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Phylogenetic relationships of the suckermouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae

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A phylogenetic analysis of nearly all genera of the Hypostominae and the Ancistrinae is provided based on osteology, external anatomy, and digestive tract anatomy. The results suggest that the Hypostominae is a paraphyletic assemblage. *Delturus* and *Upsilodus* form a monophyletic group sister to all other loricariids. *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, and *Pareiorhina* form a monophyletic group with *Neoplecostomus* and the Hypoptopomatinae and are transferred to the Neoplecostominae. The remainder of the Hypostominae is made paraphyletic by the continuing recognition of the Ancistrinae. Ancistrinae is returned to the Hypostominae and recognized as a tribe, Ancistrini. In addition, four new tribes (Corymbophanini, Hypostomini, Pterygoplichthini, and Rhinelepini) are described. *Hypostomus* is also paraphyletic, the bulk of it forming a monophyletic clade with *Aphanotorulus*, *Cochliodon*, and *Isorineloricaria*. All of the potential monophyletic groups within *Hypostomus* grade into one another; therefore, *Aphanotorulus*, *Cochliodon*, and *Isorineloricaria* are placed in the synonymy of *Hypostomus*. *Pterygoplichthys* and *Glyptoperichthys* are also polyphyletic, and *Liposarcus* and *Glyptoperichthys* are recognized as synonyms of *Pterygoplichthys*. Sister to *Pterygoplichthys* is the *Hemiancistrus annectens* group (including *Hypostomus panamensis*) which represents an undescribed genus. The phylogeny presented is compared with previous hypotheses. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **141**, 1–80.

ADDITIONAL KEYWORDS: Ancistrini – Corymbophanini – Hypoptopomatinae – *Hypostomini* – *Hypostomus* – Loricariinae – Neoplecostominae – *Pterygoplichthini* – *Rhinelepini* – systematics.

INTRODUCTION

The Loricariidae is a fascinating group of catfishes from South and Central America (Fig. 1). Unlike most other catfishes, loricariids are armour-plated and possess a mouth that is modified into a sucking disk. The Loricariidae is the largest family of catfishes and is among the largest of all fish families, with *c*. 646 species currently considered valid. Only Gobiidae, Cyprinidae, Cichlidae, and Labridae are larger (Isbrücker, 1980; Nelson, 1994; pers. observ.).

The Loricariidae is placed into the superfamily Loricarioidea along with the Astroblepidae, Scoloplacidae, Callichthyidae, Trichomycteridae, and Nematogenyidae (Baskin, 1973; Schaefer, 1987; de Pinna, 1992; Fig. 2). The monophyly of the Loricarioidea is supported mainly by the presence of integumentary teeth (odontodes) on the outside of the body, and the group is one of the few groups of families of catfishes for which a phylogeny has been well established. Of the loricarioids, the Scoloplacidae, the Callichthyidae, and the Loricariidae possess bony plates, and the Astroblepidae shares the suctorial mouth with the Loricariidae. The phylogenetic position of the Astroblepidae (Fig. 2) suggests that astroblepids have lost armour plating.

Within the Loricariidae there are four large, wide-ranging subfamilies: Hypoptopomatinae (60 spp.), Loricariinae (191 spp.), Hypostominae (182 spp.) and Ancistrinae (208 spp.) (number of species in each family is based on Isbrücker, 1980 and subsequent papers by that author). The final subfamily, Neoplecostominae, has a single genus and six species from coastal streams in south-eastern Brazil. The monotypic Lithogeninae is considered a subfamily of either the Loricariidae (e.g. Schaefer, 1987; Burgess, 1989) or the

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Figure 1. Range of the Loricariidae (shaded area).

Astroblepidae (Nijssen & Isbrücker, 1986; Nelson, 1994).

Unfortunately, little cladistic work has been performed on loricariids as a whole and published studies have suffered from a lack of some of the putatively basal genera (Howes, 1983; Schaefer, 1986, 1987). The first study to examine loricariids using cladistic methodology was that of Howes (1983), who provided a phylogenetic analysis based on muscles and bones and a tree that differed significantly from the taxonomy *sensu* Isbrücker (1980) (Fig. 3). The main difference was the recognition of Chaetostomatinae (misspelled as Chaetostominae by Howes – Nijssen & Isbrücker, 1986) for the ancistrines *Chaetostoma* Tschudi, *Lasiancistrus* Regan, and *Lipopterichthys* Norman and the hypostomine *Hemipsilichthys* Eigenmann and Eigenmann. The placement of the Chaetostomatinae in a monophyletic group with the Loricariinae, the Hypoptopomatinae, and the Neoplecostominae is based mainly on the presence of a bone Howes identified as the interopercle.

Schaefer (1986, 1987, 1988) re-examined some of the characters of Howes (1983), and determined that the putative interopercle contained part of the laterosensory canal system and is not homologous to the interopercle of other catfishes. In addition, this bone, termed the canal plate, was found in all loricariids examined by Schaefer. Schaefer (1986) also provided one of the most complete treatments of the genera of ancistrines and hypostomines to date using osteology. One of the main conclusions of his study was that the Hypostominae was made paraphyletic by the continuing recognition of the Ancistrinae; however, he retained the Ancistrinae as a valid taxon (Fig. 4). Schaefer (1986, 1987) provided a detailed description of loricariid skeletal anatomy used in skeletal descriptions below.

Weber (1991, 1992) suggested that *Pterygoplichthys* Gill, *sensu* Isbrücker (1980), was a paraphyletic assemblage closely related to *Megalancistrus* Isbrücker. To rectify the paraphyly, Weber redescribed the genus *Liposarcus* Günther and described a new genus, *Glyptoperichthys*, which he considered to be the sister to *Megalancistrus* (Fig. 5).

Montoya-Burgos *et al.* (1997, 1998) provided the first molecular phylogenies for loricariid catfishes using partial sequence data from mitochondrial 12S and 16S ribosomal RNA genes (Fig. 6). The results of both studies are incongruent with the bulk of the morphological data available. According to Montoya-Burgos *et al.* (1998): (1) *Chaetostoma* was sister to a clade consisting of the bulk of the Hypostominae (except those species placed in the Neoplecostominae below), the Ancistrinae, and the Loricariinae; (2) *Aphanotorulus* Isbrücker and Nijssen, *Cochliodon* Heckel, *Glyptoperichthys*, *Hypostomus* Lacépède, *Isorineloricaria* Isbrücker, and *Pterygoplichthys* were derived from a paraphyletic Ancistrinae; (3) *Pseudorinelepis* Bleeker (Hypostominae) was sister to the Loricariinae; (4) *Kronichthys* Miranda-Ribeiro, *Hemipsilichthys*, and *Isbrueckerichthys* Derjist were closely related to *Neoplecostomus* Eigenmann and Eigenmann; (5) *Pareiorhina* Gosline was related to the hypoptopomatines. *Hemipsilichthys gobio* (Lütken) (= *Upsilodus victori* Miranda Ribeiro) was the most basal member of the Loricariidae they examined.

Armbruster (1998c) suggested that *Pogonopoma* Regan, *Pogonopomoides* Gosline, *Pseudorinelepis*, and *Rhinelepis* Agassiz form a monophyletic group (termed the *Rhinelepis* group) based on the presence of a large, oesophageal diverticulum. Armbruster (1998b) presented a phylogenetic analysis of the genera of the *Rhinelepis* group (Fig. 7), concluding that the phylogenetic relationships followed the proposed evolution of the diverticulum; however, no information was provided on the phylogenetic position of the *Rhinelepis* group within the Hypostominae. Quevedo & Reis (2002) reanalysed Armbruster's (1998c) data with the addition of a new species of the *Rhinelepis* group. The

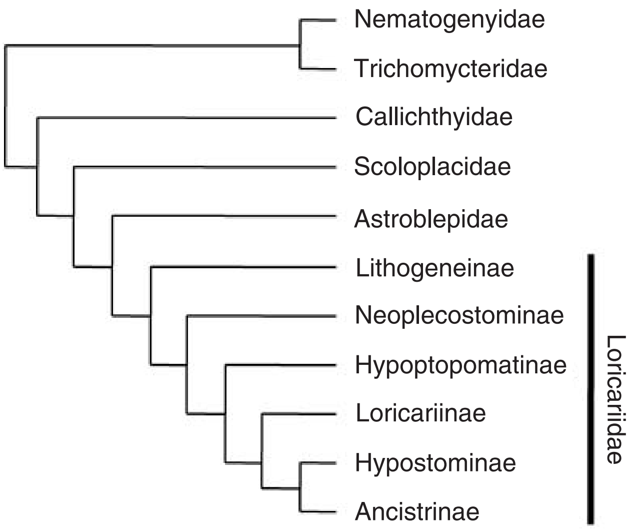

Figure 2. Phylogeny of the loricariid subfamilies (Schaefer, 1987) and the loricarioid families (de Pinna, 1992).

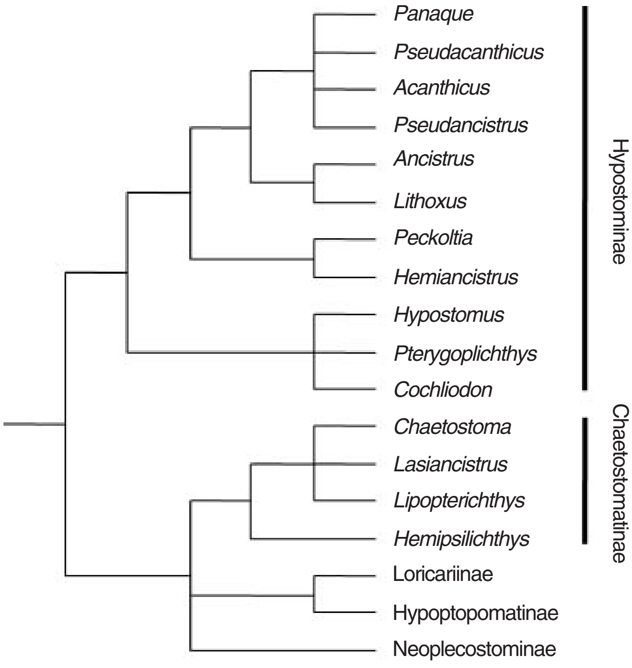

Figure 3. Phylogeny from Howes (1983) based on osteology and myology.

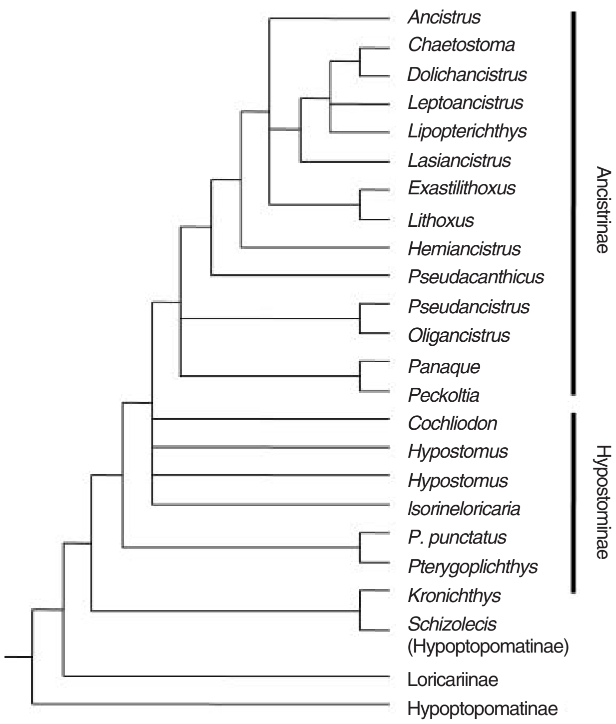

Figure 4. Phylogeny from Schaefer (1986) based on osteology. Some names have been changed from those reported by Schaefer to update taxonomy (*Oligancistrus* was formerly in *Parancistrus*) and to correct misidentifications (one of the *Hypostomus* was listed as *Corymbophanes*, *Schizolecis* was listed as *Pogonopomoides*, and *Pterygoplichthys punctatus* was listed as *Megalancistrus*).

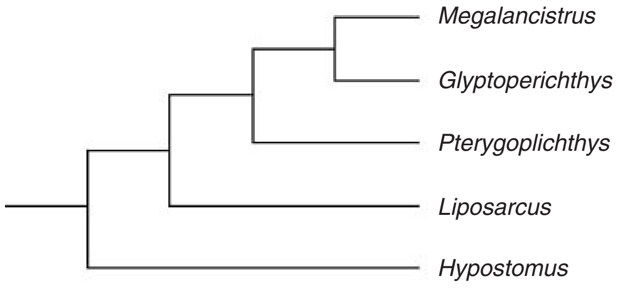

Figure 5. Phylogeny of *Pterygoplichthys* and related genera from Weber (1992) based on osteology and external features.

new species, described as *Pogonopoma obscurum*, was sister to *Pogonopoma* + *Pogonopomoides*. *Pogonopomoides* was placed in the synonymy of *Pogonopoma*.

Isbrücker *et al.* (2001) described 14 new genera of the Loricariidae. This study did not include phylogenetic analysis. I therefore defer recognition of any of the genera described in it until a phylogenetic analysis can prove that they should be recognized. Synonymies of these genera as well as all others are provided in the descriptions section below.

