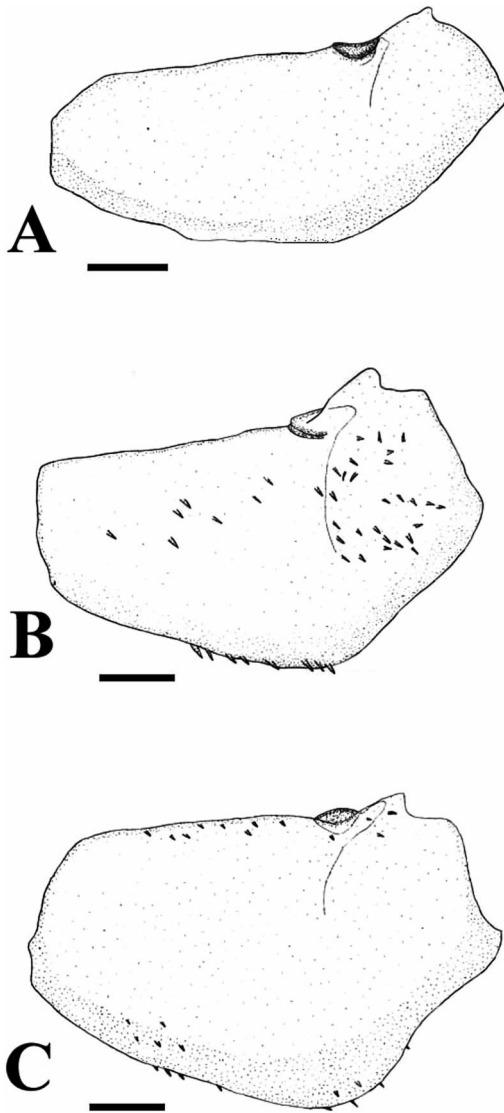
Fig. 16. Opercle, lateral view. **A,** *Corydoras ornatus*, MCP 14259, 39.0 mm SL; **B,** *Corydoras difluviatilis*, UFRJ 4656, 32.3 mm SL; **C,** *Aspidoras rochai*, MCP 19402, 40.0 mm SL. Scale bar = 1 mm.

downwards (state 1). All corydoradines. Discussed in Reis (1998a).

Laterosensory Canals

46. Epiphyseal branch of the supraorbital canal on the frontal bone: short (state 0; Fig. 3A, C); long (state 1; Fig. 3B). All *Aspidoras* (except *A. virgulatus*), *Corydoras vittatus*, *C. acutus*, *C. septentrionalis*, *C. ellisae*, *C. stenocephalus*, *C. macropterus*, *C. barbatus* I and II, *Corydoras* sp. A, and *C. aurofrenatus*.

Among the Loricarioidea, the length of the epi-

physeal branch of the supraorbital canal running inside the frontal, shows some degree of variation ranging from a long canal branch, reaching the suture between frontals, to complete absence. The Nematogenyidae, *Trichogenes*, *Copionodon*, some species of *Trichomycterus*, and the subfamily Callichthyinae have a short epiphyseal branch with its corresponding pore far from the frontal fontanel. In *Aspidoras* and some *Corydoras* species, the branch is longer and its pore is closer to the frontal fontanel. Reis (1998a) proposed that the unique pore opening on the frontals corresponds to the parietal branch of supraorbital. According to Arratia and Huaquin (1995) this branch is lost in the Loricarioidea and the unique frontal pore corresponds to that of the epiphyseal branch of the supraorbital.

47. Number of nasal pores: two (state 0); three (state 1; Lima and Britto, 2001: fig. 2A). All *Aspidoras*, except *A. microgalaeus* and *A. belenos*, *Corydoras vittatus*, *Corydoras* sp. A, and *C. paleatus*.

Representatives of the Loricarioidea have the nasal bone with two pores: one on its posterior tip, which contacts the frontal laterosensory canal segment, and another on its anterior tip where it opens into the nostril. In *Aspidoras*, *Corydoras vittatus*, *Corydoras* sp. A, and *C. paleatus*, the nasal has a third pore located in the middle of the bone, sometimes closer to the posterior pore, and opening into the olfactive capsule. Although this condition is widespread among Siluriformes, it does not occur in any other loricarioid. This character was not checked in *Corydoras elegans* due to the bad conditions of the cleared-and-stained material, and was coded as a question mark ("?"; Table 1).

48. Position of preopercular pore 5: on the middle of bone (state 0; Fig. 11A); on anterior tip of bone (state 1; Fig. 11B, C; Fig. 12A, B). All corydoradines.

In *Nematogenys* Girard, the preopercle has a canal with five pores. This condition is also present in some non-loricarioid families (Schaefer, 1988, 1990; Arratia and Huaquin, 1995). The Astroblepidae, some members of the Loricariidae, and the subfamily Callichthyinae have a preopercular canal with only three pores: one on the posterior tip of the bone, one on the middle, and a third between them. *Scoloplax dicra* has a more reduced condition with only two openings, one located on the middle and the other on the posterior tip of the bone (Schaefer, 1990). In the remaining species of *Scoloplax*, some species of the Trichomycteridae (Schaefer, 1990), and several taxa in the Loricariidae (Arratia and Huaquin, 1995) there is no laterosensory canal on the preopercle. Despite doubts concerning the homology of the two posterior pores within the superfamily, in all these members of the Loricarioidea the anteriormost opening is homologous with pore

5 of other Siluriformes (Schaefer, 1988) and is always observed on the middle of the preopercle. Representatives of the Corydoradinae also have only three openings on the preopercular laterosensory canal, but in these taxa pore 5 is located on the anterior tip of the bone, close to the quadrate-anguloarticular joint.

49. Second lateral line ossicle: tubular (state 0); with expansions (state 1). All corydoradines. Discussed in Reis (1998a).

Weberian Apparatus and Axial Skeleton

50. Lateral expansions on the aortic channel: absent (state 0); present (state 1). All corydoradines. Discussed in Reis (1998a).

51. Total number of free vertebrae: 22 or more (state 0); 21 or less (state 1). *Corydoras rabauti, C. eques, C. zygatus, C. hastatus, C. pygmaeus, C. undulatus, C. nanus, C. napoensis, C. elegans, C. panda, C. xinguensis, C. punctatus, C. bicolor, C. trilineatus, C. polystictus, C. ephippifer, C. julii, C. araguaiensis, C. leucomelas, C. baderi, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. metae, C. atropersonatus,* and *C. ambiacus.*

The total number of vertebrae is somewhat variable within the Loricarioidea. The Nematogenyidae and Trichomycteridae have 40 or more vertebrae. This number also occurs in some non-loricarioid catfishes, *e.g., Diplomystes* Bleeker (Azpelicueta, 1994) and *Mystus* Scopoli (Roberts, 1994). The typical count for the Loricariidae, Astroblepidae, and the subfamily Callichthyinae is approximately 30 vertebrae. *Scoloplax dicra* (Schaefer, 1990) and most Corydoradinae have 27–28 vertebrae. Schaefer (1990) indicated that a reduction of the total vertebral count (24–26) is derived for the Loricarioidea. According to that author, these counts include the five first vertebrae of the Weberian apparatus. Recently, in a study on the ontogeny of the Weberian apparatus of *Corydoras paleatus,* Coburn and Grubach (1998) showed that this species lacks vertebrae 1 and 2, and their derivatives (claustrum, scaphium and intercalarium), with the tripus being the only remaining functional Weberian ossicle. Furthermore, Coburn and Grubach (1998) demonstrated that the tripus in *Corydoras paleatus* is an ossification of the paravertebral sac and dorsal myoseptum of vertebra 3, and proposed the new name "myoseptal tripus" instead of the formerly used "tripus-scaphium" (according to those authors, a misnomer since there is loss of the scaphium). In that same study, those authors also indicated that part of the tripus of *Corydoras paleatus,* based on its double origin, is not homologous with the typical otophysan tripus, being rather a neomorphic structure. In addition, callichthyid catfishes show few differences

in the ontogeny of the Weberian apparatus (Hoedeman, 1960b; Alexander, 1964), which suggests that this set of ontogenetic characters could be synapomorphies for the family. Regardless of these considerations, if vertebral counts are taken so as not to include the Weberian apparatus, it is still possible to detect the same pattern of reduction in the number of vertebrae within the Loricarioidea as reported by Schaefer (1990). In this case, the derived number of vertebrae is 19–21 with the first free vertebra counted being the sixth. As observed by Schaefer (1990), this condition is seen in the species of *Scoloplax,* excluding *S. dicra.* In addition, several species of *Corydoras* (listed above) have this same derived condition. Character-states are variable ("v") in *Corydoras aeneus* and *C. bondi.*

52. Total number of ribs: eight or more (state 0); 5–7 (state 1). All corydoradines, except *Brochis multiradiatus* and *Corydoras garbei.*

As observed for total vertebral count (character 51) total rib count is also variable within the Loricarioidea. Most loricarioid families have eight or more pairs of ribs. In almost all members of the Corydoradinae this number is slightly reduced with the total number of ribs varying from five to seven. A reduced number of ribs also occurs in several taxa in the Loricariidae.