In the present study, a phylogenetic analysis for the genera of the Hypostominae and the Ancistrinae is provided based on osteology and broad comparison with members of the other subfamilies of the Loricariidae. The purpose of this study is to provide a phylogenetic framework upon which future generic level

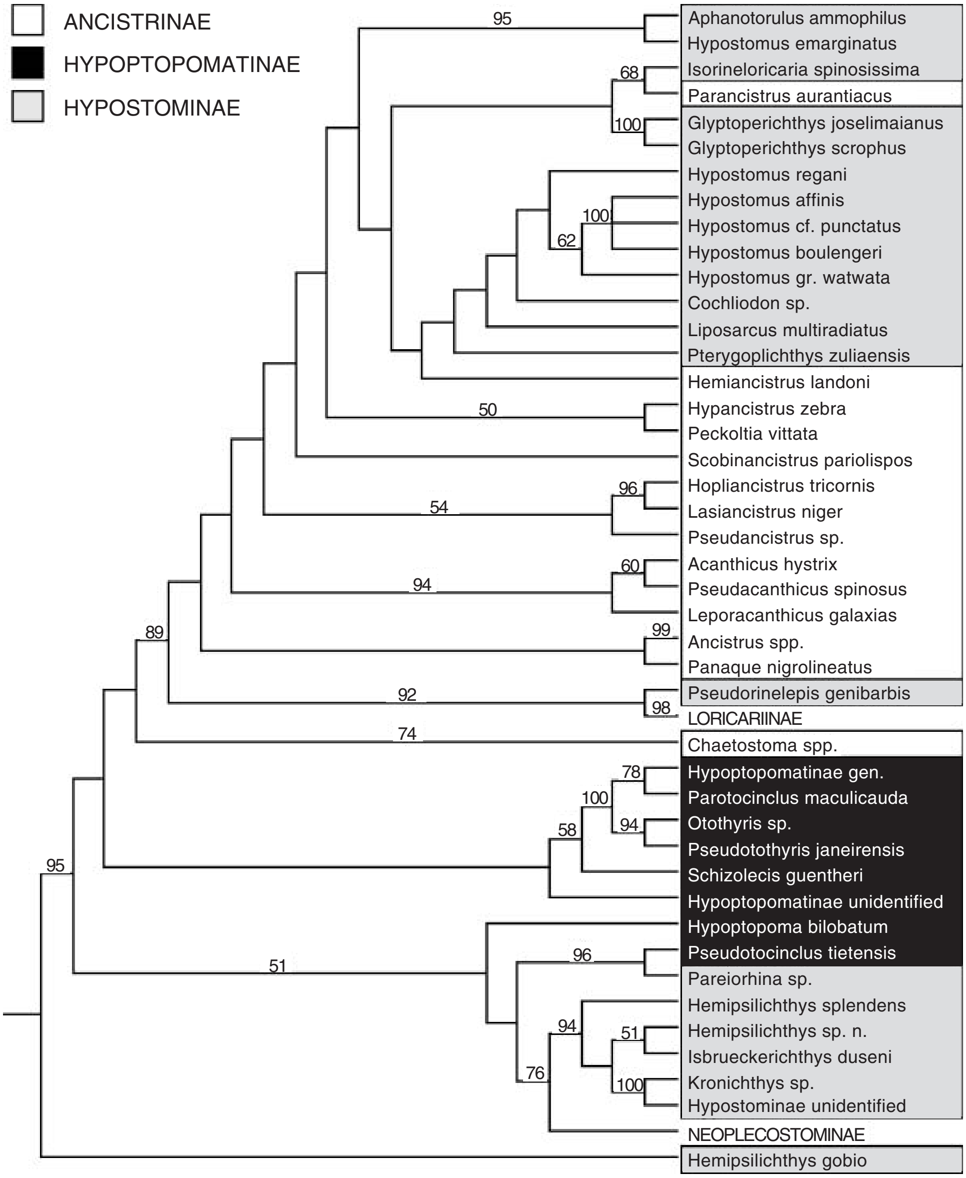

Figure 6. Phylogeny from Montoya-Burgos *et al.* (1998) based on sequence data from mitochondrial 12S and 16S; phylogeny is a composite of figures 4 and 6 in Montoya-Burgos (1998). Numbers above branches are bootstrap values. *Ancistrus*, *Chaetostoma*, and the Loricariinae are represented by more than one species in the analysis.

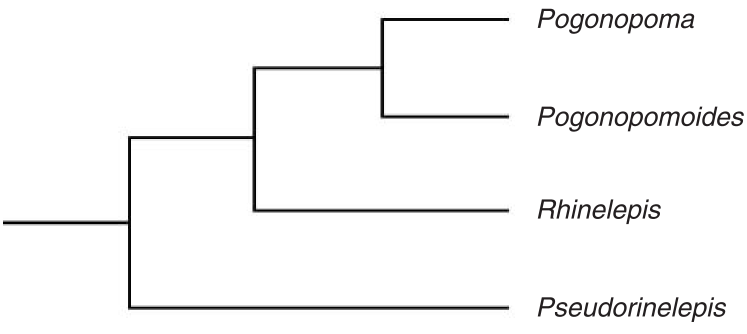

Figure 7. Phylogeny of the *Rhinelepis* group from Armbruster (1998b) based on osteology and digestive tract anatomy.

taxonomic studies can be based. The analysis below demonstrates that many genera are of dubious validity. The phylogeny suggests that several genera should be placed into synonymy and that other monophyletic groups represent undescribed genera.

In addition, several changes at the level of the subfamily are made. The Ancistrinae is returned to the synonymy of the Hypostominae, and the Hypostominae is broken into five tribes, three of them new: Ancistrini Kner, Corymbophanini new tribe, Hypostomini Kner, Pterygoplichthini new tribe, and Rhinelepini new tribe. In previous papers I have described the Rhinelepini (Armbruster, 1998b) and the Corymbophanini and its sole genus, *Corymbophanes* (Armbruster *et al.*, 2000). The Hypostomini and its sole genus, *Hypostomus*, are described below, and papers detailing the Pterygoplichthini and the Ancistrini are in preparation. Several genera currently in the Hypostominae (*Hemipsilichthys*, *Kronichthys*, *Isbrueckerichthys*, and *Pareiorhina*) appear to be unrelated to hypostomines, and are placed in the Neoplecostominae. *Delturus* and *Upsilodus* Miranda Ribeiro form a monophyletic group sister to all the other loricariids in the analysis. It is suggested that a new subfamily be described; a manuscript is in preparation describing *Delturus* + *Upsilodus* as a new subfamily.

MATERIAL AND METHODS

Fishes were cleared and double-stained with Alcian blue for cartilage and Alizarin red for bone according to procedures derived from Taylor & Van Dyke (1985). Examination of the digestive tract was completed on specimens in which the pelvic girdle, abdominal skin and musculature, and intestines were removed (Armbruster, 1998c). Drawings were prepared with the aid of a Wild MZ8 stereomicroscope and a camera lucida. Specimens examined are listed in Appendix 1. Institutional abbreviations follow Leviton *et al.* (1985).

Outgroups for the majority of the phylogenetic analyses were the callichthyids *Corydoras*, *Dianema*, and *Hoplosternum*. One species of the Scoloplacidae (*Scoloplax dicra*) was also examined. Due to the extreme miniaturization of scoloplacids, many of the character states were not comparable and not codable, although an analysis with *Scoloplax* included in the outgroup was performed. The character states of *Scoloplax* are not included in the character descriptions, and the tree with *Scoloplax* was not used to trace the evolution of the characteristics. As the morphology of *Scoloplax* is unique, due to its miniaturization, I felt that its inclusion might lead to erroneous interpretations of character evolution.

Homology assessment followed the rules laid down by Patterson (1982). Characteristics were first considered homologous based on similarity and lack of conjunction, while final assessment was via congruence based on the results of the phylogenetic analysis. Phylogenetic analysis was performed using PAUP ver. 4.0b4a (Swofford, 2000) using the tree bisection-recombination algorithm of the heuristic search. The ingroup included most genera of the Ancistrinae, the Hypostominae, and the Neoplecostominae, representative members of the Loricariinae and the Hypoptopomatinae, and *Astroblepus* and *Lithogenes*. An attempt was made to include as many species per genus as possible to test the monophyly of the genera.

Characters are unordered unless otherwise noted; where ordered, the reasoning for doing so is explained. For characters that consist of counts or extent (e.g. small, medium, large), it is most parsimonious to assume that number or size increased or decreased in a stepwise fashion rather than jumping between steps. A heuristic search with 1000 replicates was performed. Based on Schaefer (1987) and de Pinna (1992) the tree was rooted with the ingroup treated as monophyletic and the outgroup as a monophyletic sister group to the ingroup. The data matrix for the phylogenetic analysis is provided in Appendix 2. Character state evolution was examined using MacClade ver. 3.08a (Maddison & Maddison, 1999). As character state evolution can only be traced on a most parsimonious tree and the order of the trees received from PAUP is random, the first tree in the resultant dataset from PAUP was used to trace character evolution (Appendix 3). Ordering characters remains contentious (Hauser & Presch, 1991; Wilkinson, 1992; Slowinski, 1993); however, where a clear transformational series could be hypothesized, it was considered best to treat the character as ordered rather than remove useful information. To test ordering, 100 replicates of the heuristic search were run on a dataset with all characters unordered. To test the effects of the addition of *Scoloplax* on the outgroup, 100 replicates of the heuristic search were run on the ordered dataset.

A decay analysis was performed for the ordered data-set with the aid of TreeRot for the Macintosh (Sorenson, 1999). TreeRot produces constraint trees for each resolved node in a consensus tree. In constraint trees the node of interest is monophyletic, while all of the taxa above it form an unresolved polytomy. Multiple searches were then performed in PAUP, each with a different constraint tree loaded; the only trees saved were those not consistent with the constraint tree. For this study, 40 replicates were performed per node and 100 trees were saved during each replicate. Decay indices (DI), based on Bremer (1988), represent the length of the shortest trees obtained that are not consistent with the constraint tree, minus the number of steps in the most parsimonious tree.

Skeletal anatomy follows Schaefer (1987). Descriptions of characters and character states are provided.

They pertain only to those specimens listed in Appendix 1 unless otherwise indicated. The taxon names used are those considered valid based on this study. Abbreviations used in the figures are listed below.

In the character discussion below, some clades are referred to by group names, as follows:

(1) *Acanthicus* group: *Acanthicus* Agassiz, *Leporacanthicus* Isbrücker and Nijssen, *Megalancistrus,* and *Pseudacanthicus* Bleeker.

(2) *Hemiancistrus annectens* group: *Hemiancistrus holostictus* (Regan), *Hemiancistrus maracaiboensis* Schultz, and *Hypostomus panamensis* (Eigenmann) in this analysis (Armbruster, 1998c).

(3) *Hypostomus cochliodon* group: *Cochliodon sensu* Isbrücker (1980) and Armbruster & Page (1997), *H. cochliodon*, *H. hondae* (Regan), and *H. plecostomoides* (Eigenmann) in the analysis.

(4) *Hypostomus emarginatus* group: *H. ammophilus* (Armbruster & Page) (formerly *Aphanotorulus*), *H. emarginatus* Valenciennes, *H. spinosissimus* (Steindachner) (formerly *Isorineloricaria*), *H. squalinus* Schomburgk, and *H. unicolor* (Steindachner) (formerly *Aphanotorulus*).

(5) *Hypostomus unicolor* group: *Aphanotorulus sensu* Armbruster & Page (1996) and Armbruster (1998a), *H. ammophilus* and *H. unicolor*.

(6) *Lithoxus* group: *Exastilithoxus* Isbrücker and Nijssen and *Lithoxus* Eigenmann.

(7) *Pterygoplichthys multiradiatus* group: *Liposarcus sensu* Weber (1991, 1992), *P. multiradiatus* (Hancock) and *P. pardalis* (Castelnau) in the analysis.

ABBREVIATIONS USED IN FIGURES

AA	angulo-articular
AC	accessory crest of APC
AH	anterohyal
AF	abductor fossa
ALP	anterolateral process of pelvic basipterygium
AMP	anteromesial process of pelvic basipterygium
AP	accessory process
APC	levator arcus palatini crest
APG	articulating facet for the pectoral girdle
APM	anterior process of metapterygoid
APT	anterior process of pterotic-supracleithrum
AS	adipose-fin spine
AV	adductor ventralis
BL	Baudelot's ligament
CB	ceratobranchial
CL	cleithrum
CNB	connecting bone
CO	coracoid
COS	lateral strut of coracoid
CP	canal plate
D	dentary
DF	dorsal fin
DNP	dentary plug of cartilage
DPT	dorsal process of tripus
DP1	dorsal-fin pterygiophore
DS1	first dorsal-fin spine or spinelet
DS2	second dorsal-fin spine
EB	epibranchial
EO	evertible odontodes
FMA	foramen for afferent mandibular artery
H	hypural plate
HF	articulating facet of hyomandibula
HH	hypohyal
HP	posterior process of hyomandibula
HRP	process of preoperculo-hyomandibular ridge
HY	hyomandibula
HYP	hyoid plug
IH	interohyal
IO	infraorbital
IOML	interoperculo-mandibular ligament
IOP	interopercle
LER	lateral ethmoid ridge for articulation with metapterygoid
LP	lateral plate
LPC	lateral wall of the pterygoid channel
LPT	lateral process of tripus
LSPJ	lateral shelf of the upper pharyngeal jaw
LV	last vertebra
LVR	ridge of last vertebra
MB	maxillary barbel
MBT	main body of tripus
MC	metapterygoid condyle of lateral ethmoid
ME	mesethmoid
MED	mesethmoid disk
MEP	mesethmoid cartilaginous plug
MF	articulating facet of metapterygoid
MP	metapterygoid
MPC	mesial wall of the pterygoid channel
MX	maxilla
NP	nuchal plate
O	orbit
OC	opercular condyle of hyomandibula
OP	opercle
PAP	preadipose plate
PDM	dorsal-fin membrane posterior to last ray
PF	fenestra of pelvic basipterygium
PH	posterohyal
PHR	preoperculo-hyomandibular ridge
PMX	premaxilla
POP	preopercle
POPC	preopercular canal
PPCO	posterior process of coracoid
PPP	posterior process of pelvic basipterygium
PR	prootic
PS	pectoral-fin spine
PT	pterotic-supracleithrum
PTS	strut of pterotic-supracleithrum
PVRP	posteroventral ridge of pelvic basipterygium
Q	quadrate

QP	quadrate process for articulation with canal plate
R6	expanded rib of sixth vertebra
SF	symplectic foramen
SP	sphenotic
SPC	suprapreopercle
T	tripus
TPD	transverse process of dorsal-fin pterygiophore
TPWA	transverse process of the Weberian apparatus
UPJ	upper pharyngeal jaw
VRPB	ventral ridge of pelvic basipterygium
WCC	Weberian complex centrum
WO	whiskerlike odontodes

CHARACTERS

The character descriptions below refer only to specimens examined in this analysis. Statements such as 'most Loricariinae' refer only to most of those species of the Loricariinae examined.

HYOID AND BRANCHIALS

Anterohyal

1. Anterohyal shape: (0) greatest width less than half of length; (1) greatest width greater than half of length. CI = 0.06.

In *Corydoras*, *Lithogenes* Eigenmann, most Ancistrini, Hypoptopomatinae, some *Hypostomus*, *Isbrueckerichthys*, most Loricariinae, *Neoplecostomus*, some *Pterygoplichthys*, and some Rhinelepini, the greatest width of the anterohyal is less than half its length (state 0; Fig. 8B–D). In *Hoplosternum*, *Dianema*, *Astroblepus*, some Ancistrini, *Corymbophanes* Eigenmann, *Harttia*, most Neoplecostominae, most Pterygoplichthini, and most Rhinelepini, the greatest width is greater than half its length (state 1: Fig. 8A, E). Length and width are defined, respectively, as the distances along the longest and shortest axes of the hyoid arch.

2. Anterohyal shape: (0) anterior edge flat or with a single hump; (1) anterior edge sinusoidal. CI = 0.20.

In callichthyids, Astroblepus, Lithogenes, and most loricariids, the anterior edge of the anterohyal gently slopes anterolaterally from its anterior contact with the hypohyal or is flat (state 0; Fig. 8A, C–E). In most *Chaetostoma*, *Exastilithoxus fimbriatus* (Steindachner), *Lithoxancistrus* Isbrücker, Nijssen, and Cala, and *Lamontichthys*, the anterior margin of the anterohyal is wide mesially, then narrows, and then widens again so that the anterior margin appears sinusoidal (state 1; Fig. 8B).

Basibranchials

3. Basibranchial 2: (0) ossified; (1) cartilaginous; (2) absent. CI = 0.10.

In callichthyids, the *Acanthicus* group, the *Chaetostoma* group, some *Hypostomus*, *Lithoxancistrus*, the Loricariinae, some *Panaque* Eigenmann and Eigenmann, and some *Peckoltia* Miranda Ribeiro the second basibranchial is ossified (state 0). In *Hemipsilichthys*

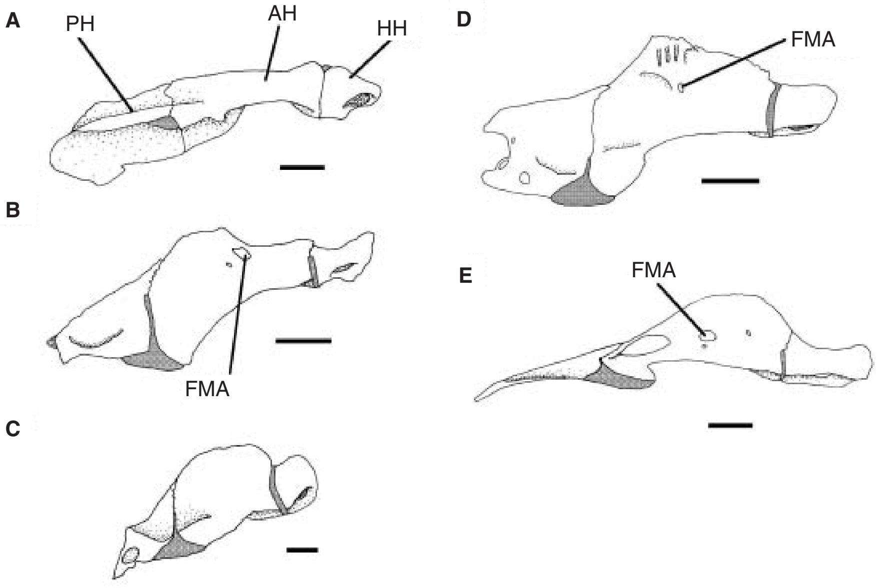

Figure 8. Hypohyal, anterohyal, and posterohyal bones, right side, ventral view. A, *Astroblepus* sp., USNM 302674. B, *Chaetostoma sovichthys*, INHS 34957. C, *Hypostomus unicolor*, USNM 319355. D, *Lasiancistrus maracaiboensis*, INHS 60465. E, *Leporacanthicus galaxias* Isbrücker and Nijssen, INHS 40910. Scale bars = 1 mm. Shaded area is cartilage.

cameroni and most Hypostominae it is cartilaginous (state 1). In *Astroblepus,* the Hypoptopomatinae, some *Hypostomus*, *Lithoxus*, most of the Neoplecostominae, *Peckoltia oligospila* (Günther), some *Pterygoplichthys*, and the Rhinelepini, it is absent (state 2). This state was not observable in *Lithogenes*.

4. Basibranchial 3, shape: (0) elongate; (1) short and wide, almost square. CI = 0.25.

In callichthyids, *Astroblepus*, and most loricariids, the third basibranchial is elongate anteroposteriorly (state 0). In *Crossoloricaria*, *Hemipsilichthys*?, the *Hypostomus unicolor* group, and *Isbrueckerichthys*, it is short and wide, almost square (state 1; Armbruster, 1998a). This state was not observable in *Lithogenes*.

Branchiostegals

5. Number of branchiostegals: (0) four; (1) three. CI = 0.67.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are four (state 0). In *Lasiancistrus s.s* and *Lithoxancistrus* there are three (state 1).

6. Mesial facing process on branchiostegal 3: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the branchiostegals are gently curving structures (state 0). In the *Chaetostoma* group, the third basibranchial has a process mesially at the point of greatest curvature (state 1; Schaefer, 1986).

Ceratobranchials

7. Length of accessory process of ceratobranchial 1 (ordered): (0) absent; (1) less than length of main body of ceratobranchial; (2) same length as ceratobranchial. CI = 0.18.

In callichthyids, *Astroblepus, Lithogenes*, and some loricariines, the first ceratobranchial (CB1) lacks an accessory process (state 0; Fig. 9A). In most loricariids, CB1 has a sheetlike anterior accessory process (Schaefer, 1986). In *Delturus*, most hypoptopomatines, some loricariines, most neoplecostomines, *Leporacanthicus*, the *Lithoxus* group, and *Upsilodus* the process is not as long as the main body of the ceratobranchial (state 1; Fig. 9B, C). In some hypoptopomatines, some neoplecostomines, and hypostomines, it is at least as long (state 2; Fig. 9D, E). The accessory process supports additional gill rakers. In most loricariids, the gill rakers are covered in an epithelium which helps trap food particles (Schaefer, 1986, 1987). It is hypothesized that the greater the size of the accessory process, the more gill tissue that can be supported, and that the process has expanded through evolution to increase the ability of the fishes to strain food; hence, this character is coded as ordered.

8. Width of accessory process of ceratobranchial 1 (ordered): (0) absent; (1) thin; (2) wide. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and some loricariines, the first ceratobranchial (CB1) lacks an accessory process (state 0; Fig. 9A). In *Delturus*, most hypoptopomatines, some hypostomines, some loricariines, most neoplecostomines, *Leporacanthicus*, the *Lithoxus* group, and *Upsilodus* the process is a thin structure less than the width of the main body of the ceratobranchial (state 1; Fig. 9B–D). In most hypostomines, some neoplecostomines, and some *Otocinclus*, it is wider than the main body of the ceratobranchial (state 2; Fig. 9E).

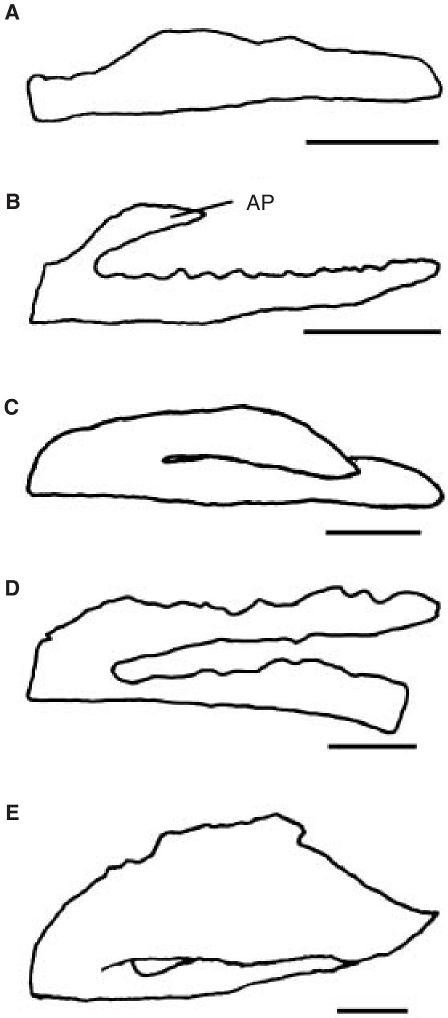

Figure 9. First ceratobranchial, right side, dorsal view. A, *Astroblepus* sp., MCNG 16251. B, *Hypoptopoma* sp., INHS 28696. C, *Lamontichthys llanero*, INHS 29957. D, *Isbrueckerichthys duseni*, UMMZ 215262. E, *Hypostomus cochliodon*, UMMZ 20338. Scale bars = 1 mm.

9. Width of ceratobranchial 3: (0) approximately same width as other ceratobranchials; (1) at least twice the width of the other ceratobranchials. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the third ceratobranchial is approximately the same width as the other ceratobranchials (state 0). In most of the Loricariini examined, it is at least twice the width (state 1).

10. Shape of ceratobranchial 5: (0) thin, uniform width; (1) wide. CI = 0.10.

In callichthyids, *Astroblepus, Lithogenes*, some of the Ancistrini, *Delturus*, some hypoptopomatines, most loricariines, neoplecostomines, and *Upsilodus*, the fifth ceratobranchial is a narrow structure with a nearly uniform width (state 0; Fig. 10A). In some hypoptopomatines, most of the Hypostominae, and most of the Loricariinae, it is widened at least anteriorly to form a hatchetlike structure (state 1; Fig. 10B).

11. Posteromedial invagination of ceratobranchial 5: (0) absent, (1) present. CI = 0.19.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posteromedial edge of the fifth ceratobranchial is without an invagination (state 0). In some loricariines, *Otocinclus*, and several hypostomines an invagination is present on the fifth ceratobranchial, giving it a battle-axe shape (state 1; from Schaefer, 1986 and Schaefer & Stewart, 1993).

12. Connections of ceratobranchial 5: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the fifth ceratobranchials do not contact one another mesially, and the teeth are fine (state 0; Fig. 11A). In *Crossoloricaria* and *Loricaria* the fifth ceratobranchials are enlarged, thickened, and sutured or held tightly to one another and have large, molariform teeth (state 1; Fig. 11B). There are pulverized seeds in the guts of *Crossoloricaria* and *Loricaria*, suggesting that the molariform teeth and strengthened pharyngeal jaws are adaptations for granivory. All of the seeds found in the guts examined are highly mot-

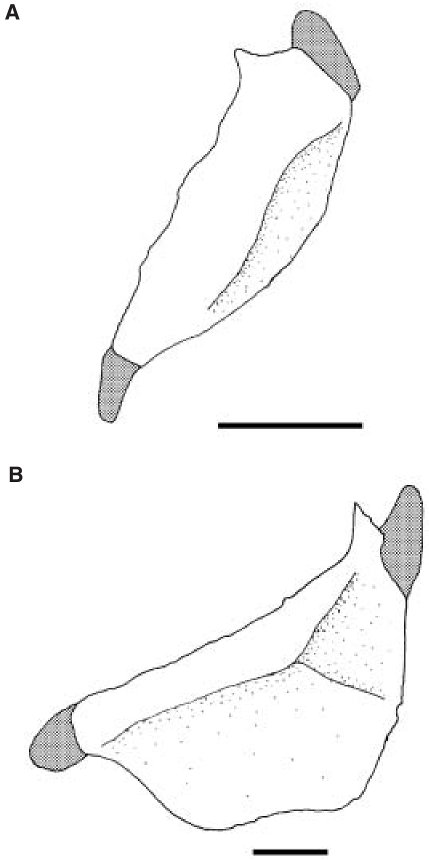

Figure 10. Fifth ceratobranchial, right side, ventral view. A, *Kronichthys* sp., MZUSP 35286. B, *Pseudorinelepis genibarbis* (Valenciennes), INHS 36938. Scale bars = 1 mm. Shaded area is cartilage.

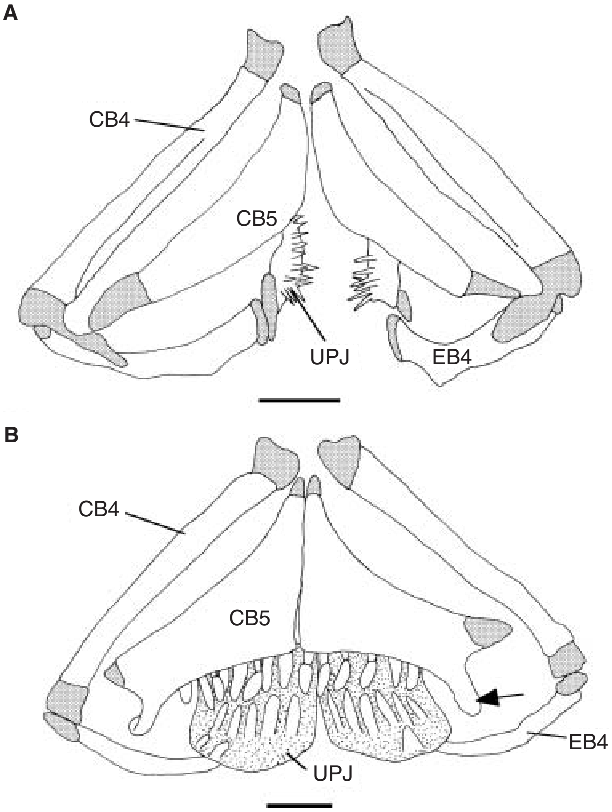

Figure 11. Pharyngeal jaws, ventral view. A, *Hemipsilichthys cameroni*, USNM 279585. B, *Loricaria* sp., INHS 31689. Scale bars = 1 mm. Shaded area is cartilage. Arrow indicates postero-lateral process.

tled, a condition stated by Goulding (1980) to be found in plants that do not have fruits. Goulding suggests that the mottling of the seeds is for camouflage from granivores; however, the guts of *Crossoloricaria* and *Loricaria* attest to a well-developed ability to find the seeds. Because the seeds are all crushed, it is apparent that the granivorous loricariines are not dispersing viable seeds.