53. Anterior expansions of haemal spines: absent (state 0); present (state 1). Scoloplacidae, Loricariidae, Astroblepidae, *Corydoras rabauti, C. eques, C. zygatus, C. pygmaeus, C. vittatus, C. acutus, C. septentrionalis, C. undulatus, C. nanus, C. napoensis, C. elegans, C. punctatus,* and *C. habrosus.*

In the Nematogenyidae, Trichomycteridae, and most Callichthyidae, the haemal spines are shaft-like and flattened without any expansions along their margins. Scoloplacidae, Loricariidae, and Astroblepidae have haemal spines much wider than in the remaining members of the Loricarioidea (Schaefer, 1987, 1990). These spines are somewhat square-shaped and with a laminar expansion along their anterior borders. The anterior laminar expansions also occur in the species of *Corydoras* listed above. However, in these species, the expansions are much smaller than those in the Scoloplacidae, Astroblepidae, and Loricariidae. Character-states are variable ("v") in *Corydoras aeneus* and *C. ephippifer.*

Unpaired Fins

54. Nuchal plate: covered by skin (state 0); exposed (state 1). All corydoradines. Discussed in Reis (1998a).

55. Length of dorsal spine: equal in size or smaller than adjacent branched dorsal-fin rays (state 0); longer than dorsal-fin rays (state 1). *Corydoras*
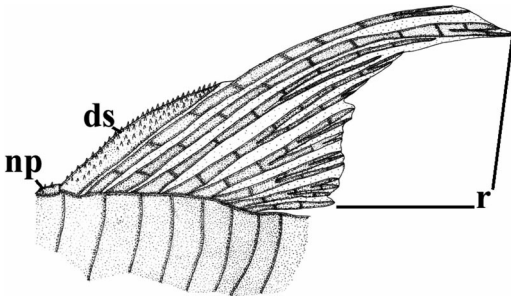
Fig. 17. Dorsal fin of *Corydoras macropterus*, UFRJ 0202, male, 47.0 mm SL, lateral view (*ds,* dorsal spine; *np,* nuchal plate; *r,* rays).

reticulatus, C. bicolor, C. ornatus, C. paleatus, C. atropersonatus, and *C. loretoensis.*

The Loricariidae, Astroblepidae, Scoloplacidae and almost all members of the Callichthyidae have a dorsal spine of the same size or slightly smaller than the first two or three branched dorsal-fin rays. In *Corydoras reticulatus, C. bicolor, C. ornatus, C. paleatus, C. atropersonatus,* and *C. loretoensis* the dorsal spine is strengthened along its main axis, and it is much longer than the dorsal-fin rays. This character was coded as uncomparable ("-") for Nematogenyidae and Trichomycteridae due to the reduction of the dorsal spine in those families.

56. First three branched dorsal-fin rays: no difference between males and females, rays with same size as dorsal spine (state 0); sexually dimorphic, with rays of males much longer than dorsal spine (state 1; Fig. 17). *Aspidoras virgulatus, Corydoras macropterus, C. barbatus* I and II, and *Corydoras* sp. A.

Males of the species listed above have the first three branched dorsal-fin rays much longer than the dorsal spine (about twice as long), giving the fin a lanceolate shape. As explained above (character 55),

in the primitive condition, dorsal-fin rays of males are typically the same size or just a little longer than the dorsal spine.

57. Number of branched dorsal-fin rays: 6–8 (state 0); more than 10 (state 1). All *Brochis.* Discussed in Reis (1998a).

58. Anal-fin rays: thin (state 0; Fig. 18); thick (state 1; Fig. 19). All *Brochis, Corydoras rabauti, C. eques,* and *C. leucomelas.*

In the species listed above, all anal-fin rays are thickened, with a notably reduced interradial area. A similar condition is also seen in some members of the Loricariidae (*e.g., Hypostomus*).

59. Proximal segment of second unbranched anal-fin ray: narrow (state 0; Fig. 18); thick (state 1; Fig. 19). All *Brochis, Corydoras rabauti, C. eques, C. zygatus, C. leucomelas,* and *C. arcuatus.*

The second unbranched anal-fin ray segment in almost all members of the Loricarioidea is a narrow structure and much longer than the remaining segments. In the above listed species this proximal segment displays a pronounced thickening. This condition is difficult to perceive in the species that shows a thickening of all fin rays (character 58).

60. Shape of caudal fin: rounded or truncate (state 0); bilobed (state 1). All corydoradines. Discussed in Reis (1998a).

61. Caudal-fin rays: thin (state 0; Fig. 20); thick (state 1; Fig. 21). All *Brochis* and *Corydoras vittatus.*

The Trichomycteridae, Scoloplacidae, Astroblepidae, most Loricariidae, and Callichthyidae have thin caudal-fin rays. In some larger specimens of the Loricariidae (*e.g., Hypostomus*), *Lepthoplosternum* Reis, *Megalechis* Reis, and *Hoplosternum,* the procurrent and unbranched caudal-fin rays are thicker than the branched rays. *Brochis* species and *Corydoras vittatus* show a thickening in all caudal-fin rays, resulting in a very small interradial area.
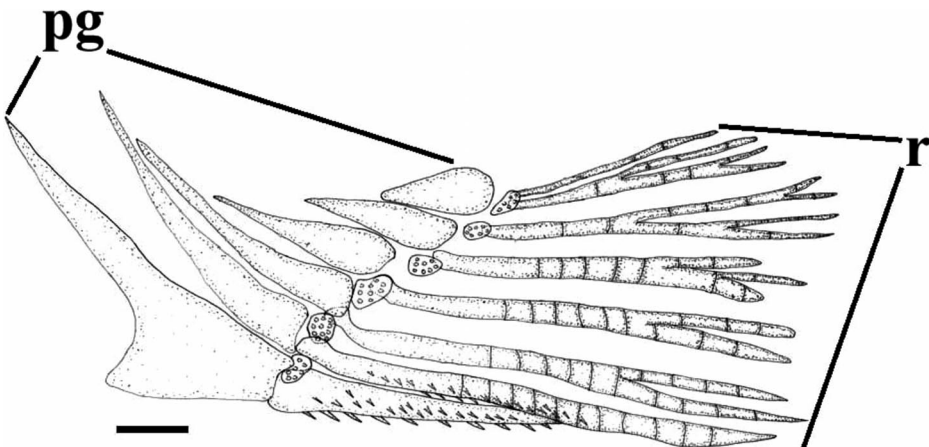

Fig. 18. Anal fin of *Corydoras punctatus*, MCP 16138, 32.0 mm SL, lateral view (*pg,* pterygiophores; *r,* rays). Scale bar = 1 mm.
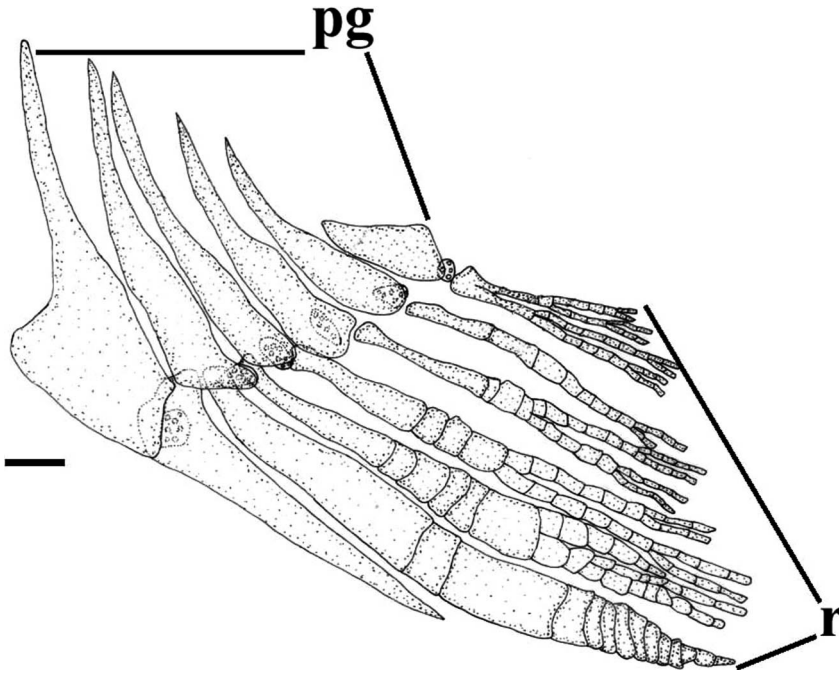
Fig. 19. Anal fin of *Brochis britskii*, UFRJ 3850, 100.0 mm SL, lateral view (*pg*, pterygiophores; *r*, rays). Scale bar = 1 mm.

Pectoral Girdle and Fins

62. Medial expansion of coracoid: covered by skin (state 0); exposed (state 1). All *Brochis* and *Corydoras*, except by *C. macropterus*, *C. barbatus* I and II, and *Corydoras* sp. A.

The medial expansion of the posterior process of coracoid is not externally visible, with a thick layer of skin covering it, in the majority of the members of the Loricarioidea. In the subfamily Callichthyinae, only *Callichthys* shows this primitive condition. The medial expansions in the remaining genera are exposed and sometimes well developed. Within the Corydoradinae this latter condition is shared by *Bro-*

chis and almost all species of *Corydoras* except those listed above.

63. Medial expansions of coracoids: small (state 0); large (state 1). All *Brochis*, *Corydoras rabauti*, *C. eques*, and *C. zygatus*.

Among members of the Loricarioidea, well-developed expansions of coracoids are observed only in the family Callichthyidae. This derived condition appears only in some genera that have exposed me-
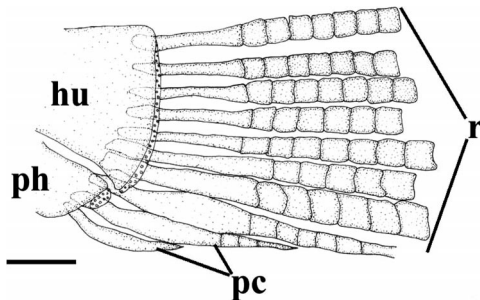

Fig. 20. Lower lobe of caudal fin of *Corydoras punctatus*, MCP 16138, 32.0 mm SL, lateral view (*hu*, hypurals 1+2 (fused); *pc*, procurrent rays; *ph*, parhypural; *r*, principal rays). Scale bar = 1 mm.
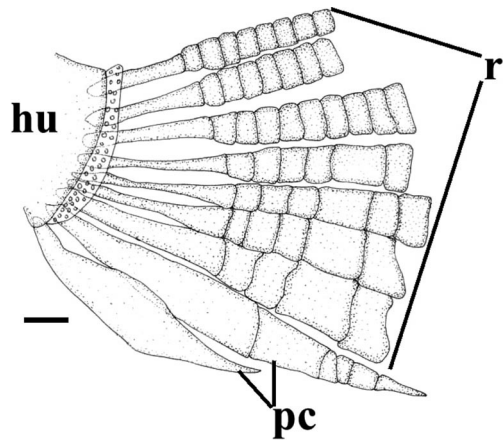

Fig. 21. Lower lobe of caudal fin of *Brochis britskii*, UFRJ 3850, 100.0 mm SL, lateral view (*hu*, hypurals 1+2 (fused); *pc*, procurrent rays; *r*, principal rays). Scale bar = 1 mm.

dial expansions (character 62). In these taxa, the degree of development of the coracoid expansions is much greater than in any member of the Loricarioidea with the expansions contacting each other at the ventral midline of body. Within the subfamily Corydoradinae, this condition occurs in all species of *Brochis* and in the *Corydoras* species listed above.