13. Posterolateral process on ceratobranchial 5: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the fifth ceratobranchial does not have a posterolateral process (state 0; Fig. 11A). In *Crossoloricaria* and *Loricaria*, there is a posterolateral process on the fifth ceratobranchial that appears to be associated with the increased musculature needed for crushing seeds (state 1; see 12; Fig. 11B).

Epibranchials

14. Accessory process on first epibranchial: (0) absent; (1) thin; (2) broad. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, *Hemiancistrus megacephalus* (Günther), most hypoptopomatines, the *Lithoxus* group, and some loricariines, the first epibranchial lacks an accessory process (state 0). In *Delturus*, most neoplecostomines, most hypostomines, *Otocinclus*, and *Upsilodus*, there is a small, thin accessory process located anteromesially on the first epibranchial (state 1; Schaefer, 1986, 1987). In the Loricariini, there is also an accessory process; however, it is very broad (state 2).

15. Mesial surface of epibranchial 1: (0) rounded; (1) forms a blade. CI = 0.09.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the ventral surface of the first epibranchial is rounded or slightly keeled (state 0). In most hypoptopomatines and several groups of hypostomines, the ventral surface is highly keeled with the mesial edge expanded such that it appears blade-like (state 1).

16. Anterior-facing process on epibranchial 4 located basally to the gill rakers: (0) absent or short; (1) very long. CI = 0.10.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the fourth epibranchial either does not have an anterior-facing process or the process is short, not much longer than wide (state 0; Fig. 12A). In most of the Ancistrini, the Corymbophanini, hypoptopomatines, some *Hypostomus*, and neoplecostomines the process is very long, at least four times longer than wide (state 1; Fig. 12B).

17. Posterior shelf of epibranchial 4: (0) absent; (1) present. CI = 0.20.

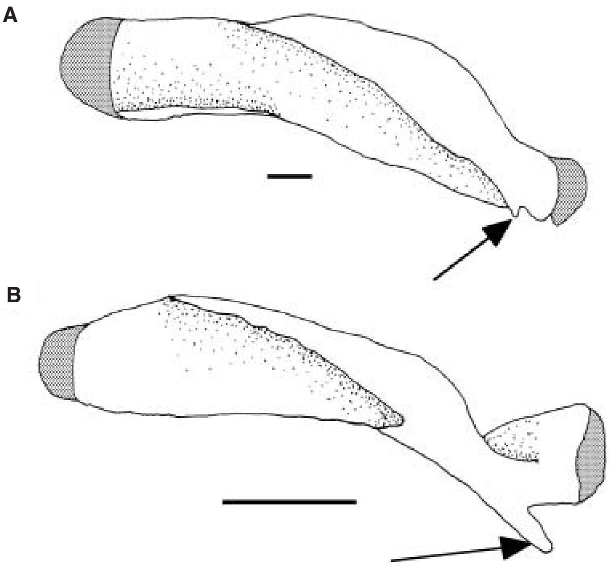

Figure 12. Fourth epibranchial, right side, dorsal view (slightly twisted anteriorly). A, *Pterygoplichthys multiradiatus*, INHS 29787. B, *Hemipsilichthys cameroni*, USNM 279585. Scale bars = 0.5 mm. Shaded area is cartilage. Arrows indicate anterior processes.

In most callichthyids, *Astroblepus, Lithogenes*, *Delturus*, *Leporacanthicus*, the *Lithoxus* group, the Loricariini, and *Upsilodus*, the fourth epibranchial lacks a posterior shelf and is cylindrical (state 0). In *Hoplosternum* and most loricariids, a posterior shelf is present and short (state 1).

18. Gill rakers on epibranchial 4: (0) absent; (1) present. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and some loricariines, there are no gill rakers on the fourth epibranchial (state 0). In most loricariids, they are present (state 1).

Hypohyal

19. Anteromesial projections on hypohyal: (0) absent; (1) present. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the hypohyal does not have anteromesial projections (state 0). In *Pogonopoma* and *Rhinelepis*, there are projections that nearly contact one another along the midline (state 1; (Armbruster, 1998b).

20. Width of hypohyal: (0) wide; greatest width approximately equal to or greater than length; (1) narrow, greatest width less than length. CI = 0.06.

In callichthyids, *Lithogenes*, and hypoptopomatines, some hypostomines, most loricariines, and some neoplecostomines, the hypohyal is wide, with the greatest width approximately equal to or greater than the length (state 0, Fig. 8C). In most loricariids, the hypohyal is narrow, with the greatest width less than the length (state 1, Fig. 8A, B, D, E). Length and width are defined, respectively, as the distances along the longest and shortest axes of the hyoid arch.

21. Hypohyal, spindle-shaped: (0) no; (1) yes. CI = 0.13.

In callichthyids, *Lithogenes*, and most loricariids, the hypohyal is roughly square to circular, with the anterior and posterior edges straight to convex (state 0; Fig. 8A, C–E). In *Astroblepus, Lithogenes*, and several groups of the Ancistrini, the anterior and posterior edges of the hypohyal are concave, making it spindle-shaped (state 1; Fig. 8B).

Hypobranchials

22. Hypobranchial 1: (0) rectangular to square, sometimes thinner at one end; (1) fan-shaped, lateral end much wider than the mesial end. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the first hypobranchial is rectangular to square, sometimes thinner at one end (state 0). In some of the Loricariini it is fan-shaped, with the lateral end much wider than the mesial end (state 1).

23. Hypobranchial 1: (0) short and stout; (1) elongated. CI = 0.06.

In callichthyids, *Lithogenes*, and most loricariids, the first hypobranchial is short and stout (state 0). In *Astroblepus*, *Acanthicus*, *Delturus*, the *H. emarginatus* group, the *Lithoxus* group, *Leporacanthicus*, some loricariines, *Nannoptopoma* Schaefer, most neoplecostomines, *Rhinelepis*, and *Upsilodus*, it is elongated (state 1; Armbruster & Page, 1996).

24. Hypobranchial 2: (0) short and stout; (1) elongated. CI = 0.33.

In callichthyids, *Lithogenes*, and most loricariids, the second hypobranchial is short and stout (state 0). In *Astroblepus*, *Hemipsilichthys nudulus* Reis and Pereira, and the *Hypostomus unicolor* group, it is elongated (state 1; Armbruster & Page, 1996).

Infrapharyngobranchials

25. Infrapharyngobranchial 4: (0) no process; (1) with lateral process. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the fourth infrapharyngobranchial is circular-shaped, orientated dorsoventrally (state 0). In some *Hypostomus*, some *Pterygoplichthys multiradiatus*, *Loricariichthys*, *Pogonopoma*, and *Rhinelepis*, it has a lateral process located approximately in the centre (state 1).

Interhyal

26. Interhyal: (0) on or behind hyomandibula; (1) contacts the cartilaginous section between the hyomandibula and the quadrate; (2) contacts bony part of quadrate. CI = 0.13.

In *Astroblepus, Lithogenes*, *Acanthicus*, *Dekeyseria* Rapp Py-Daniel, *Delturus*, hypoptopomatines, some *Hypostomus*, *Leporacanthicus*, most loricariines, neoplecostomines, *Pterygoplichthys*, the Rhinelepini, and *Upsilodus*, the interhyal is located posterior to the cartilaginous section between the quadrate and the hyomandibula or is absent (state 0; Fig. 13B). In callichthyids, some *Hypostomus*, most loricariines, *Megalancistrus*, *Parancistrus* Castelnau, and *Pseudacanthicus*, the anterior margin of the interhyal contacts the cartilaginous section between the quadrate and hyomandibula but does not contact the bony part of the quadrate (state 1). In most of the Ancistrini, the *Hemiancistrus annectens* group, most of the Hypostomini, *Sturisoma*, and *Sturisomatichthys*, the anterior margin of the interhyal contacts the bony part of the quadrate or reaches a point just ventral to the posteroventral corner of the bony part of the quadrate (state 2; Fig. 13A, C, D).

27. Interhyal: (0) large; (1) medium; (2) very small or absent. CI = 0.15.

In *Astroblepus*, the *Chaetostoma* group, *Delturus*, *Pseudolithoxus*, loricariines, *Lithoxancistrus*, *Panaque albomaculatus* Kanazawa, and *Upsilodus*, the interhyal is large, almost rectangular (state 0; Fig. 13A). In callichthyids, *Lithogenes,* and most loricariids, it is medium-sized, rod-shaped or oval (state 1; Fig. 13B–D). In *Hemipsilichthys* sp., hypoptopomatines, some *Hypostomus*, *Kronichthys*, *Pareiorhina* sp., *Pterygoplichthys*, and *Pseudorinelepis* the interhyal is a diminutive ossification or is absent (state 2).

28. Interhyal: (0) ventral; (1) dorsal. CI = 0.33.

In callichthyids, *Astroblepus*, and most loricariids, the interhyal is located at or below the ventral margin of the hyomandibula (state 0; Fig. 13). In *Lithogenes, Delturus*, loricariines, *Pseudolithoxus*, and *Upsilodus*, it is located well above the ventral margin of the hyomandibula (state 1).

Pharyngeal jaw

29. Upper pharyngeal jaw: (0) without invagination in shelf; (1) with invagination in shelf. CI = 0.13.

In most loricariids, the upper pharyngeal jaw consists of a bulbous section and a mesial shelf or is stout across the entire length (see also 30). In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the mesial shelf is complete or is absent (state 0; Fig. 14A, C). In several groups of the Ancistrini, *Delturus*, *Hartia*, most hypoptopomatines, most neoplecostomines,

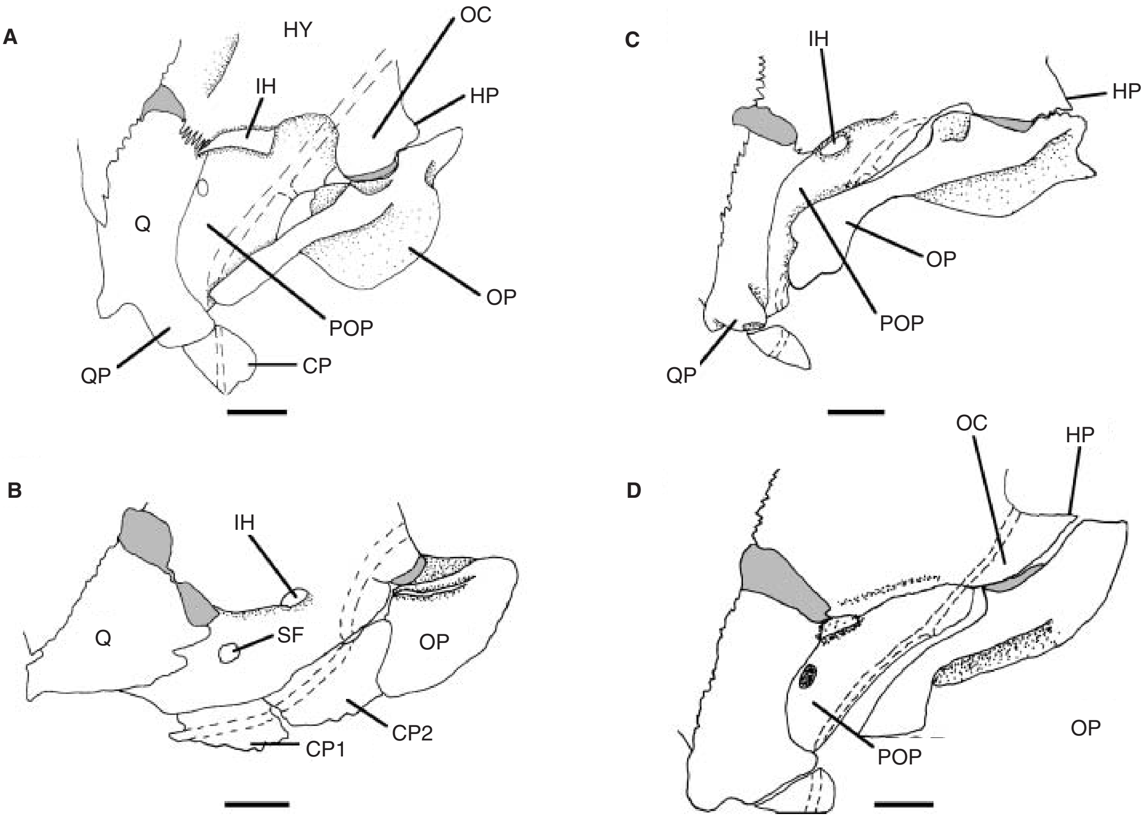

Figure 13. Suspensorium, right side, mesial view. A, *Cordylancistrus torbesensis*, MCNG 8066. B, *Isbrueckerichthys duseni*, UMMZ 215262. C, *Lasiancistrus maracaiboensis*, INHS 60465. D, *Neblinichthys pilosus* Ferraris, Isbrücker, and Nijssen, AMNH 56138SW. Scale bars = 1 mm. Shaded area is cartilage.

and *Upsilodus*, the shelf has an invagination (state 1; Fig. 14B, arrowed).

30. Upper pharyngeal tooth plate: (0) round, teeth uniformly distributed; (1) with a mesial shelf and a raised bulbous area, teeth restricted to bulbous area and posterior edge of shelf. CI = 0.13.