64. Anteroventral portion of cleithrum: covered by skin (state 0); exposed (state 1). All *Brochis*, *Corydoras rabauti*, *C. eques*, *C. zygatus*, *C. hastatus*, *C. nanus*, and *C. elegans*.

In addition to the medial expansion of the coracoids (character 62), most Loricarioidea also have the anteroventral portion of cleithrum covered by skin. The species listed above have this anteroventral portion exposed. Furthermore, all pectoral girdle elements are externally visible. Some *Corydoras* species have an ossified region in the anteroventral portion of the breast, which resembles an exposed part of cleithrum. However, in these specimens, this ossified area is formed by small dermal bony plates. Furthermore, this latter condition is variable and occurs only in larger individuals, representing perhaps a senescent condition.

65. Pectoral spine: equal in size on both sexes (state 0); sexually dimorphic, with males having a much larger spine than female (state 1). *Aspidoras virgulatus*, *Corydoras macropterus*, *C. barbatus* I and II, and *Corydoras* sp. A.

Representatives of the Loricarioidea show no sexual dimorphism related to pectoral spine morphology, which has the same size in both sexes, or it is slightly larger in males. Within the Callichthyinae, *Hoplosternum littorale* and species of *Megalechis* have a sexually dimorphic enlargement of the pectoral spine of males (Reis, 1997). This derived condition also occurs in *Aspidoras virgulatus*, *Corydoras macropterus*, *C. barbatus* I and II, and *Corydoras* sp. A. However, in these species, the strengthening of the pectoral spine takes place in the non-ossified portion of the spine (see character 66). Males of *Corydoras geoffroy* also have elongate pectoral spines (Nijssen, 1970), but in this species the enlargement occurs only in the ossified portion, as in representatives of *Hoplosternum* and *Megalechis*.

66. Ossified portion of pectoral spine: equal in size to the first branched rays (state 0); slightly reduced in size (state 1); strongly reduced (state 2). State 1: *Corydoras vittatus*, *C. macropterus*, *C. barbatus* I, *Corydoras* sp. A, *C. prionotos*, and *C. aurofrenatus*. State 2: all *Aspidoras*.

According to Reis (1998a), species of *Aspidoras* have the pectoral spine formed by a proximal ossified portion and a well-developed segmented non-ossified distal portion. Furthermore, Reis observed that in *Aspidoras* the ossified portion is smaller than the adjacent branched pectoral-fin rays. A

similar condition occurs in *Nematogenys* (de Pinna, 1992). The Loricariidae, Scoloplacidae, and most Callichthyidae have the pectoral spine nearly or entirely ossified, with its length equal or somewhat shorter than the branched rays. A reduced ossified portion of the pectoral spine is also shared by *Corydoras vittatus*, *C. macropterus*, *C. barbatus* I, *Corydoras* sp. A, *C. prionotos*, and *C. aurofrenatus*. However, in these species, the ossified part is longer than half the length of the first branched pectoral-fin ray. *Aspidoras* shows a more extreme condition, with the proximal portion of the pectoral-fin ray highly reduced and always smaller than half the length of the first branched pectoral-fin ray.

67. Inner margin of pectoral spine: serrated along its entire length (state 0); serrated only along its proximal margin (state 1); without serrations (state 2). State 1: *Corydoras difluviatilis*. State 2: *Corydoras garbei*.

In most Siluriformes the first pectoral-fin ray has its components co-ossified into a rigid and non-segmented spine, bearing serrations along its inner margin (Reed, 1924; de Pinna, 1992). Within the Loricarioidea, Nematogenyidae, some members of the Loricariidae, *Scoloplax dolicolophia* (Schaefer, 1990), and the Callichthyidae show well-developed serrations on the inner margin of the pectoral spine. In the Trichomycteridae, Astroblepidae, and some members of the Loricariidae the first pectoral-fin ray is not modified into a spine. The remaining species of *Scoloplax* (Schaefer, 1990) and *Corydoras garbei* have the pectoral spine lacking serrations along its inner margin, which is entirely smooth. A putative intermediate condition is observed in *Corydoras difluviatilis*, which has serrations restricted to the proximal portion of the pectoral spine.

Pelvic Girdle

68. Shape of internal arm of the basipterygium: sharp (state 0; Fig. 22A); expanded (state 1; Fig. 22B, C, D). All corydoradines.

Among catfishes the primitive condition of the pelvic girdle is a basipterygium bearing two anterior arms (Fink and Fink, 1981). This condition is observed in several families of the Loricarioidea. The Trichomycteridae, Nematogenyidae, Loricariidae and Astroblepidae have a sharp free tip on the internal arm. The pelvic girdle of the Scoloplacidae is strongly modified and there are no distinct internal and external arms (Schaefer, 1990: fig. 23). The Callichthyidae also displays several modifications of the pelvic girdle (Reis, 1998a). In this family the internal arm is close to the midline of the girdle and it has a dorsal expansion. The external arm is reduced, has a laminar shape, and is laterally displaced. A sharp internal process of basipterygium is
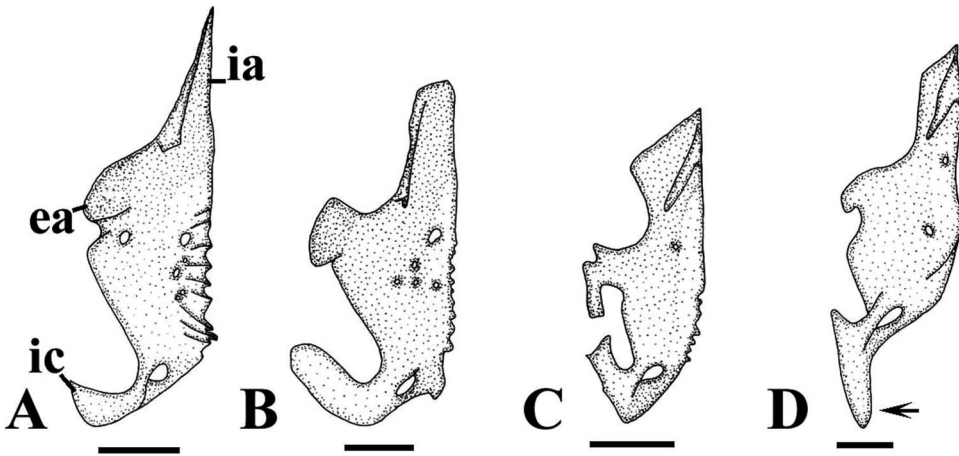
Fig. 22. Pelvic girdle (basipterygium), dorsal view (*ea,* external arm; *ia,* internal arm; *ic,* ischiac process; *arrow,* narrow expansion of ischiac process). **A,** *Callichthys callichthys,* UFRJ 2014, 48.0 mm SL; **B,** *Aspidoras rochai,* MCP 19402, 40.0 mm SL; **C,** *Corydoras leucomelas,* MCP 14249, 27.0 mm SL; **D,** *Brochis multiradiatus,* MCP 16502, 50.0 mm SL. Scale bar = 1 mm.

also observed in representatives of the subfamily Callichthyinae. In the Corydoradinae the internal arm has its free tip expanded and laminar in shape.

69. Shape of external arm of basipterygium: narrow (state 0); laminar (state 1; Fig. 22A, B, D); falciform (state 2; Fig. 22C). State 1: all callichthyids except by those, which present state 2. State 2: *Corydoras panda, C. xinguensis, C. punctatus, C. bicolor, C. trilineatus, C. bondi, C. osteocarus, C. polystictus, C. ephippifer, C. julii, C. araguaiensis, C. maculifer, C. leucomelas, C. paleatus, C. flaveolus, C. baderi, C. habrosus, C. axelrodi, C. cochui, C. nattereri, C. ehrhardti, C. metae, C. atropersonatus, C. ambiacus,* and *C. loretoensis.*

In the Loricarioidea the external arm of the basipterygium is narrow, notably elongate, and located anteriorly. The Callichthyidae has this process reduced, laminar in shape and shifted laterally. Another derived condition occurs in some *Corydoras* species. In these species the external arm has a posterior expansion, which gives the process a falciform shape. Character-states were treated as non-additive since it was not possible to perceive an evident ordering sequence from a less to a more extreme condition.

70. Shape of ischiac process: small or posteriorly elongate (state 0; Schaefer, 1987: fig. 14; Arratia et al., 1978: fig. 5); falciform (state 1; Fig. 22A, B, D); falciform and strongly developed (state 2; Fig. 22C). State 1: all callichthyids, except by those presenting state 2. State 2: *Corydoras panda, C. punctatus, C. bicolor, C. trilineatus, C. ephippifer, C. julii, C. araguaiensis, C. leucomelas, C. cochui, C. metae, C. atropersonatus, C. ambiacus,* and *C. loretoensis.*

In addition to the internal and external arm, the ischiac process of basipterygium in Callichthyidae is highly modified. In this family, the process is divided into dorsal and ventral portions (Reis, 1998a). *Copionodon, Trichogenes,* and some members of the Trichomycterinae display a highly reduced ischiac process. In the Astroblepidae and Loricariidae, this process is elongated posteriorly, having a laminar shape in the Loricariidae. The Callichthyidae has an ischiac process with a falciform shape in its ventral portion. In some species of *Corydoras* a more extreme condition occurs in which the ventral portion of the process is well developed, almost contacting the external arm of the basipterygium (state 2).

71. Posterior margin of ischiac process: smooth (state 0; Fig. 22A, B, C); with a narrow expansion (state 1; Fig. 22D). All *Brochis, Corydoras rabauti, C. eques, C. zygatus, C. aeneus, C. reticulatus, C. garbei, C. ornatus, C. paleatus,* and *C. habrosus.*

Despite modifications on the shape of the ischiac process, representatives of the subfamily Callichthyinae and most members of the Corydoradinae lack expansions along the posterior margin of the process. Species of *Brochis* and some *Corydoras* species have the ischiac process with a conspicuous narrow expansion situated along its posterior border. Character-states were coded as not comparable ("-") in Nematogenyidae, Trichomycteridae, Scoloplacidae, Loricariidae, and Astroblepidae, due to the shape of the ischiac process in these taxa (character 70).

Coloration

In this section character-states related to color patterns are discussed. To avoid unnecessary repetitive discussion on each topic, brief comments are

made at this point on choices made relative to these characters.