In callichthyids, *Astroblepus, Lithogenes*, *Corymbophanes*, some hypoptopomatines, *Leporacanthicus*, the *Lithoxus* group some loricariines, and *Neoplecostomus*, the upper pharyngeal tooth plate is rounded, with the teeth evenly distributed across the surface (state 0; Fig. 14C). In most loricariids it has a mesial shelf and a raised bulbous area; the teeth are restricted to the bulbous area and the posterior edge of the shelf (state 1; Fig. 14A, B).

31. Upper pharyngeal tooth plate, shelf lateral to the bulbous section: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the upper pharyngeal tooth plate is either round or has a rounded bulb with a mesial shelf (state 0). In the Rhinelepini, an additional lateral shelf is present (state 1; Armbruster, 1998b).

Posterohyal

32. Lateral edge of posterohyal: (0) pointed, forming pouch with a lateral wall (Fig. 8A–C, E); (1) Lateral wall of pouch absent or reduced so that the posterohyal forms a half cylinder (Fig. 8D). CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterohyal is pointed laterally and has a ventral pouch formed from a thickened lateral wall of the posterohyal (state 0; Fig. 8A–C, E). In *Ancistrus* Kner, *Lasiancistrus*, the *Lithoxus* group, and *Neblinichthys* Ferraris, Isbrücker, and Nijssen, the lateral wall of the pouch is reduced or absent and the lateral margin of the posterohyal is concave and widened so that the posterohyal appears to form a half cylinder (state 1; Fig. 8D).

SUSPENSORIUM

Hyomandibula

33. Contact of mesial surface of hyomandibula with quadrate posteroventrally: (0) none; (1) project toward one another or sutured. CI = 0.18.

In callichthyids, *Astroblepus, Lithogenes*, some of the Ancistrini, *Delturus*, hypoptopomatines, most lori-

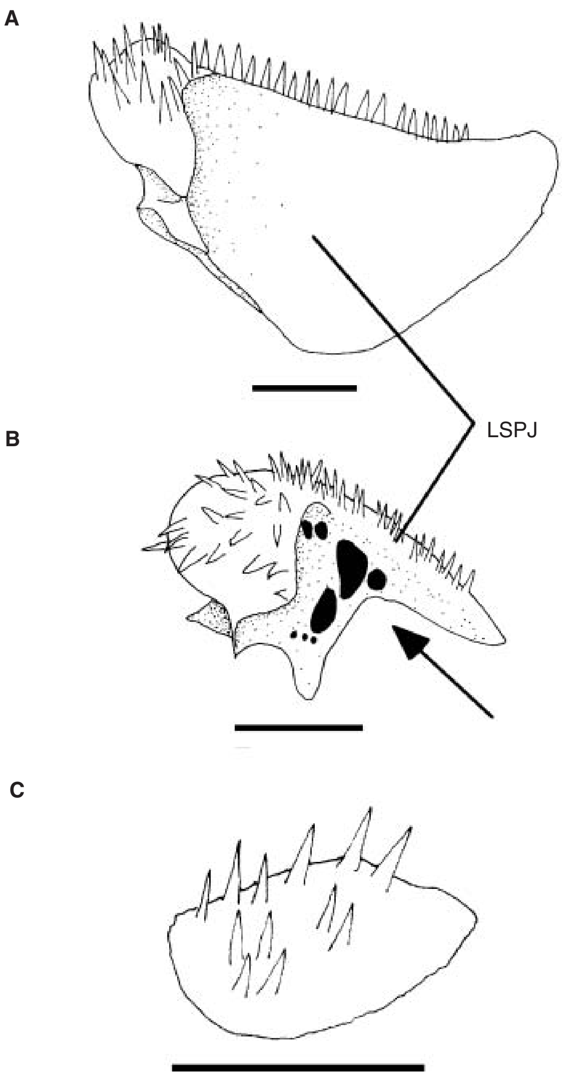

Figure 14. Upper pharyngeal jaw, right side, ventral view. A, *Hypostomus emarginatus* 1, FMNH 96957. B, *Panaque maccus*, INHS 29906. C, *Lithoxus lithoides*, BMNH 1972.7.17 : 66–115. Scale bars = 0.5 mm. Arrow indicates invagination of the lateral shelf (LPJ). Blackened areas in B are holes.

cariines, neoplecostomines, and *Upsilodus*, the mesial surfaces of the hyomandibula and the quadrate do not have a bony contact with one another mesially (state 0; Fig. 13B). In most of the Ancistrini, the Hypostomini, *Lamontichthys*, and most of the Pterygoplichthini, the hyomandibula, quadrate, or both develop mesial processes that project toward one another and may form a suture (state 1; Fig. 13A, C).

34. Hyomandibula sutured to pterotic-supracleithrum posterior to cartilaginous condyle of hyomandibula: (0) absent; (1) present. CI = 0.25.

In callichthyids, *Astroblepus*, most basal loricariids, *Chaetostoma*, *Hemiancistrus megacephalus*, and *Pseudancistrus* Bleeker, the hyomandibula and the pterotic-supracleithrum are not sutured together (state 0). In *Lithogenes,* most of the Ancistrini, the Hypostomini, *Loricariichthys*, and the Pterygoplichthini, the hyomandibula is sutured to the pterotic-supracleithrum posterior to the cartilaginous condyle to the hyomandibula (state 1). Based on Schaefer (1986).

35. Hyomandibula contacts prootic: (0) yes; (1) no, pterotic-supracleithrum only. CI = 0.11.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the hyomandibula has a cartilaginous condyle dorsally to the prootic or to the prootic and the pterotic-supracleithrum (state 0). In most *Hemipsilichthys*, *Pogonopoma*, *Chaetostoma platyrhyncha*, *Hemiancistrus megacephalus*, *Nannoptopoma*, *Otocinclus*, and *Pseudancistrus*, the contact is solely on the pterotic-supracleithrum (state 1).

36. Anterior margin of hyomandibula sutured to posterior metapterygoid along entire length: (0) yes, no notch between the two; (1) no, slight to large notch between the two. CI = 0.13.

In callichthyids, *Astroblepus*, the *Acanthicus* group (except *Megalancistrus*), the *H. cochliodon* group, *Panaque*, *Pareiorhina* sp., *Pogonopoma parahybae*, *Scobinancistrus* Isbrücker and Nijssen, and *Spectracanthicus* Nijssen and Isbrücker, the entire anterior edge of the hyomandibula dorsal to the cartilaginous intersection of the metapterygoid, hyomandibula, preopercle, and quadrate is sutured to the metapterygoid or there is a cartilaginous contact throughout their entire contact surfaces (state 0; Fig. 15A, H, I). In *Lithogenes* and most loricariids, the anterodorsal section of the hyomandibula is not sutured to the metapterygoid leaving a slight to large notch between the two bones (state 1; Fig. 15B–G).

37. Opercular condyle of hyomandibula on a process extended beyond posterior margin: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the opercular condyle of the hyomandibula is either flush with the posterior edge of the lateral face or anterior to the posterior margin (state 0; Fig. 13A–C). In *Neblinichthys* the condyle is separated by a pedicle from the main body of the hyomandibula so that it is posterior to the posterior margin of the lateral face (state 1; Fig. 13D).

38. Length of opercular condyle of hyomandibula: (0) short; (1) long. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the opercular condyle of the hyomandibula does not extend far below the posterior margin of the

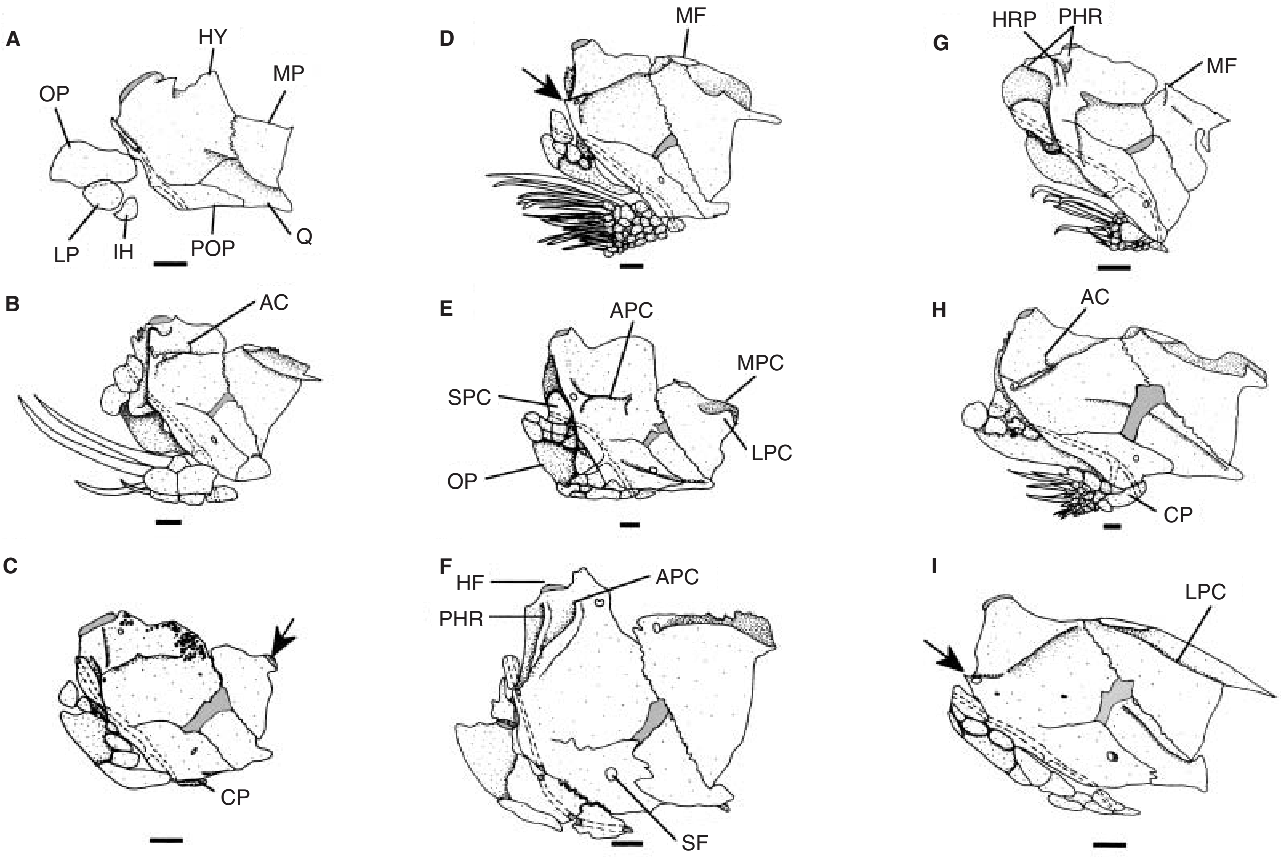

Figure 15. Suspensorium, right side, lateral view. A, *Astroblepus* sp., USNM 302674. B, *Dolichancistrus cobrensis* (Schultz), MCNG 6470. C, *Delturus anguilicauda* (Steindachner), USNM 318209. D, *Hemiancistrus* sp. 1, UF 77850. E, *Hypostomus unicolor*, FMNH 101120. F, *Isbrueckerichthys duseni*, UMMZ 215212. G, *Lithoxus lithoides*, BMNH 1972.7.17 : 66–115. H, *Pseudacanthicus leopardus* (Fowler), FMNH 95554. I. *Spectracanthicus murinus*, MZUSP 34279. Scale bars = 1 mm. Shaded area is cartilage. In B, the lateral wall of the pterygoid channel is deflected at a right angle so that it appears as a ridge in the drawing when it is as tall as the mesial wall. Arrows point to highly deflected preoperculo-hyomandibular crests in D and I and to a furrow in the metapterygoid that is the precursor to the pterygoid channel in C.

hyomandibula and is shorter than it is wide (state 0; Fig. 13B–D). In the *Chaetostoma* group, *Hypostomus francisci*, and *Peckoltia ucayalensis* (Fowler), it is elongated and longer than it is wide (Fig. 13A).

39. Thin, posterior process on hyomandibula just dorsal to opercle: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the hyomandibula either has a broad extension posterior to the condyle for articulation with the opercle, or its posterior border is flush with that of the condyle for articulation with the opercle (state 0; Fig. 13B). In some of the Ancistrini, there is a pointed process extending posteriorly from the condyle to which the opercle has a secondary attachment. It is present in *Ancistrus*, the *Chaetostoma* group, *Dekeyseria*, *Lasiancistrus*, the *Lithoxus* group, and *Neblinichthys* (state 1; Fig. 13A, C, D; HP). The process acts as a pivot point for the opercle when the opercle is used to evert the cheek plates. The *Lithoxus* group is coded as state 1 although the condition in the group appears to be a further modification of the process as is discussed in character 41.

40. Posterior part of hyomandibula beyond opercle: (0) not well developed; (1) developed into a shelf. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterior section of the hyomandibula is not particularly well developed (state 0; Fig. 15A–F, H, I). In *Ancistrus*, *Lasiancistrus*, the *Lithoxus* group, and *Parancistrus*, it is developed into a shelf dorsally such that the suture to the pterotic-supracleithrum is nearly at a right angle to the preoperculo-hyomandibular ridge (state 1; Fig. 15G).

41. Posterior process of hyomandibula incorporated within hyomandibula: (0) either absent or not incorporated; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterior process of the hyomandibula is either absent or is not incorporated into the posterior section of the hyomandibula (state 0; see 39). In the *Lithoxus* group the thin posterior process described in 39 is incorporated into an expanded posterior shelf of the hyomandibula (state 1).

42. Posterior region of hyomandibula greatly deflected: (0) absent; (1) present. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the hyomandibula is not deflected to moderately deflected mesially, but the opercle is always orientated parallel or nearly parallel to the main body axis (state 0). In most of the Ancistrini the posterior margin of the hyomandibula is strongly deflected mesially (state 1) causing the opercle to almost sit at a right angle to the main body axis.

43. Ridge on mesial side of hyomandibula located anterodorsally: (0) present; (1) absent. CI = 0.11.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there is no ridge present on the mesial side of the hyomandibula that runs from about the centre of the bone to the dorsal edge a few millimetres posterior to the anterior edge (state 0). In some hypoptopomatines, some *Hypostomus*, some loricariines, some neoplecostomines, and most of the Pterygoplichthini such a ridge is present (state 1).

44. Levator arcus palatini crest (ordered): (0) absent; (1) short; (2) tall. CI = 0.12.

In callichthyids, *Astroblepus*, some loricariines, and some hypoptopomatines, the levator arcus palatini crest is absent (state 0; Fig. 15A). In most loricariids, there is a short to tall ridge on the hyomandibula for attachment of the levator arcus palatini (Fig. 15B–I). In most loricariids, the ridge is rounded and short (state 1). In *Lithogenes,* most of the Ancistrini, some *Hypostomus*, *Isbrueckerichthys*, *Neoplecostomus*, and *Pareiorhina*, the ridge forms a tall shelf (state 2). It is most parsimonious to suggest that the crest first evolved as a short, rounded ridge and then became more pronounced; hence, this character is coded as ordered.

45. Levator arcus palatini crest of hyomandibula: (0) without strong dorsal upswing, straight; (1) with strong dorsal upswing. CI = 0.33.

Generally, when present, the levator arcus palatini crest has an accessory ridge dorsally that is perpendicular to it. This ridge is usually shorter in height than the crest and may be indistinct. In *Lithogenes, Exastilithoxus fimbriatus*, *Hemipsilichthys nudulus*, *Isbrueckerichthys*, *Leptoancistrus*, and some *Pareiorhina* sp., the ridge is the same height as the crest; the latter either does not continue beyond the ridge or becomes very short beyond it. This modification makes the crest appear curved such that it ends near the dorsal, cartilaginous condyle of the hyomandibula (state 1, Fig. 15E). Species without a crest or a ridge, or with a ridge shorter than the crest are coded as state 0 (Fig. 15A–D, F–I).

46. Hyomandibula deflected beyond posterior margin: (0) not deflected; (1) deflected. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the preoperculo-hyomandibular ridge is not strongly deflected (state 0; Fig. 15A–C, E-H). In some of the Ancistrini, *Hemipsilichthys* sp., and some *Hypostomus*, it is deflected posteriorly such that is passes beyond the posterior margin of the hyomandibula and is visible when the mesial surface of the hyomandibula is viewed (state 1; Fig. 15D, I).

47. Process on preoperculo-hyomandibular ridge: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there is no process on the preoperculo-hyomandibular ridge (state 0; Fig. 15A–F, H, I). In *Lithoxus* there is a small process located along the ridge, above the levator arcus palatini crest (state 1; Fig. 15G, HRP).

48. Preoperculo-hyomandibular ridge continuous: (0) yes; (1) no, ridge branches. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the preoperculo-hyomandibular ridge is continuous (state 0; Fig. 15A–F, H, I). In *Ancistrus*, *Lasiancistrus*, *Leptoancistrus*, the *Lithoxus* group, *Parancistrus*, and *Pseudorinelepis*, the ridge branches dorsally into anterior and posterior sections (state 1; Fig. 15G).

49. Ridge on hyomandibula (contiguous with ridge on quadrate): (0) absent; (1) present. CI = 0.25.

In callichthyids, *Astroblepus*, and most loricariids, there is no ridge on the ventrolateral part of the hyomandibula (state 0; Fig. 15A–G, I). In *Lithogenes, Hypancistrus* Isbrücker and Nijssen, *Leporacanthicus*, *Megalancistrus*, and *Pseudacanthicus*, there is a short ridge on the ventrolateral part of the hyomandibula that is contiguous with a ridge on the quadrate (state 1; Fig. 15H; see character 67); in *Pseudacanthicus* this ridge is much better developed than in the other species.

Metapterygoid

50. Zipperlike connection of metapterygoid to lateral ethmoid: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the metapterygoid does not contact the lateral ethmoid or the contact is simple (state 0, see 51). In the Loricariini there is a serrated, zipperlike connection between the metapterygoid and the lateral ethmoid (state 1).

51. Anterior connection between metapterygoid and lateral ethmoid: (0) absent; (1) present. CI = 0.25.

In callichthyids, *Astroblepus*, *Hypancistrus*, and *Otocinclus*, the metapterygoid does not contact the lateral ethmoid anteriorly (state 0). In *Lithogenes* and most loricariids, the metapterygoid has an anterior, bony contact with the lateral ethmoid or is held tightly to the lateral ethmoid by ligament (state 1). Typically, there are no modified contact surfaces, and the metapterygoid and the lateral ethmoid simply touch; however, some loricariids have developed a more well-developed contact surface (see 50). Based on Schaefer (1986, 1987).

52. Metapterygoid channel: (0) absent; (1) dorsal surface of metapterygoid split and forming slight furrow; (2) dorsal surface of metapterygoid split to the anterior process of the metapterygoid and forming a channel (ordered). CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, *Ixinandria*, *Neoplecostomus microps* (Steindachner), *Otocinclus*, and *Rineloricaria*, the metapterygoid lacks a channel laterally (state 0; Fig. 15A). In *Delturus*, *Exastilithoxus*, *Lithoxus*, *Scobinancistrus*, and *Upsilodus*, the dorsal margin of the metapterygoid is split and forms a slight furrow (state 1, Fig. 15C, arrowed). The split of the metapterygoid creates a larger and stronger contact surface with the lateral ethmoid, but does not form a channel for the passage of the levator arcus palatini muscle. In most loricariids, the dorsal margin is further split to the anterior process of the metapterygoid, which results in the presence of a channel for passage of the levator arcus palatini muscle (state 2; Fig. 15B, D–F, H, I). It is hypothesized that the dorsal surface of the metapterygoid became further split through evolution, and that what had originally evolved as an increase in the attachment of the metapterygoid secondarily became a channel for the levator arcus palatini muscle; hence, this character is coded as ordered. Presence of a channel would limit the lateral movement of the muscle, allowing it to pull the palatine posteriorly and thus pull the premaxilla posteriorly more strongly and efficiently. Some loricariids have only a slight ridge to denote the lateral wall of the pterygoid channel, but are coded as possessing the channel. *Lithoxus* has state 1, but the furrow is not visible in Figure 15G.

53. Lateral wall of metapterygoid channel: (0) absent; (1) long and rounded along entire length; (2) triangular; (3) broad ridge, perpendicular to metapterygoid; (4) just a slight ridge. CI = 0.27.

In callichthyids, *Astroblepus, Lithogenes*, *Delturus*, *Exastilithoxus*, *Lithoxus*, *Ixinandria*, *Neoplecostomus microps*, *Otocinclus*, *Rineloricaria*, *Scobinancistrus*, and *Upsilodus*, the channel is absent (state 0; Fig. 15A, G). In some loricariids, the channel is present with the lateral wall long and convex (state 1; Fig. 15B, F). In most loricariids, the lateral wall is roughly triangular (state 2; Fig. 15D, E, H). In *Spectracanthicus murinus* Nijssen & Isbrücker, the wall is present, but as a low, broad ridge perpendicular to the metapterygoid (state 3; Fig. 15I). In *Hypancistrus*, some loricariines, and *Megalancistrus*, the wall exists only as a low weak ridge (state 4). The morphology of states 3 and 4 is similar, but distinct enough to suggest that they evolved separately.

54. Walls of metapterygoid channel: (0) lateral wall slightly smaller to just slightly larger than mesial wall, or absent; (1) lateral wall taller. CI = 0.33.

In most loricariids, either the lateral and mesial walls of the channel are approximately the same height or the lateral wall is absent (state 0). In *Hypoptopoma*, *Lamontichthys*, *Nannoptopoma*, and *Pogonopoma*, the lateral wall is much taller than the mesial (state 1; Armbruster, 1998c). Species without a channel are coded as state 0 because it is hypothesized that it first developed as a furrow (52); in species with a furrow, both sides are equal in height.

55. Walls of metapterygoid channel: (0) lateral wall slightly smaller to just slightly larger than mesial wall, or absent; (1) mesial wall much taller. CI = 0.11

In most loricariids, either the lateral and mesial walls of the channel are approximately the same height, or the lateral wall is absent or shorter (state 0). In most of the *Chaetostoma* group [except *Cordylancistrus torbesensis* (Schultz)], *Hemiancistrus* sp. 1, *Hemipsilichthys* sp., *Hypancistrus*, some hypoptopomatines, some loricariines, *Megalancistrus*, *Parancistrus*, *Spectracanthicus*) the lateral wall is much shorter than the mesial (state 2). Species without a channel are coded as state 0 because it is hypothesized that it first developed as a furrow (52); in species with the furrow, both sides are equal in height.

56. Section of metapterygoid dorsal to the anterior process: (0) short; (1) very tall. CI = 0.20.

In most loricariids, the walls of the channel are not particularly tall and in those species without the channel, the section above the anterior process of the metapterygoid that is homologous to the two walls of the channel is short (state 0). In *Hemiancistrus megacephalus*, *Loricariichthys*, *Pseudancistrus*, some *Pterygoplichthys*, and *Dekeyseria pulcher* (Steindachner), both walls are tall (state 1).

57. Articulating surface between metapterygoid and lateral ethmoid: (0) absent; (1) present, not directly

connected to wall of metapterygoid; (2) present, directly connected via a straight ridge. CI = 0.13.

In callichthyids, *Astroblepus, Lithogenes*, *Delturus*, some hypoptopomatines, some loricariines, and *Upsilodus*, the metapterygoid lacks an articulating facet for contact with the lateral ethmoid (state 0; Fig. 15A, C). In some *Hemipsilichthys*, some *Hypostomus*, *Leporacanthicus*, the *Lithoxus* group, *Neoplecostomus microps*, *Parancistrus*, *Pogonopoma*, and most of the Pterygoplichthini, a facet is present, but not directly connected to the lateral wall of the metapterygoid channel (state 1; Fig. 15E–G). In most loricariids, the lateral wall continues as a low ridge onto the articulating facet (state 2; Fig. 15B, D, H, I).

58. Anterior process on metapterygoid: (0) pointed or absent; (1) spoon-shaped, straight; (2) spoon-shaped, angled ventrally; (3) curved, wider anteriorly than posteriorly (*Corydoras* only). CI = 0.50.

In *Dianema*, *Hoplosternum*, *Astroblepus, Lithogenes*, and most loricariids, the anterior process of the metapterygoid is either absent or pointed (state 0; Fig. 15A–C, E, F, H). In *Corymbophanes*, *Hemiancistrus* sp., *Hemiancistrus megacephalus*, *Lithoxancistrus*, *Pseudancistrus*, and *Spectracanthicus* (state 1; Fig. 15D; in *Spectracanthicus* the metapterygoid is angled such that the spoon-shaped process cannot be seen in Fig. 15I), the anterior process is straight and widened anteriorly making it appear spoon-shaped. In *Lithoxus* the anterior process is also spoon-shaped, but it is angled ventrally (state 2; Fig. 15G). The state in *Corydoras* (curved, wider anteriorly than posteriorly) is not directly comparable to other loricarioids and was coded as state 3.

Palatine

59. Ventromesial process of palatine: (0) short; (1) long. CI = 1.00

In loricariids, *Astroblepus, Lithogenes*, and callichthyids, the palatine has a mesial and a lateral process ventrally. In most, the mesial process is short (state 0). In *Pareiorhina* and the Rhinelepini it is elongated (state 1).

60. Palatine: (0) elongate; (1) with mesial flap, very wide. CI = 1.00.

In most loricariids the palatine is long and slender (state 0). In the Loricariini it has a mesial flap which makes it appear very wide (state 1).

Preopercle

61. Orientation of preopercle: (0) horizontal; (1) almost vertical. CI = 0.08.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterior section of the preopercle is long and the preopercle appears to be orientated horizontally if the ventral edge of the quadrate is taken as the horizon (state 0). In some of the Ancistrinae, *Pogonopoma*, *Rhinelepis*, *Loricaria*, and *Rineloricaria*, the posterior section is very short, giving the preopercle the appearance of being orientated at an angle to almost vertically (state 1; Armbruster, 1998b).

62. Exit of preopercular latero-sensory canal: (0) posterior to posteroventral edge of quadrate; (1) anterior to posteroventral edge of quadrate; (2) latero-sensory canal does not enter preopercle. CI = 0.15.

In *Astroblepus, Lithogenes* and most loricariids, the exit is located posterior to the posterior edge of the quadrate (state 0). In callichthyids, most of the Ancistrini, *Corymbophanes*, some loricariines, and most of the Rhinelepini, it is located anterior to the posteroventral edge of the quadrate (state 1; Armbruster, 1998b). In some hypoptopomatines and in *Hemipsilichthys nudulus*, the preopercle does not have a section of the latero-sensory canal system (state 2).

63. Preopercular latero-sensory canal extended posteriorly: (0) no; (1) yes. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the canal is flush with the posterior edge of the hyomandibula at the posterior opening of the canal (state 0). In *Corymbophanes*, the Hypoptopomatinae, and the Neoplecostominae, the preopercle is extended posteriorly as a shelf at the posterior opening of the canal.

Quadrate

64. Quadrate: (0) thin; (1) wide; (2) very wide. CI = 0.22.

In *Corydoras*, *Astroblepus, Lithogenes*, and most loricariids, the quadrate is roughly triangular, its width approximately half its length (state 1). In *Ancistrus*, *Dekeyseria scaphirhyncha* (Kner), *Lasiancistrus s.s.* and *Rineloricaria*, the quadrate is very narrow, its width approximately one quarter its length (state 0). In *Dianema*, *Hoplosternum*, some *Chaetostoma*, *Delturus*, *Otocinclus*, *Pseudorinelepis*, and *Upsilodus*, the quadrate is nearly as wide as long (state 2).

65. Ventral process on quadrate for articulation with canal plate: (0) absent; (1) present. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the quadrate does not have a ventral process that articulates with the canal plate (state 0; Fig. 13B, D). In the *Chaetostoma* group, *Hemiancistrus* sp., *Lasiancistrus s.s.*, *Lithoxus*, *Neblinichthys*, and *Peckoltia oligospila*, a process is present on the quadrate that articulates with the canal plate (state 1; Fig. 13A, C).