Members of the Loricarioidea show a great variety of coloration patterns. Coloration characters included in the present analysis (72 to 78) are those that are absent in basal clades of Loricarioidea families, being therefore derived for the Corydoradinae. Some of these coloration patterns also occur in other more derived clades within families of the Loricarioidea, phylogenetic distant from basal taxa. Considering the present knowledge of the relationships within the Loricarioidea (Baskin, 1973; Howes, 1983; Schaefer, 1990), these cases represent convergences.

72. Area between tip of snout and interorbital region: similar in males and females, without any conspicuous color markings (state 0); sexually dimorphic, with a mid-dorsal white stripe (state 1; Glaser et al., 1996: p. 98). *Corydoras barbatus* I and II, and *Corydoras* sp. A.

73. Dorsal region of head and body: with a uniform coloration or with blotches and/or spots (state 0); with an arch-like dark brown stripe from snout to caudal peduncle (state 1; Glaser et al., 1996: p. 64). *Corydoras gracilis* and *C. arcuatus*.

74. Dorsal region of body between the anterior portion of the nuchal plate and the caudal-fin base: with a uniform coloration or with blotches and/or spots (state 0); with an oblique dark brown stripe (state 1; Glaser et al., 1996: p. 111). *Corydoras rabauti* and *C. zygatus*.

75. Junction of lateral body plates: without any conspicuous color marks or showing some blotches (state 0); with a dark brown stripe (state 1; Glaser et al., 1996: p. 93). *Aspidoras virgulatus*, *Corydoras hastatus*, *C. pygmaeus*, *C. bondi*, *C. nattereri*, and *C. prionotos*. Character-states variable ("v") in *Corydoras osteocarus*.

76. Caudal-fin base: without any conspicuous color markings (state 0); with a dark brown diamond-shaped spot bordered by two white stripes (state 1; Schaefer et al., 1989: fig 14). *Corydoras hastatus* and *C. pygmaeus*. Discussed in Schaefer et al. (1989).

77. Area between pelvic- and anal-fin origins: without conspicuous color markings (state 0); with a dark brown stripe (state 1; Schaefer et al., 1989: fig 14). *Corydoras hastatus* and *C. pygmaeus*. Discussed in Schaefer et al. (1989).

78. Caudal-peduncle region: without conspicuous color markings (state 0); with a conspicuous large dark brown spot (state 1; Glaser et al., 1996: p. 116). *Corydoras panda*, *C. habrosus*, and *C. guapore*.

Miscellaneous

79. Area at the corner of mouth, ventral to the maxillary barbels: smooth (state 0); with a fleshy flap (state 1). *Corydoras vittatus*, *C. acutus*, *C. septentrionalis*, *C. ellisae*, *C. stenocephalus*, *C. macropterus*, *C. barbatus* I and II, *Corydoras* sp. A, and *C. aurofrenatus*.

Representatives of the Loricarioidea show some variation in the degree of development of their maxillary barbels, ranging from two well-developed pairs, in the Callichthyinae, to a small papilla at the corner of the mouth, in some members of the Loricariidae (*e.g.*, *Corumbataia* Britski). However, a fleshy expansion of the maxillary barbels is absent in almost all loricarioids. In the *Corydoras* species listed above, a conspicuous fleshy flap is located ventral to the maxillary barbels. *Corydoras geoffroy* has a third, well-developed maxillary barbel in the same place as the fleshy flap found in other *Corydoras* species (Nijssen, 1970), probably an autapomorphy for this species. Nijssen (1970) pointed out that *Corydoras septentrionalis* also displays a third pair of maxillary barbels. This condition, however, was not seen in any specimen of *Corydoras septentrionalis* examined in the present study.

80. Shape of lower lip: skin fold, without barbels (state 0); with one barbel on each side (state 1). All corydoradines. Discussed in Reis (1998a).

81. Preopercular-opercular region: smooth, similar in males and females (state 0); sexually dimorphic, with odontodes in males (state 1; Burgess, 1989: p. 651). *Aspidoras virgulatus*, *Corydoras macropterus*, *C. barbatus* I and II, *Corydoras* sp. A and *C. prionotos*.

Sexually dimorphic development of odontodes on the preopercular-opercular region is unknown in the Nematogenyidae, Trichomycteridae, Scoloplacidae, Astroblepidae or the subfamily Callichthyinae. In *Aspidoras virgulatus*, *Corydoras macropterus*, *C. barbatus* I and II, *Corydoras* sp. A, and *C. prionotos*, adult males have odontodes inserted in small fleshy papillae on the preopercular-opercular region, sometimes reaching anteriorly to the snout. This derived condition also occurs in some representatives of the Loricariidae (*e.g.*, *Rineloricaria* Bleeker). Other members of Loricariidae also show sexually dimorphic development of odontodes on other body regions (*e.g.*, *Otocinclus flexilis* and *O. vittatus*; Aquino, 1994).

82. Shape of genital papilla of males: narrow (state 0; Fig. 23A); lanceolate (state 1; Fig. 23B). All corydoradines.

The genital papilla in males of the Loricarioidea has a narrow or rod-like shape. In these taxa, the papillae of males are distinguished from those of females only in length being longer in males. In females of the Corydoradinae, the shape of genital papilla is similar to that observed in other members of the Loricarioidea. However, in males of that subfamily the papilla is lanceolate in shape.
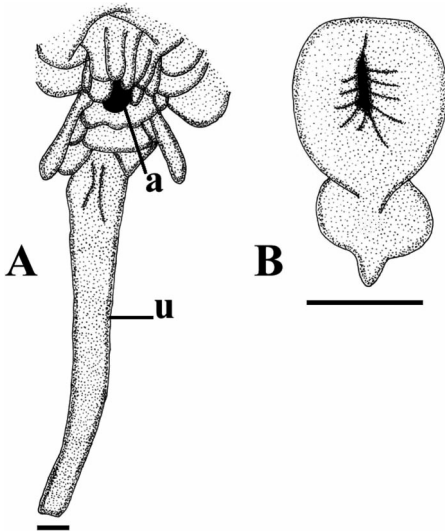
Fig. 23. Anus (*a*) and urogenital papilla (*u*), ventral view. **A,** *Hoplosternum littorale*, DBAV.UERJ 1018, male, 150 mm SL; **B,** *Corydoras barbatus*, UFRJ 0591, male, 70.0 mm SL. Scale bar = 1 mm.

83. Swimming behavior: close to the bottom (state 0); on mid-water (state 1). *Corydoras hastatus* and *C. pygmaeus*. Discussed in Reis (1998a).

DISCUSSION

Several new hypotheses on the interrelationships of corydoradine catfishes are expressed in the consensus cladogram of 1403 trees on Figure 24. To allow a better visualization of the main assemblages detailed below, a few clades were pointed out on the cladogram and are presented separately (as clade I to IX). One of the results of the present study is the non-monophyletic nature of the genus *Corydoras* as currently defined. Historically, problems concerned with the name *Corydoras* began since the original description of the genus by Lacépède (1803), as noted by numerous authors (Valenciennes, in Cuvier and Valenciennes, 1840; Bleeker, 1862; Myers, 1940; Nijssen, 1970; Nijssen and Isbrücker, 1967; Nijssen and Isbrücker, 1980). Until now *Corydoras* was diagnosed only as a member of the Corydoradinae that lacked the diagnostic features of *Aspidoras* and *Brochis*. Reis (1998a) suggested on the basis of a cladistic analysis that *Corydoras* is not monophyletic if *Brochis* is recognized.

Although the present hypothesis agrees with Reis (1998a) as it regards non-monophyly of *Corydoras*, the two differ in detail. According to Reis (1997, 1998a), *Brochis* and all species of *Corydoras* he examined form a monophyletic assemblage, which is the sister-group of *Aspidoras*. Thus, that author indicated Corydoras as a paraphyletic group. In the present study, however, some *Corydoras* species are hypothesized to form a monophyletic group with *Brochis*, while others are more closely related to *Aspidoras*. Thus, according to the present study, non-monophyly of *Corydoras* is a consequence of its polyphyly rather than its paraphyly.

The tribe Aspidoradini was originally proposed by Hoedeman (1952) to include only *Aspidoras*. Reis (1998a) corroborated the monophyly of *Aspidoras*. According to the present study, a small monophyletic group of species so far assigned to *Corydoras* is the sister-group of *Aspidoras*. One taxonomic option would be to synonymize this group with *Aspidoras*, thus expanding the concept of the latter. However, this action would fail to express the monophyly of both groups. An alternative option proposed herein is to maintain the current concept of *Aspidoras* and to amplify the tribe Aspidoradini to encompass *Aspidoras* and its sister-group. This action would require a generic name for the sister-group of *Aspidoras*. *Scleromystax* (type-species *Callichthys barbatus*) is available for this assemblage, including *Corydoras prionotos* as the sister-group of the clade (*Corydoras macropterus* (*Corydoras* sp. A (*C. barbatus* I and II))) (clade I) defined by five synapomorphies: anterior process of the frontal short (character 5); contact between the quadrate and metapterygoid by means of small interdigitation (character 33); first three branched dorsal-fin rays much longer than dorsal spine in males (character 56); expansion of the non-ossified portion of the pectoral spine in males (character 65); and fleshy flap hidden below maxillary barbels (character 79). A close relationship among these species was previously hypothesized by Nijssen and Isbrücker (1980), who also included some other species of *Corydoras* in that group. A close relationship between *Corydoras prionotos*, *C. barbatus* and *C. macropterus* than with other *Corydoras* species was also proposed by Oliveira et al. (1992, 1993) based on cytogenetic data. The present study corroborates the latter hypothesis with evidence from morphological data.

The Corydoradini as here redefined consists of the majority of species belonging to *Corydoras* and *Brochis*. A new species of *Corydoras*, *C. difluviatilis* (Britto and Castro, 2002), is considered the sister-group to all the rest of the Corydoradini, showing several plesiomorphic features when compared to the remaining *Corydoras* species.