66. Quadrate with flap extending below symplectic foramen: (0) absent; (1) present. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the quadrate is a triangular bone and without a flap underneath the symplectic foramen (state 0). In the Hypostomini, the Pterygoplichthini, and most of the Ancistrini (except the *Acanthicus* group and *Exastilithoxus*), it has a ventral flap that extends below the symplectic foramen (state 1).

67. Articulating condyle of quadrate: (0) thin, pointed; (1) wide, blunt. CI = 0.14.

In callichthyids, *Lithogenes*, and most loricariids, the condyle of the quadrate that articulates with the lower jaw is thin and pointed, half as wide as long or less (state 0). In *Astroblepus*, the *Chaetostoma* group, some *Hemipsilichthys*, *Leporacanthicus*, *Lithoxancistrus*, *Panaque*, and *Scobinancistrus*, the articulating condyle is very wide and blunt, approximately as wide as long (state 1).

68. Longitudinal ridge running the length of the quadrate laterally: (0) absent; (1) present. CI = 0.10.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the quadrate is smooth laterally (state 0; Fig. 15A–G). In the *Acanthicus* group, *Chaetostoma pearsei* Eigenmann, *Hemiancistrus landoni* (Eigenmann), some *Hypostomus*, *H. panamensis*, *Hypancistrus*, *Leporacanthicus*, the *Lithoxus* group, *Megalancistrus*, *Panaque*, *Parancistrus*, most *Peckoltia*, and *Scobinancistrus*, there is a ridge running the length of the quadrate laterally (state 1; Fig. 15H, I).

JAWS

Lower jaw

69. Angle of dentaries: (0) oblique; (1) acute or right angle. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the dentaries meet to form an oblique angle (usually >90°; state 0; Fig. 16A). In *Hypancistrus*, the *Hypostomus cochliodon* group, *Leporacanthicus*, the *Lithoxus* group, the Loricariini, *Megalancistrus*, *Panaque*, *Parancistrus*, *Peckoltia*, *Pseudancistrus*, and *Spectracanthicus*, the jaws typically meet at an acute angle (usually = 80°; state 1; Fig. 16B).

Upper jaw

70. Angle of maxilla: (0) angled dorsally to slightly angled ventrally; (1) well angled ventrally, almost forming right angle. CI = 0.08.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the maxilla ranges from being angled slightly ventrally to slightly dorsally (state 0; Fig. 17A, B, D). In some *Hypostomus*, *Hemiancistrus holostictus*, *Hemiancistrus landoni*, most *Panaque*, some *Peckoltia*, *Pseudacanthicus*, *Pterygoplichthys punctatus* (Kner), *Scobinancistrus*, and *Spectracanthicus punctatissimus* (Steindachner), the maxilla is strongly angled ventrally to almost form a right angle (state 1; Fig. 17C).

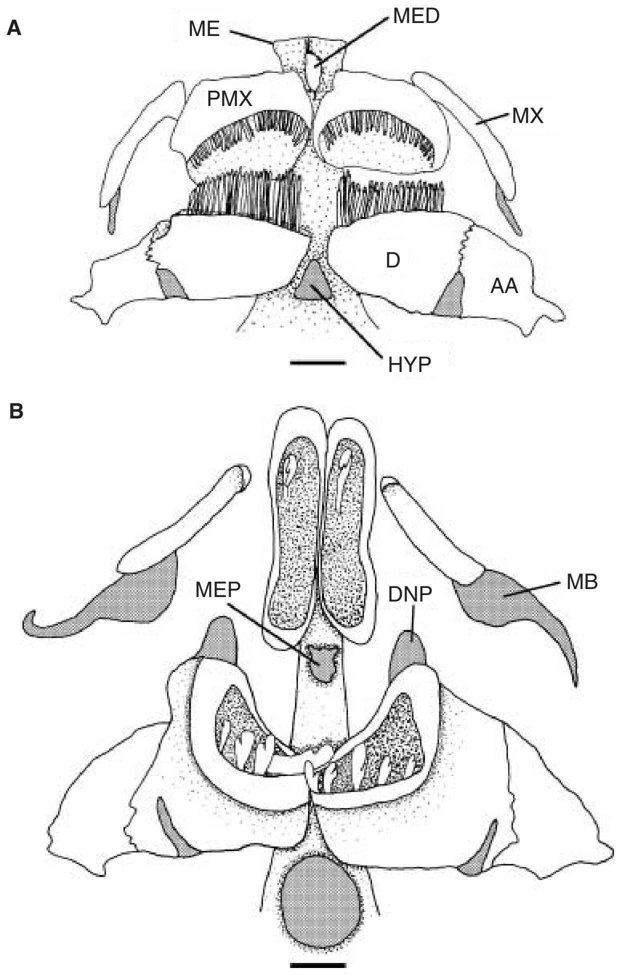

Figure 16. Jaws, ventral view. A, *Kronichthys* sp., MZUSP 35286. B, *Leporacanthicus galaxias*, INHS 40910. Scale bars = 1 mm. Shaded area is cartilage.

71. Shape of maxilla: (0) long, narrow, uniformly wide; (1) resembling a bowling pin. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the maxilla is long and narrow and is uniformly wide (state 0; Fig. 17A–C). In the *Lithoxus* group, *Leporacanthicus*, and *Spectracanthicus murinus*, the maxilla is wide and rounded distally, narrows proximally to form a neck, and then widens slightly to form a head, much like a bowling pin (state 1; Fig. 17D).

72. Premaxilla with cartilaginous connection to mesethmoid: (0) no; (1) yes. CI = 1.00.

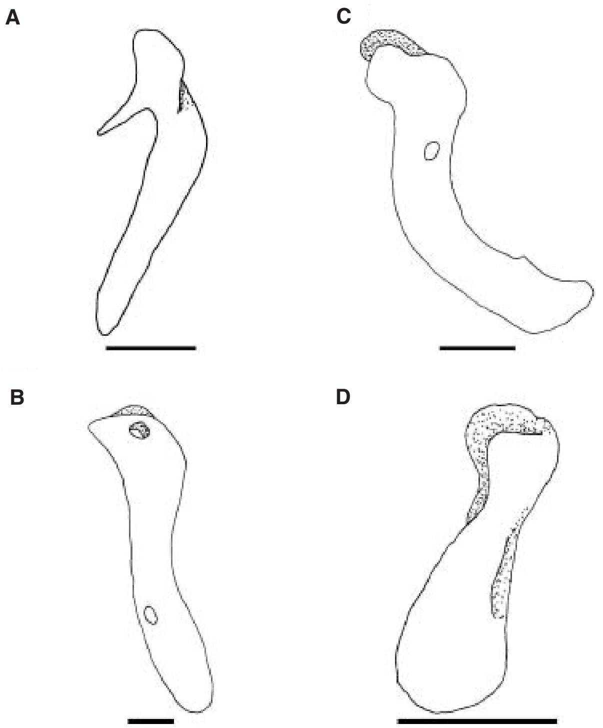

Figure 17. Maxilla, right side, lateral view. A, *Astroblepus* sp., FMNH 70017. B, *Hypostomus plecostomus*, YPM 4194. C, *Panaque maccus*, INHS 29862. D, *Lithoxus lithoides*, BMNH 1972.7.17 : 66–115. Scale bars = 1 mm.

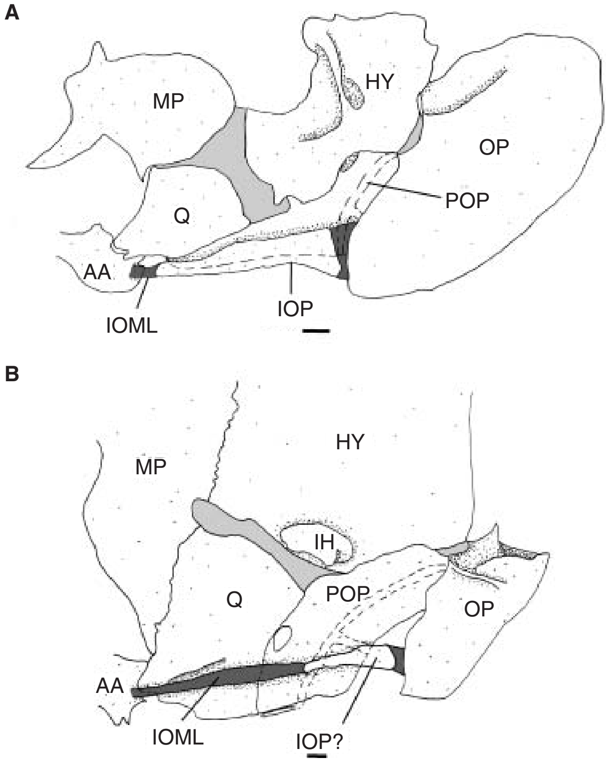

Figure 18. Suspensorium, mesial view. A, *Hoplosternum littorale* INHS 69360. B, *Delturus anguilicauda* USNM 318180. Scale bars = 1 mm.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the premaxilla contacts the mesethmoid directly (state 0). In the Loricariini, the premaxillas have a cartilaginous contact with one another and the mesethmoid (state 1).

OPERCULAR SERIES

Interopercular elements

73. Interopercular sesamoid: (0) absent; (1) present. CI = 0.17.

Schaefer (1986, 1987, 1988) and Schaefer & Lauder (1986, 1996) state that loricariids have lost both the interopercle and the interoperculo-mandibular ligament. In *Deltuus*, *Harttia*, *Lithogenes*, *Neoplecostomus*, *Pogonopoma*, and *Upsilodus*, there is a small ossification mesial to the preopercle and connected by a ligament to the opercle and the anguloarticular (state 1, Fig. 18A). Homologies of the bone are difficult to ascertain. In *Delturus*, the bone has the same shape as the interopercle of *Hoplosternum*, but is smaller (Fig. 18B) suggesting that it may be a true interopercle. In *Lithogenes, Harttia*, *Neoplecostomus*, and *Pogonopoma*, the bone is likely a neomorph and is probably a sesamoid ossification based on its size, shape, and the fact that it develops at what appears to be a friction point on the interoperculo-mandibular ligament. There has been some contention as to the presence or absence of the interopercle in Loricarioids. Schaefer (1988) suggested that a bone located ventrolaterally to the opercle in *Astroblepus* is homologous to the interopercle based on positional homology; however, the putative interopercle is lateral to the opercle instead of directly ventral and slightly mesial as in callichthyids. It is most likely that the putative interopercle of Schaefer (1988) is actually a bony plate. A similar plate is found in *Lithogenes* and it often supports odontodes. As the position of an interopercle in *Lithogenes* could be denoted by the presence of an interoperculo-mandibular ligament, it is very unlikely that the plate near the opercle in both *Astroblepus* and *Lithogenes* is the interopercle. In order to be as unbiased as possible, the bone occasionally found inside of the interoperculo-mandibular ligament was coded as a unique ossification and not the interopercle, and all callichthyids, *Astroblepus*, and all loricariids not mentioned above are coded as state 0. Further discussion of this characteristic can be found below.

74. Interoperculo-mandibular ligament: (0) present; (1) absent. CI = 0.06.

The presence of an interoperculo-mandibular ligament in loricariids is actually quite widespread: *Lithogenes,* most of the *Acanthicus* group, *Delturus*, *Harttia*, *Hemipsilichthys bahianus* (Gosline), most *Hypostomus*, *Isbrueckerichthys alipionis* (Gosline), some loricariines, *Neoplecostomus*, the *Hemiancistrus annectens* group, *Pogonopoma*, some *Pterygoplichthys*, and *Upsilodus*. Given that the ligament does not have an interopercle associated with it, it is possible that the ligament found in loricariids is not homologous to the interoperculo-mandibular ligament of other catfishes; however, it is also possible that basal loricariids lost the interopercle, but not the ligament, the ligament acquiring a new attachment directly to the opercle. The ligament shares a positional and operational homology with the interoperculo-mandibular ligament, it acts as a mechanical couple between the opercle and the angulo-articular. Given that the ligament is present in *Lithogenes*, it is most likely that it is the interopeculo-mandibular ligament. *Astroblepus* and several groups of loricariids lost the ligament; the loss may not be a synapomorphy for *Astroblepus* + loricariids as suggested by Schaefer (1987) and Schaefer & Lauder (1986, 1996). Most loricariids and *Astroblepus* lack the interoperculo-mandibular ligament (state 1).

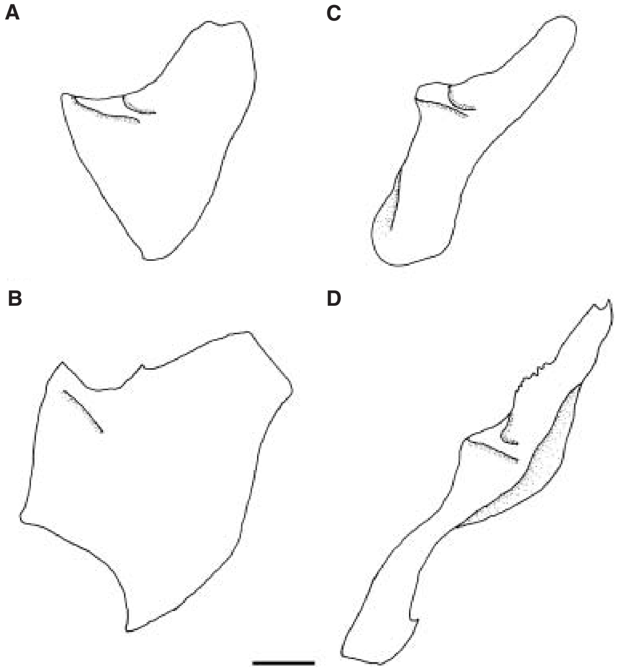

Figure 19. Opercle, right side, mesial view. A, *Hemiancistrus maracaiboensis*, EBRG 2855. B, *Hypostomus taphorni* (Lilyestrom), ANSP 16195. C, *Peckoltia* sp., FMNH 70863. D, *Ancistrus pirareta* Müller, UMMZ 206085. Scale bars = 1 mm.