The sister-group of all remaining *Corydoras* species is a clade composed of (*C. agassizi* (*C. ornatus* (*C. ellisae* (*C. acutus* ((*C. stenocephalus* plus *C. septentrionalis*)(*C. aurofrenatus* plus *C. vittatus*)))))) (clade II). Five synapomorphies support the relationships between clade II and the remaining *Corydoras*: contact between supraoccipital and nuchal plate (character 11); reduced inner expansion of in-

Fig. 24. Strict consensus tree showing the phylogenetic relationships within the subfamily Corydoradinae (trees 1403 [overflow], length 336, CI 0.29, RI 0.71), pointing out some of its clades (I to IX).

fraorbitals 1 (character 16) and 2 (character 17); hypobranchial 2 well ossified (character 21); and posterior expansion on pharyngobranchial 3 concave or rounded (character 28). Only one reversal (*i.e.,* lateral ethmoid elongate in shape; character 4) supports the monophyly of clade II. However, the clade (*Corydoras ellisae* (*C. acutus* ((*C. stenocephalus*, *C. septentrionalis*)(*C. aurofrenatus*, *C. vittatus*)))) (clade III) is supported by eight derived conditions: contact between second infraorbital and pterotic-supracleithrum by means of triangular expansion on former bone (character 18); continuous posterior expansion of third ceratobranchial (character 23); falciform dorsal lamina on anguloarticular (character 37); laminar process for insertion of *retractor tentaculi* muscle on maxilla (character 39); palatine slender (character 40); epiphyseal branch of supraorbital canal long (character 46); and fleshy flap hidden

below maxillary barbels (character 79). Nijssen (1970) placed *Corydoras acutus* and *C. aurofrenatus* together with other species in his "*acutus*" group based on the presence of a grayish color pattern and serrated pectoral spine. Subsequently, Nijssen and Isbrücker (1980) placed *Corydoras acutus*, *C. aurofrenatus*, *C. septentrionalis*, *C. ellisae*, *C. vittatus*, and some other *Corydoras* in a redefined "*acutus*" group.

The remaining species of *Corydoras* are grouped in a large assemblage with *C. reticulatus* as the most basal taxon. This group is supported by only one synapomorphy (anterior portion of mesethmoid short; character 1). The group formed by the remaining *Corydoras* species, exclusive of *C. reticulatus*, is supported by five synapomorphies: posterior half of mesethmoid wide (character 2); uncinate process of third epibranchial curved mesially (character 27); absence of dorsal lamina on anguloarticular (char-

acter 37); 19–21 free vertebrae (character 51); and falciform external arm of basipterygium (character 69). Relationships within this assemblage are poorly resolved. Although some groups are delimited within this clade, a basal polytomy remains. This is a consequence of the placement of constituent species in different phylogenetic positions in several fundamental cladograms, resulting in a "soft" polytomy in the consensus (Maddison, 1989). Six monophyletic assemblages are delimited within this large unresolved clade. One of them is composed of *Corydoras hastatus* and *C. pygmaeus* (clade IV). Four exclusive synapomorphies corroborate clade IV: suture between metapterygoid and hyomandibular reduced (character 31); dark brown diamond-shaped spot outlined by two white stripes on the caudal fin (character 76); dark brown stripe between pelvic and anal fins (character 77); and mid-water swimming behavior (character 83). These two species were first grouped together by Nijssen (1970) based on their minute size. Schaefer et al. (1989) also indicated that these two species are sister-groups, hypothesizing that their minute size arose in their common ancestor. In addition, Nijssen and Isbrücker (1980) included these two species and some other *Corydoras* together in their "*elegans*" group.

Another group is composed of *Corydoras atropersonatus* and *C. loretoensis* (clade V) and is supported by two characters: the dorsal spine longer than the dorsal-fin rays (character 55); and the ischiac process falciform and strongly developed (character 70). Nijssen and Isbrücker (1980) placed *Corydoras atropersonatus* in their "*punctatus*" species group. Later, the same authors (1986b) indicated that *Corydoras loretoensis* also belonged in the "*punctatus*" group and somewhat resembled *C. armatus*. This latter hypothesis was not confirmed herein.

A second assemblage is formed by *Corydoras osteocarus*, *C. ephippifer*, and *C. axelrodi* (clade VI); with the latter two as sister-species. Clade VI is supported by only one reversed character, which is the mesethmoid bearing reduced lateral cornua (character 3). Nijssen and Isbrücker (1980) placed *Corydoras osteocarus*, *C. axelrodi* and other *Corydoras* in their "*aeneus*" group, apart from *C. ephippifer*, which they assigned to the "*punctatus*" group.

Corydoras cochui, *C. julii*, *C. bicolor*, and *C. habrosus* constitute the third clade (clade VII), with *C. cochui* as sister-group of the remaining. Within this group, *Corydoras julii* is the sister-group of *C. bicolor* plus *C. habrosus*. Three characters support the monophyly of clade VII: presence of a pointed process on anterolateral margin of frontal bone (character 7; reversed in *Corydoras bicolor*); an interdigitating suture along the upper half of posterior edge of metapterygoid (character 30); and the ischiac process falciform and strongly developed (character

70; not developed in *C. habrosus*). In his 1970's papers, Nijssen grouped *Corydoras julii*, *C. bicolor* and *C. habrosus* within his "*punctatus*" group. However, each one was assigned to a different subgroup, according to morphometric and pigmentation data. Subsequently, Nijssen and Isbrücker (1980) maintained *Corydoras julii* and *C. bicolor* in that same group, but placed *C. habrosus* in their "*aeneus*" group. A monophyletic group formed by these four species has not been previously hypothesized.

A fourth clade consists of *Corydoras xinguensis* (the most basal species), *C. panda*, *C. trilineatus*, *C. arcuatus*, *C. baderi*, *C. flaveolus*, *C. gracilis*, *C. undulatus*, and *C. garbei* (clade VIII), and is supported by the inner expansion on infraorbital 2 large (character 17); a continuous posterior expansion of ceratobranchial 3 (character 23); and preopercle without odontodes (character 35). Within this clade, there is an assemblage composed of *C. panda*, *C. trilineatus*, *C. arcuatus*, *C. baderi*, *C. flaveolus*, *C. gracilis*, *C. undulatus*, and *C. garbei*. Two monophyletic groups are recognized within this assemblage. One includes (*C. trilineatus* (*C. arcuatus* plus *C. baderi*)), and the other (*C. flaveolus* (*C. gracilis* (*C. undulatus* plus *C. garbei*))). These two groups form a tritomy with *Corydoras panda*. *Corydoras garbei*, *C. flaveolus*, *C. undulatus* and other *Corydoras* species were placed by Nijssen (1970) in his "*barbatus*" group. Nijssen and Isbrücker (1980) kept *Corydoras garbei* and *C. flaveolus* in the "*barbatus*" group, but included *Corydoras undulatus* together with *C. gracilis* and other species in their "*elegans*" group. In addition, these authors placed several species of *Corydoras* (e.g., *C. arcuatus*, *C. panda*, and *C. baderi*) in their "*aeneus*" group. *Corydoras trilineatus* and *C. xinguensis*, in turn, were placed in Nijssen and Isbrücker's (1980) largest assemblage, the "*punctatus*" group. Subsequently, Oliveira et al. (1992), based on cytogenetic data, delimited a group formed by *Corydoras arcuatus*, *C. undulatus*, and other species.

The fifth monophyletic group includes *Corydoras aeneus*, *C. zygatus*, *C. rabauti*, *C. eques*, and the species previously assigned to *Brochis* (clade IX). This assemblage is supported by the following features: the anterior expansion of infraorbital 1 very large (character 15); contact between infraorbital 2 and pterotic-supracleithrum by means of a triangular expansion of the infraorbital (character 18); the free margin of opercle angulated (character 43); the external arm of basipterygium laminar (character 69); and the posterior margin of ischiac process with a narrow expansion (character 71). According to the present study, two exclusive characters support the monophyly of the species currently assigned to *Brochis*: presence of bony plate anterior to first infraorbital (character 14) and the possession of more than ten branched dorsal-fin rays (character 57).
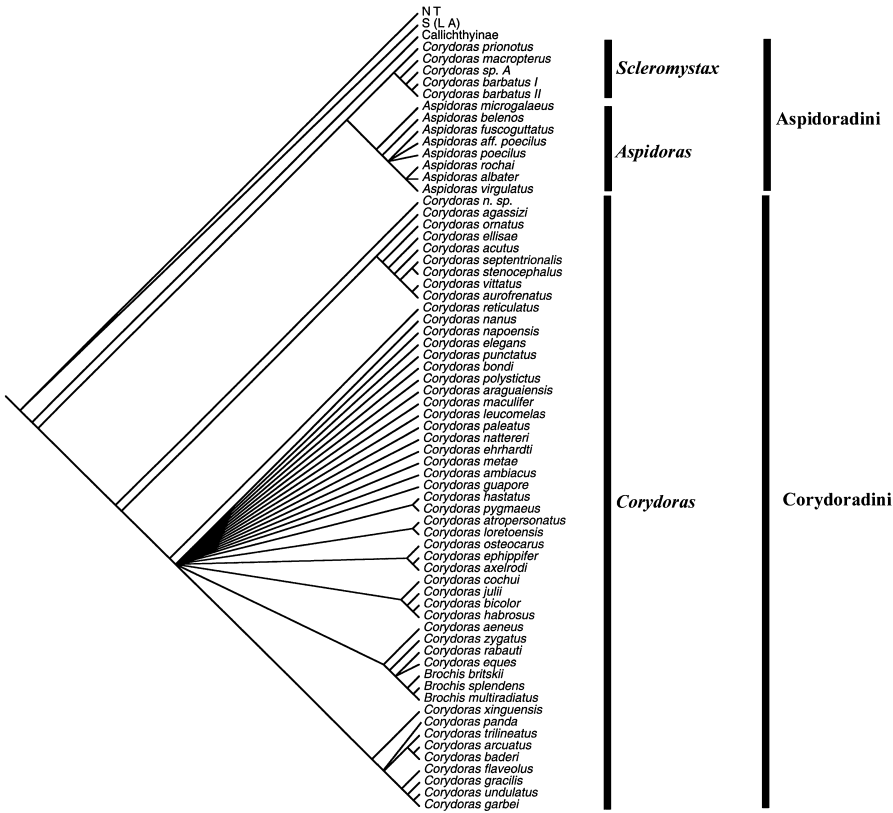
Fig. 25. Classification superimposed on the consensus cladogram of Fig. 24.

This taxon is included in a more inclusive group forming a tritomy with *Corydoras rabauti* and *C. eques*, with *C. zygatus* as its sister-group. The genus *Brochis* has been broadly used in ichthyological publications and is easily recognized. However, the usage of *Brochis* would render *Corydoras* non-monophyletic. In order to overcome this problem it would be necessary to create and/or resurrect at least four genera in order to accommodate species in proximate sister-groups. Given these factors, the option adopted herein is to synonymize *Brochis* under *Corydoras*.

A NEW CLASSIFICATION

A new classification of the subfamily Corydoradinae is proposed based on the results obtained from the phylogenetic analysis conducted in the present study (Fig. 25). As a consequence of the hypothesized non-monophyletic status of the genus *Corydoras* as previously defined, taxonomic modifications were necessary in order to reflect relationships. Proposed changes in the classification aimed at minimizing the number of alterations in the current nomenclature of Callichthyidae following the conven-

tion 2 for annotated Linnaean classifications proposed by Wiley (1981).

A new classification for the Corydoradinae is presented below, followed by a phylogenetic diagnosis for each proposed taxa. In the diagnosis, the character-states result from optimizations in each of the presented nodes (*i.e.,* the proposed taxa), including all states that support these nodes, and not only unique unreversed character-states. Some non-derived features are also provided in subsequent paragraphs to facilitate recognition of the taxa.

Subfamily Corydoradinae
    Tribe Aspidoradini
        Aspidoras
        Scleromystax
    Tribe Corydoradini
        Corydoras

    Subfamily CORYDORADINAE Hoedeman, 1952

Corydoradinae Hoedeman, 1952: 4 (key diagnosis)
Type-genus: *Corydoras* Lacépède, 1803

Diagnosis.—Narrow frontal bones (character 6);

odontodes on both infraorbitals (character 13); anterior expansion on infraorbital 1 well-developed (character 15); dorsal hypohyal present (character 19); hypobranchial 1 deep (character 20); anterior process on ceratobranchial 1 (character 22); anterior tip of ceratobranchial 5 long (character 24); anterior projection on epibranchial 1 (character 25); hyomandibular slender (character 29); suture between hyomandibular and metapterygoid interdigitating along entire extension of posterior edge of metapterygoid (character 30); infraorbitals articulated with hyomandibular (character 32); preopercle exposed (character 34); odontodes on preopercle (character 35); dorsal process on premaxilla (character 38); laminar process for insertion of *retractor tentaculi* muscle on maxilla (character 39); ventral keel on opercle for insertion of *levator operculi* muscle (character 45); preopercular pore 5 located on anterior tip of the bone (character 48); expansions on second lateral line ossicle (character 49); lateral expansions on the aortic channel (character 50); five to seven pairs of ribs (character 52); nuchal plate exposed (character 54); caudal fin bilobed (character 60); internal arm of basipterygium expanded (character 68); one barbel on each side of the lower lip (character 80); genital papilla lanceolate in males (character 82).

Tribe ASPIDORADINI Hoedeman, 1952

Aspidoradidi Hoedeman, 1952: 4 (key diagnosis)
Type-genus: *Aspidoras* Ihering, 1907

Diagnosis.—Anterior projection of frontal bone long (character 5); hypobranchial 2 well-ossified (character 21); free margin of opercle angulated (character 43); epiphyseal branch of the supraorbital canal running inside the frontal bone long (character 46); ossified portion of pectoral spine reduced (character 66).

In addition, representatives of this tribe have somewhat longer bodies, compared to the Corydoradini and, except for *Scleromystax prionotos*, have medial expansion of the coracoid covered by skin and not visible externally.
Included genera. Aspidoras and *Scleromystax.*

Genus **Aspidoras** Ihering, 1907

Aspidoras Ihering, 1907: 30–31 (type-species *Aspidoras rochai* Ihering, 1907, by original designation and monotypy)

Diagnosis.—Posterior portion of mesethmoid wide (character 2); frontal fontanel reduced (character 8); supraoccipital fontanel present (character 10); opercle compact (character 42); ossified portion

of pectoral spine strongly reduced, less than half the length of the first branched pectoral-fin ray (character 66).

Aspidoras has eyes somewhat smaller than in the remaining members of the Corydoradinae and, except for *A. belenos*, has no contact between the supraoccipital and the nuchal plate.

Genus **Scleromystax** Günther, 1864

Scleromystax Günther, 1864: 225 (type species *Callichthys barbatus* Quoy and Gaimard, 1824, by monotypy; key diagnosis, originally proposed as a subgenus of *Callichthys*, ranked to genus by Eigenmann and Eigenmann, 1888: 164)

Diagnosis.—Lateral ethmoid long (character 4); contact between supraoccipital and nuchal plate (character 11; reversal in *Scleromystax macropterus* and *S. barbatus* I); palatine slender (character 40); odontodes on preopercular-opercular region of males (character 81).

In addition, *Scleromystax* differs from *Aspidoras* in its reduced ossified portion of pectoral spine, which is longer than half the length of the first branched pectoral-fin ray, and in its somewhat more elongate snout. Individuals of this genus also posses a conspicuous coloration pattern characterized by small striated blotches all over dorsum and sides of head (less conspicuous in *Scleromystax prionotos*).
Included species. Scleromystax prionotos new combination, *S. macropterus* new combination, *Scleromystax* sp. A and *S. barbatus.*

Tribe CORYDORADINI Hoedeman, 1952

Corydoradidi Hoedeman, 1952: 4 (key diagnosis)
Type-genus: *Corydoras* Lacépède, 1803

Diagnosis.—Same as for the genus *Corydoras.*

Genus **Corydoras** Lacépède, 1803

Corydoras Lacépède, 1803: 147–149 (type-species *Corydoras geoffroy* Lacépède, 1803, by monotypy).
Cordorinus Rafinesque, 1815: 89 (unnecessary emendation of *Corydoras* Lacépède, 1803).
Hoplisoma Swainson, 1838: 336 (type-species *Cataphractus punctatus* Bloch, 1794, by original designation).
Hoplosoma Agassiz, 1846: 186 (emendation of *Hoplisoma* Swainson, 1838).
Brochis Cope, 1871: 112 (type-species *Brochis coeruleus* Cope, 1872 = *Callichthys splendens* Castelnau, 1855, by subsequent designation of Cope, 1872: 278), new synonymization.
Gastrodermus Cope, 1878: 681 (type-species *Cory-*

doras elegans Steindachner, 1877, by subsequent designation of Gosline, 1940: 10).

Osteogaster Cope, 1894: 102 (type-species *Corydoras eques* Steindachner, 1877, by original designation).

Diagnosis.—Complex vertebra compact in shape (character 12); posterior expansion of ceratobranchial 3 with a notch (character 23); dorsal lamina on anguloarticular triangular in shape (character 37); medial expansion of coracoid exposed (character 62).

In addition, the ossified portion of pectoral spine is of the same size, or somewhat longer than the first branched pectoral-fin ray.

A NOTE ON THE FOSSIL RECORD OF THE CALLICHTHYIDAE

The first known fossil record of the family Callichthyidae is a specimen from Sunchal, Jujuy Province, Argentina. The species *Corydoras revelatus* was described by Cockerell in 1925. Later, Bardack (1961), based on another specimen of *C. revelatus* from Salta, Argentina, provided an illustration and added more morphological information to the species. Additional specimens of *C. revelatus* were recorded in Ferraris (1991), who presented a picture showing a fossilized school of this species. Although all these studies pointed out that the Argentinean callichthyid fossil referred to *Corydoras*, only Bardack (1961) presented explicit support for this generic assignment, based on Gosline's (1940) characters. A critical analysis of that placement was made recently by Reis (1998b). That author pointed out three derived conditions referring *C. revelatus* to the Corydoradinae, such as a well-developed anterior expansion on the first infraorbital, the exposed nuchal plate, and the bilobed caudal fin. Reis (1998b) also assigned *C. revelatus* to the clade *Corydoras* plus *Brochis* based on the contact between the supraoccipital and nuchal plate. Finally, Reis (1998b) discussed the tentative generic assignment of that callichthyid fossil on the basis of the absence of synapomorphies of *Brochis*.

According to the present study, and illustrations in Bardack (1961: figs. 3 and 4), *Corydoras revelatus* exhibits some derived features of the subfamily Corydoradinae as pointed out by Reis (1998b). The placement of that callichthyid fossil in *Corydoras* as defined in the present study, is uncertain, because the unique feature indicated by Reis (the contact between the supraoccipital and nuchal plate) would assign the fossil to the resurrected genus *Scleromystax* as well as to a less inclusive clade within *Corydoras* (see "Discussion"). Nevertheless, the conclusions regarding the age of the Callichthyidae (Reis, 1998b)

do not change. The unambiguous placement of the Argentinean fossil in the Corydoradinae indicates that the lineages leading to subfamilies Callichthyinae and Corydoradinae occurred at least on the late Paleocene, as proposed by Reis (1998b). Thus, the phylogenetic position of the callichthyid fossil within the superfamily Loricarioidea might suggest an earlier differentiation of loricarioids in comparison to other catfishes, or a lack of older fossils of other Neotropical groups.

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APPENDIX 1

Material examined

Abbreviations for institutions are: AMNH, American Museum of Natural History, New York; DBAV.UERJ, Departamento de Biologia Animal e Vegetal da Universidade do Estado do Rio de Janeiro, Rio de Janeiro; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MCP, Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MNRJ, Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NRM, Naturhistoriska Riksmuseet, Stockholm; UFRJ, Laboratório de Ictiologia Geral e Aplicada da Universidade Federal do Rio de Janeiro, Rio de Janeiro; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Nematogenyidae: *Nematogenys inermis* (Guichenot) USNM 259095, 3 ex. (1 cs).

Trichomycteridae: *Copionodon pecten* de Pinna MZUSP 48962, 1 cs; *Copionodon orthiocarinatus* de Pinna MZUSP, 1 ex.; *Trichogenes longipinnis* Britski and Ortega UFRJ 0590, 1 ex.; UFRJ 0682, 2 cs; UFRJ 0861, 3 ex.; UFRJ 0894, 9 ex.; UFRJ 1639, 2 ex.; *Trichomycterus alternatus* (Eigenmann) UFRJ 0080, 9 ex.; *T. albinotatus* Costa UFRJ 1294, 7 ex.; *T. brasiliensis* Reinhardt UFRJ 1150, 2 ex.; *T. itatiayae* Ribeiro UFRJ 3400, 3 ex.; *T. mirisumba* Costa UFRJ 3366, 7 ex.; *T. reinhardti* (Eigenmann) UFRJ 1309, 6 ex.; *T. zonatus* (Eigenmann) UFRJ 3822, 13 ex. (2 cs).

Scoloplacidae: *Scoloplax distolothrix* Schaefer, Weitzman and Britski UFRJ 1213, 51 ex. (2 cs); UFRJ 1337, 35 ex.; *S. dolicolophia* Schaefer, Weitzman and Britski UFRJ 3946, 2 ex.

Astroblepidae: *Astroblepus chotae* (Regan) UMMZ 179260, 5 ex. (2 cs); *A. grixalvii* Humboldt UMMZ 143369, 5 ex.; *A. orientalis* (Boulenger) UMMZ 145378, 5 ex. (1 cs); *Astroblepus* sp. AMNH 20873, 3 ex.

Loricariidae: *Ancistrus stigmaticus* Eigenmann and Eigenmann UFRJ 0182, 1 ex.; UFRJ 2267, 2 ex.; *Ancistrus* sp. UFRJ 0302, 6 ex.; UFRJ 1014, 1 cs; UFRJ 1841, 1 ex.; UFRJ 3220, 4 ex.; UFRJ 3259, 4 ex.; *Chaetostomus* sp. UFRJ 0507, 1 ex.; UFRJ 1014, 6 ex.; UFRJ 1967, 2 ex.; *Cochliodon cochliodon* (Kner) UFRJ 1028, 1 ex.; *Corymbophanes bahianus* Gosline UFRJ 0545, 2 ex.; *Farlowella* sp. UFRJ 0323, 1 ex.; UFRJ 1730, 4 ex.; UFRJ 3871, 3 ex.; *Hypoptopoma* sp. UFRJ 0331, 6 ex.; UFRJ 3924, 6 ex.; *H. commersonii* Valenciennes UFRJ 0747, 1 ex.; *Hypostomus margaritifer* (Regan) UFRJ 0746, 3 ex.; *H. punctatus* Valenciennes UFRJ 0447, 2 ex.; UFRJ 1690, 5 ex.; UFRJ 2273, 2 ex.; *Hypostomus* sp. UFRJ 1016, 8 ex.; UFRJ 1403, 6 ex.; UFRJ 1502, 7 ex.; UFRJ 1745, 2 ex.; UFRJ 1790, 1 ex.; UFRJ 2211, 2 cs; *Ixinandria* sp. UFRJ 0134, 1 ex.; *Kronichthys* sp. UFRJ 0858, 1 ex.; UFRJ 2150, 5 ex. (1 cs); UFRJ 3985, 3 ex.; *Limatulichthys* sp. UFRJ 0951, 2 ex.; UFRJ 0960, 2 ex.; *Lipopterichthys* sp. UFRJ 0506, 5 ex.; *Loricaria* sp. UFRJ 0515, 1 ex.; UFRJ 1812, 1 ex.; UFRJ 2228, 1 ex.; UFRJ 3328, 1 ex.; *Loricariichthys* sp. UFRJ 0638, 1 ex.; UFRJ 1740, 4 ex.; UFRJ 2285, 1 ex.; *Microlepidogaster notatus* (Eigenmann and Eigenmann) UFRJ 0531, 6 ex.; *Microlepidogaster* sp. UFRJ 0831, 9 ex.; UFRJ 1621, 6 ex.; *Neoplecostomus* sp. UFRJ 0067, 1 ex.; UFRJ 0078, 4 ex.; UFRJ 0169, 1 ex.; UFRJ 0601, 3 ex.; UFRJ 0617, 2 ex.; UFRJ 0665, 1 cs; UFRJ 0673, 2 ex.; UFRJ 3324, 3 ex.; UFRJ 3975, 6 ex.; *Otocinclus vittatus* Regan UFRJ 1460, 6 ex.; *Otothyris lophophanes* (Eigenmann and Eigenmann) UFRJ 0007, 6 ex.; *Otothyris* sp. UFRJ 0020, 6 ex; UFRJ 1779, 8 ex.; UFRJ 2017, 6 ex.; *Pareiorhina rudolphi* (Ribeiro) UFRJ 0549, 2 ex.; UFRJ 0663, 6 ex.; UFRJ 0675, 3 ex.; *Pareiorhina* sp. UFRJ 0581, 1 cs; UFRJ 0666, 3 ex.; UFRJ 1295, 5 ex.; UFRJ 1301, 6 ex.; *Parotocinclus maculicauda* (Steindachner) UFRJ 0883, 1 ex.; *Parotocinclus* sp. UFRJ 3357, 6 ex.; UFRJ 3987, 5 ex.; *Planiloricaria* sp. UFRJ 0920, 2 ex.; *Pseudoloricaria* sp. UFRJ 1036, 1 ex.; *Reganella* sp. UFRJ 3870, 6 ex.; *Rineloricaria* sp. UFRJ 0852, 2 ex.; UFRJ 0922, 1 cs; UFRJ 1436, 2 ex.; UFRJ 1896, 1 ex.; UFRJ 2289, 2 ex.; UFRJ 3348, 1 ex.; *Schizolecis guentheri* (Ribeiro) UFRJ 0311, 6 ex.; UFRJ 2005, 5 ex.; *Schizolecis* sp. UFRJ 0855, 5 ex.; UFRJ 3971, 6 ex.; *Upsilodus victori* Ribeiro UFRJ 3459, 3 ex.

Callichthyinae: *Callichthys callichthys* UFRJ 0018, 1 ex.; UFRJ 0522, 2 ex.; UFRJ 0851, 1 ex.; UFRJ 1201, 1 ex.; UFRJ 1306, 1 ex.; UFRJ 1908, 10 ex.; UFRJ 1993, 1 ex.; UFRJ 2002, 1 ex.; UFRJ 2014, 2 ex. (1 cs); UFRJ 3168,

15 ex. (2 cs); UFRJ 3535, 6 ex.; UFRJ 3636, 1 ex.; *Dianema longibarbis* Cope MCP 19403, 3 cs; MZUSP 27593, 4 ex. (2 cs); MZUSP 35573, 2 ex.; *D. urostriata* Ribeiro MCP 19404, 2 cs; MZUSP 35558, 2 ex.; MZUSP 41671, 4 ex. (2 cs); *Hoplosternum littorale* (Hancock) DBAV.UERJ 1018, 1 ex.; UFRJ 1005, 3 ex.; UFRJ 1010, 2 ex; UFRJ 1026, 3 ex.; UFRJ 3650, 1 ex.; UFRJ 3792, 8 ex. (2 cs); *Lepthoplosternum pectorale* (Boulenger) UFRJ 3700, 9 ex. (2 cs); UFRJ 3651, 1 ex.; UFRJ 3652, 2 ex.; UFRJ 3700, 9 ex.; *Megalechis thoracata* (Valenciennes) UFRJ 3661, 1 ex.; UFRJ 3945, 2 ex.; *Megalechis personata* (Ranzani) UFRJ 1993, 1 ex..

Corydoradinae: *Aspidoras*. *Aspidoras albater* Nijssen and Isbrücker MCP 15974, 5 ex. (1 cs); MNRJ 12571, 26 ex.; MNRJ 12581, 45 ex. (3 cs); *Aspidoras belenos* Britto MCP 19294, paratypes, 3 ex.; MZUSP 51208, paratypes, 3 ex.; UFRJ 1206, paratypes, 2 ex.; UFRJ 3861, paratypes, 3 ex. (2 cs); *A. fuscoguttatus* Nijssen and Isbrücker MCP 14253, 7 ex.; MCP 19401, 3 cs; MNRJ 12649, 11 ex. (2 cs); MZUSP 35833, 2 ex.; *A. lakoi* Ribeiro MNRJ 5293, 4 ex. (2 cs); *A. menezesi* Nijssen and Isbrücker MZUSP 49952, 2 ex.; *Aspidoras microgalaeus* Britto MCP 19295, paratypes, 4 ex.; MZUSP 51209, holotype.; MZUSP 51210, paratypes, 4 ex.; UFRJ 1247, paratypes, 3 ex. (2 cs); UFRJ 1385, paratypes, 2 ex.; *A.* cf. *pauciradiatus* MZUSP 14634, 2 ex.; MZUSP 30841, 4 ex.; MZUSP 31282, 2 ex.; *A. poecilus* Nijssen and Isbrücker UFRJ 1473, 10 ex. (1 cs); UFRJ 1693, 16 ex.; UFRJ 1818, 11 ex.; UFRJ 1823, 15 ex. (2 cs); UFRJ 1925, 4 ex.; *A.* aff. *poecilus* MNRJ 997, 16 ex.; MNRJ 5233, 9 ex.; MNRJ 11716, 69 ex.; MNRJ 12779, 12 ex. (3 cs); MNRJ 13045, 37 ex.; UFRJ 0201, 12 ex. (1 cs); UFRJ 2189, 7 ex.; *A. rochai* Ihering, 1907 MCP 19402, 4 cs; MZUSP 24634, 4 ex.; *A. spilotus* Nijssen and Isbrücker MNRJ 8688, paratypes, 4 ex. (2 cs); *A. virgulatus* Nijssen and Isbrücker MNRJ 4736, 14 ex. (3 cs); UFRJ 1775, 17 ex. (2 cs).

Corydoras. *Corydoras acutus* Cope USNM 305595, 4 ex. (2 cs); *C. adolfoi* Burgess MZUSP 26641, holotype; *C. aeneus* (Gill) INPA 3099, 3 ex.; MNRJ 5756, 4 ex. (1 cs); UFRJ 0095, 2 ex.; UFRJ 0605, 1 ex.; UFRJ 3017, 6 ex. (2 cs); UFRJ 3847, 15 ex.; UFRJ 3848, 8 ex.; UMMZ 169066, 15 ex.; UMMZ 205475, 8 ex.; *C. agassizi* Steindachner MZUSP 15297, 3 ex.; NRM 28589, 4 ex. (2 cs); *C. amapaensis* Nijssen MZUSP 30842, 1 ex.; MZUSP 31553, 1 ex.; MZUSP 31606, 1 ex.; MZUSP 38979, paratypes, 3 ex.; *C. ambiacus* Cope MZUSP 26016, 1 ex.; MZUSP 26053, 2 ex.; NRM 13397, 4 ex. (2 cs); *C. aprouaguensis* Nijssen and Isbrücker MZUSP 27895, paratype; MZUSP 27896, paratype; *C. araguaiensis* Knaack UFRJ 1332, 3 ex. (1 cs); UFRJ 1427, 4 ex. (1 cs); UFRJ 1458, 5 ex. (1 cs); UFRJ 1474, 5 ex. (1 cs); UFRJ 1536, 1 ex.; UFRJ 1945, 1 ex.; *C. arcuatus* Elwin NRM 13396, 4 ex.; USNM 317900, 4 ex. (2 cs); *C. atropersonatus* Weitzman and Nijssen NRM 28590, 4 ex. (2 cs); *C. aurofrenatus* Eigenmann and Kennedy MZUSP 36720, 6 ex.; NRM 23528, 4 ex. (2 cs); *C. axelrodi* Rössel USNM 246701, 4 ex. (2 cs); *C. baderi* Geisler MZUSP 38986, 4 ex. (paratypes of *C. oelemariensis* Nijssen); USNM 225587, 4 ex. (2 cs); *C. bicolor* Nijssen and Isbrücker USNM 225580, 4 ex. (2 cs); *C. bifasciatus* Nijssen MZUSP 38976, paratypes, 4 ex.; *C. blochi* Nijssen INPA 1289, 1 ex.; MZUSP 8580, paratypes, 3 ex.; *C. bondi*

Gosline INPA 1288, 5 ex. (2 cs); INPA 1639, 1 ex; INPA 7797, 5 ex.; INPA 8133, 5 ex. (2 cs); *C. britskii* Nijssen and Isbrücker MZUSP 36382, 1 ex.; UFRJ 3850, 1 cs; *C. cochui* Myers and Weitzman MZUSP 35838, 4 ex.; UFRJ 1760, 2 ex. (1 cs); *C. coppenamensis* Nijssen MZUSP 8950, paratypes, 2 ex.; *C. davidsandsi* Black MZUSP 38633, paratype; MZUSP 38634, paratype; MZUSP 38635, paratype; *C. difluviatilis* UFRJ 4655, 1 ex.; UFRJ 4656, 3 ex. (cs); *C. ehrhardti* Steindachner UFRJ 2251, 4 ex. (1 cs); UFRJ 3662, 3 ex.; *C. elegans* Steindachner MZUSP 15299, 2 ex.; MZUSP 26017, 6 ex.; MZUSP 26342, 3 ex.; UFRJ 3782, 2 ex. (1 cs); *C. ellisae* Gosline MCP 15517, 2 cs; UMMZ 206339, 4 ex. (1 cs); *C. ephippifer* Nijssen MZUSP 30844, 4 ex. (2 cs); MZUSP 38948, paratypes, 2 ex.; *C. eques* Steindachner USNM 317921, 4 ex. (2 cs); *C. flaveolus* Ihering MZUSP 47925, 4 ex. (2 cs); *C. garbei* Ihering MCP 16994, 4 ex. (2 cs); MZUSP 40184, 4 ex.; UFRJ 3064, 1 ex.; *C. geoffroy* (paratypes of *C. octocirrus* Nijssen) MZUSP 38984, 2 ex.; *C. gossei* Nijssen MZUSP 38977, paratypes, 4 ex.; *C. gracilis* Nijssen and Isbrücker INPA 7759, 5 ex. (2 cs); *C. guapore* Knaack UMMZ 204302, 7 ex. (2 cs); *C. habrosus* Weitzman USNM 220356, 4 ex. (2 cs); *C. hastatus* Eigenmann and Eigenmann MZUSP 35908, 4 ex. (2 cs); UFRJ 0384, 31 ex. (5 cs); UFRJ 1909, 2 ex.; UFRJ 3654, 6 ex. (1 cs); UFRJ 3655, 5 ex.; UFRJ 3656, 2 ex.; UFRJ 3657, 4 ex.; UFRJ 3658, 3 ex.; UFRJ 3659, 3 ex.; UFRJ 3660, 3 ex.; UFRJ 3831, 5 ex. (2 cs); *C. heteromorphus* Nijssen MZUSP 9084, paratype; MZUSP 9085, 1 ex.; *C. incolicana* Burgess MZUSP 45717, holotype; *C. julii* Steindachner UFRJ 3779, 59 ex. (2 cs); *C. leopardus* Myers MZUSP 22874, 1 ex.; *C. leucomelas* Eigenmann and Allen MCP 14249, 1 cs; UMMZ 204304, 5 ex. (2 cs); *C. loretoensis* Nijssen and Isbrücker NRM 28562, paratypes, 4 ex. (2 cs); *C. maculifer* Nijssen and Isbrücker UFRJ 0106, 28 ex. (4 cs); *C. melanistius* Regan INPA 4204, 1 ex.; INPA 6990, 5 ex.; INPA 7080, 2 ex.; INPA 8093, 1 ex.; UFRJ 3177, 2 ex. (1 cs); UFRJ 3780, 1 ex.; USNM 225582, 4 ex. (2 cs); *C. melanotaenia* Regan NRM 27872, 5 ex. (1 cs); *C. metae* Eigenmann MZUSP 47926, 4 ex.; NRM 27873, 4 ex. (2 cs); *C. multimaculatus* Steindachner MZUSP 40183, 4 ex.; MZUSP 47405, 1 ex.; *C. multiradiatus* (Orcés-Villagomez) MCP 16302, 1 cs; MZUSP 26822, 1 ex.; MZUSP 31555, 1 ex.; *C. nanus* Nijssen and Isbrücker NRM 13501, 4 ex.; NRM 28595, 4 ex.; USNM 218359, 4 ex. (2 cs); *C. napoensis* Nijssen and Isbrücker MZUSP 26341, paratype; USNM 301949, 4 ex. (2 cs); *C. nattereri* Steindachner UFRJ 0025, 8 ex.; UFRJ 0031, 8 ex.; UFRJ 0520, 26 ex. (2 cs); UFRJ 0565, 6 ex. (1 cs); UFRJ 0924, 3 ex.; UFRJ 0928, 2 ex.; UFRJ 1085, 5 ex.; UFRJ 3692, 3 ex.; *C. oiapoquensis* Nijssen MZUSP 38957, 4 ex.; *C. ornatus* Nijssen and Isbrücker INPA 4708, 1 ex.; MCP 14259, 2 cs; *C. osteocarus* Böhlke INPA 7910, 2 ex.; INPA 7916, 5 ex.; INPA 8129, 5 ex. (2 cs); *C. ourastigma* Nijssen MZUSP 38960, paratypes, 4 ex.; *C. paleatus* (Jenyns) DBAV.UERJ 0232, 1 ex.; MCP 14835, 2 cs; MZUSP 27035, 4 ex.; MZUSP 41814, 2 ex.; *C. panda* Nijssen and Isbrücker MCP 14257, 2 cs; *C. paralelus* Burgess MZUSP 45716, holotype; *C. pinheiroi* Dinkelmeyer MZUSP 48099, holotype; *C. polystictus* Regan MZUSP 44454, 4 ex. (2 cs); UFRJ 0399, 22 ex.; UFRJ 3849, 20 ex. (2 cs); UMMZ 205169, 20 ex.; *C. punctatus*

(Bloch) INPA 7814, 5 ex. (2 cs); MCP 16138, 2 cs; MZUSP 42507, 2 ex.; *C. pygmaeus* Knaack MZUSP 26344, 4 ex.; USNM 218355, 5 ex. (2 cs); *C. rabauti* La Monte MCP 14258, 1 ex. cs; MNRJ 3627, 6 ex. (paratypes of *C. myersi* Ribeiro); MZUSP 15300, 1 ex.; *C. reticulatus* Fraser-Brunner MZUSP 28752, 3 ex.; USNM 317945, 4 ex. (2 cs); *C. robiniae* Burgess MZUSP 27175, holotype; MZUSP 27176, paratype, 1 ex.; MZUSP 27177, paratype; *C. sanchesi* Nijssen and Isbrücker USNM 203810, 2 ex.; *C. sarareensis* Dinkelmeyer MZUSP 48100, holotype; *C. schwartzi* Rössel MZUSP 42506, 6 ex; *C. septentrionalis* Gosline MZUSP 27953, 8 ex. (2 cs); *C. seussi* Dinkelmeyer MZUSP 49323, paratypes, 5 ex.; *C. simulatus* Weitzman and Nijssen MZUSP 42514, 1 ex.; *C. sodalis* Nijssen and Isbrücker MZUSP 26817, paratypes, 4 ex.; *C. splendens* (Castelnau) MCP 14261, 1 cs; MZUSP 30859, 4 ex.; MZUSP 42218, 1 ex.; NRM 13431, 4 ex. (2 cs); *C. stenocephalus* Eigenmann and Allen MZUSP 25985, 3 ex.; USNM 264116, 4 ex. (2 cs); *C. sterbai* Knaack UFRJ 4424, 1 ex.; *C. trilineatus* Cope MZUSP 42510, 2 ex.; NRM 13398, 4 ex.; NRM 13492, 4 ex.; USNM 317949, 4 ex. (2 cs); *C. triseriatus* Ihering MNRJ 8608, 4 ex. (2 cs); *C. undulatus* Regan MCP 13954, 2 cs; *C. virginiae* Burgess MZUSP 45715, holotype; *C. vittatus* Nijssen UFRJ 3781, 6 ex. (1 cs); *C. xinguensis* Nijssen MCP 15633, 3 cs; MZUSP 36864, 4 ex.; MZUSP 38974, paratype; MZUSP 38980, paratype; MZUSP 38987, paratype; *C. zygatus* Eigenmann and Allen USNM 316823, 4 ex. (2 cs).

Scleromystax: *Scleromystax barbatus* I MNRJ 13723, 10 ex. (2 cs); MNRJ 14843, 10 ex. (2 cs); UFRJ 0167, 10 ex. (2 cs); UFRJ 0591, 9 ex. (1 cs); UFRJ 2268, 3 ex.; UFRJ 3204, 2 ex.; UFRJ 3344, 1 ex.; *S. barbatus* II UFRJ 1649, 3 ex.; UFRJ 2151, 3 ex.; UFRJ 3374, 1 ex.; UFRJ 3379, 1 ex.; *S. macropterus* (Regan) UFRJ 0202, 4 ex. (2 cs); *S. prionotos* (Nijssen and Isbrücker) UFRJ 0003, 11 ex. (2 cs); UFRJ 0211, 8 ex. (1 cs); UFRJ 0521, 4 ex. (1 cs); UFRJ 0568, 2 ex.; UFRJ 1084, 1 ex.; UFRJ 1781, 2 ex.; *Scleromystax* sp.A UFRJ 4303, 2 ex.; UFRJ 4309, 8 ex. (3 cs).

Note: The species indicated as "*Scleromystax* sp. A" refers to a species from rio Ribeira basin, Brazil, known in the aquarist literature as "*Corydoras* sp. baianinho II".