Opercle

75. Shape of ancistrine opercle (ordered): (0) oval or triangular; (1) sickle-shaped (*Peckoltia*-type); (2) bar-shaped (*Ancistrus*-type). CI = 0.67.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the opercle is roughly oval or triangular (state 0; Fig. 19A, B). Schaefer (1986, 1987) diagnosed the Ancistrini based on modifications of the opercle. Basally in the Ancistrini, the opercle is sickle-shaped (state 1; Fig. 19C). In *Ancistrus*, the *Chaetostoma* group, *Dekeyseria*, *Lasiancistrus*, the *Lithoxus* group, and *Neblinichthys*, the opercle is bar-shaped with the lateral section deflected laterally (state 2; Fig. 19D). Schaefer (1986, 1987) hypothesized that the opercle first lost the posterolateral shelf and then the lateral section of the opercle became deflected; hence, this character is coded as ordered. The modified opercle is in all members of the Ancistrini except *Hemiancistrus* sp. Brazil and *Spectracanthicus murinus*.

76. Double attachment of opercle: (0) absent; (1) present. CI = 1.00

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the opercle contacts the hyomandibula only at the opercular condyle of the hyomandibula (state 0; Fig. 13B). In the Ancistrini with a bar-shaped opercle (see 75: 2), the opercle has an additional posterior (and sometimes also an anterior) connection to the hyomandibula (state 1; Fig. 13A, C, D; based on Schaefer, 1986).

77. Maximum forward position of opercle (ordered): (0) below hyomandibula; (1) to posteroventral corner of quadrate; (2) to posterodorsal corner of quadrate. CI = 0.22.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the opercle is located posteriorly so that no part is located below the quadrate (state 0). In most of the Ancistrini with a bar-shaped opercle (75: 2) and *Hemiancistrus* sp. 1, the opercle is lengthened anteriorly such that the anterior border is located below the posteroventral corner of the quadrate (state 1). In *Ancistrus*, *Chaetostoma pearsei*, *Lasiancistrus*, and *Lithoxus lithoides* Eigenmann, the anterior border of the opercle is further anterior and is located below the posterodorsal corner of the quadrate (state 2). It is most parsimonious to assume that the opercle moved successively forward; hence, this character is coded as ordered.

78. Hatchet-shaped opercle: (0) absent; (1) present. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the opercle is either straight along its anterior margin or convex (state 0; Fig. 19A, C, D). In *Hypostomus*, *Kronichthys*, *Neoplecostomus*, *Hemiancistrus holostictus*, *Pareiorhina*, *Spectracanthicus*, and *Harttia*, the opercle has at least a moderately concave anteroventral margin making it shaped as a hatchet (state 1; Fig. 19B).

79. Opercle: (0) supports odontodes; (1) does not support odontodes. CI = 0.25.

In callichthyids and most loricariids, the opercle supports odontodes (state 0). In *Astroblepus, Lithogenes*, *Hypancistrus*, *Panaque*, *Parancistrus*, *Peckoltia*, and *Pterygoplichthys punctatus*, the opercle is covered by skin or plates in at least adults and does not support odontodes. In at least *Hypancistrus* and *Peckoltia*, there is an ontogenetic change in the exposure of the opercle. In most juvenile *Hypancistrus* and *Peckoltia*, the opercle supports several rows of odontodes; in the largest adults, the opercle supports few or no odontodes. The specimens examined of *Hypancistrus* and *Peckoltia* that lack odontodes on the opercle appear to be males, so it is possible that there is also sexual dimorphism in the character. All *Panaque* examined lack odontodes on the opercle. Some members of the *H. cochliodon* group not analysed in this study also lack odontodes on the opercle.

Suprapreopercle

80. Suprapreopercle: (0) absent; (1) present. CI = 0.14.

In *Astroblepus* (where it is present as an ossified tube) and most loricariids, the suprapreopercle is located posterior to the preopercle and bears a branch of the lateralis system (state 1). In callichthyids, *Lithogenes*, some hypoptopomatines, and some neoplecostomines, the suprapreopercle is absent (state 0).

81. Number of rows of plates between suprapreopercle and exposed portion of opercle (ordered): (0) none; (1) one; (2) two to three. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, *Corymbophanes*, *Exastilithoxus*, *Hemipsilichthys cameroni* (Steindachner), *H. nudulus*, hypoptopomatines, *Lithoxancistrus*, most loricariines, *Pareiorhina*, *Pogonopoma parahybae*, *Pseudorinelepis*, and *Rhinelepis* there are no plates between the suprapreopercle (or in the area the suprapreopercle would be) and the exposed opercle (state 0). In most of the Ancistrini, *Delturus*, *Harttia*, most *Hypostomus*, *Lamontichthys*, the remainder of the neoplecostomines, and *Upsilodus*, there is one plate between the suprapreopercle and the exposed opercle (state 1). In *Acanthicus*, *Ancistrus*, *Dekeyseria pulcher*, *Hypancistrus*, some *Hypostomus*, *Lasiancistrus*, *Parancistrus*, the Pterygoplichthini, and *Scobinancistrus*, there are 2–3 plates between the suprapreopercle and the exposed opercle (state 2). Because increased fragmentation of the cheek plates is concomitant with their increased evertibility (Schaefer, 1986, 1987) this character is coded as ordered. Most species without suprapreopercles are coded as state 0 because it appears as if there is not enough room for plates between where the suprapreopercle would be and the exposed opercle. In *Hemipsilichthys splendens* Bizerril, the preopercular latero-sensory canal enters the preopercle much more dorsally than in other species without suprapreopercles, and there is a plate between the area where the suprapreopercle would be and the opercle; hence *H. splendens* was coded as having state 1.

LATERO-SENSORY CANAL SYSTEM

Hemipsilichthys nudulus lacks much of the lateralis system. The lateral line canal is only a few plates long, the infraorbital canal and preopercular latero-sensory canal are missing, and the other canals of the head are weak. However, it is possible to recognize most of the plates pierced by the lateralis system in most other loricariids. Hence a canal plate and most infraorbitals are recognizable; they are coded as present and/or their position is noted.

Canal plate

82. Canal plate: (0) absent; (1) present. CI = 1.00.

Schaefer (1986, 1987, 1988) describes a plate located ventral to the preopercle that bears a portion of the canal that he terms the ‘canal plate’. Callichthyids, *Astroblepus, Lithogenes*, *Delturus* and *Upsilodus* either lack the plate or it is marked only by a slight ossification no wider than the canal (state 0). All loricariids except *Delturus* and *Upsilodus* have a plate that is larger than the canal and that generally supports odontodes (see 84: 1).

83. Canal plate, number and size: (?) absent; (0) one large; (1) one small; (2) two small. CI = 0.22.

The number, size, and shape of the canal plates in loricariids is variable. Callichthyids, *Astroblepus, Lithogenes*, *Delturus* and *Upsilodus* lack the plate and were coded as unknown (?). The plate can either be large with the ventral part deflected mesially so that it is visible from below, as in hypoptopomatines, *Leporacanthicus*, some loricariines, most neoplecostomines, and *Pogonopoma* (state 0), small, as in most other loricariids (state 1; Fig. 13A, C, D), or there may be two small plates, as in *Isbrueckerichthys*, *Pareiorhina rudolphi* Gosline, and *Rhinelepis* (state 2; Fig. 13B). In *Astroblepus*, *Delturus*, *Lithogenes*, and *Upsilodus* the canal plate is represented only by an ossified tube. Because ossified tubes occasionally occur around the lateralis system in catfishes, they are not considered to be plates, although they are used to mark the location of plates for the following characters.

84. Canal plate: (?) absent; (0) exposed, supporting odontodes; (1) covered in skin or plates, not supporting odontodes. CI = 1.00.

Callichthyids, *Astroblepus, Lithogenes*, *Delturus* and *Upsilodus* lack the canal plate and were coded as unknown (?). In most loricariids the plate supports odontodes (state 0). In the *Chaetostoma* group the plate is located slightly mesially to the lateral plates and does not have any odontodes attached to it (state 1).

85. Contact of canal plate with suspensorium: (?) no canal plate; (0) absent; (1) present. CI = 0.10.

Callichthyids, *Astroblepus, Lithogenes*, *Delturus* and *Upsilodus* lack the canal plate and were coded as unknown (?). In most loricariids, the plate does not contact the suspensorium (state 0). In several groups of loricariids (including most of the Ancistrini) the plate has a bony or ligamentous connection with the suspensorium, either on the preopercle, quadrate, or both (state 1).

86. Canal in canal plate: (0) unbranched; (1) branched. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and loricariids, the canal is not branched either in, or in the region of, the canal plate (state 0). In *Hemipsilichthys*, *Isbrueckerichthys*, *Neoplecostomus*, and *Pareiorhina* sp., the canal in the canal plate is branched (state 1).

87. Preopercular latero-sensory canal leaves preopercle at first exit and enters a plate: (0) no; (1) yes. CI = 0.25.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, this canal gives off a branch medially to the posterior of the preopercle and then continues to the ventral margin of the preopercle (state 0; Fig. 13A, C, D). In some of the Hypoptopomatinae, *Isbrueckerichthys*, *Neoplecostomus paranensis* Langeani, and *Pareiorhina rudolphi*, it exits at the level of the first branch along the posterior margin of the preopercle and does not continue to the ventral margin of the preopercle (state 1; Fig. 13B).

88. Number of cheek plates between the canal plate and opercle (ordered): (0) none; (1) one; (2) two to four; (3) five or more. CI = 0.23.

Schaefer (1986, 1987) hypothesized that the cheek plates became successively fragmented during evolution, partially assessing this from the number between the canal plate and the exposed section of the opercle. The Ancistrini and the Pterygoplichthini tend to have the most fragmented cheek plates and this may be associated with the ability to evert them. In the Ancistrini that have the opercle unexposed, counts are made to the area where the opercle normally is exposed. The above categories appear to hold phylogenetic signal. State 0 is found in *Astroblepus, Lithogenes*, some hypoptopomatines, and some neoplecostomines. State 1 is found in *Corymbophanes*, *Delturus*, most hypoptopomatines, most loricariines, most neoplecostomines, and *Upsilodus*. State 2 is found in *Ancistrus*, the *Chaetostoma* group, *Hemipsilichthys*?, the Hypostomini, the *Lithoxus* group, some loricariines, *Pseudacanthicus*, *Spectracanthicus murinus*, and the Rhinelepini. State 3 is found basally in the Ancistrini and in the Pterygoplichthini. It is hypothesized that the cheek plates became more fragmented so that the opercle could be better rotated outwards; hence, this character is coded as ordered. Callichthyids lack cheek plates and are coded as unknown (?). *Astroblepus, Lithogenes*, *Delturus*, and *Upsilodus* lack true canal plates, but there is an ossified tube denoting the position of the canal plate and allowing the number of plates between the opercle and where the canal plate would be to be counted (see 82 above).

Schaefer (1986, 1987, 1988) describes a bone in *Astroblepus* of unknown homology. Schaefer (1988) suggests that the bone, based on positional homology, is an interopercle that lacks a ligamentous contact with the angulo-articular. However, the position of the bone is ventral rather than anterior to the opercle and is lateral rather than on the same plane as (or slightly mesial to) the opercle, as is the interopercle in other catfishes (Fig. 15A). *Lithogenes* lacks plates on the anterior half of the body except for a large, odontode-bearing plate in the same area as the putative interopercle of the Astroblepidae. *Lithogenes* does have an interoperculo-mandibular ligament and a bone within it that is possibly homologous to the interopercle (see 73 above). Given that both a cheek plate similar to that of *Astroblepus* and an interopercle are present in *Lithogenes* and that the cheek plate in *Astroblepus* is not positionally or operationally homologous to the interopercle of other catfishes, the cheek plate of *Astroblepus* is not the interopercle and is coded here as the presence of a single plate between the opercle and the area where an ossified tube denotes the area of the canal plate.

Infraorbitals

Infraorbitals are numbered in loricariids starting posteriorly with IO6, because most loricariids have six infraorbital canal plates; however, some lack an IO1 and some have infraorbitals anterior to IO1; therefore, IO0 or lower is possible.

89. IO6: (0) forms only the posteroventral corner of the orbit; (1) forms entire ventral border of orbit. CI = 0.50.

In *Astroblepus, Lithogenes*, and most loricariids, the posteriormost canal plate (IO6) forms only a small portion of the posteroventral corner of the orbit with much of the ventral border formed by IO5 (state 0). In *Lasiancistrus s.s* and *Panaque nigrolineatus* (Peters), IO6 forms the entire ventral border of the orbit (state 1). The infraorbital series in callichthyids is restricted to just two plates (Reis, 1998), neither of which forms the entire ventral border of the orbit; hence, callichthyids were coded as state 0.

90. IO4: (0) absent; (1) contacts orbit through much of its posterior edge; (2) contact with orbit slight or absent. CI = 0.40.

In callichthyids, a plate homologous to IO4 in *Astroblepus, Lithogenes* and loricariids is likely absent (state 0; Reis, 1998). In most loricariids, IO4 normally forms the anterior border of the orbit (state 1). In *Astroblepus, Lithogenes*, some members of the *H. emarginatus* group, *Leporacanthicus*, and *Panaque nigrolineatus*, IO4 is either completely or partially separated from the orbit and forms little or no part of the border of the orbit (state 2).

91. Number of infraorbitals (ordered): (0) two; (1) five to six; (2) seven to ten. CI = 0.30.

Callichthyids have two infraorbital canal plates (state 0), while most loricariids have five or six (state 1). Seven to ten plates are found in *Delturus*, *Baryancistrus* Rapp Py-Daniel, some *Cordylancistrus* Isbrücker, some *Dekeyseria scaphirhyncha*, *Exastilithoxus fimbriatus*, the *H. emarginatus* group, *H. albopunctatus* (Regan), *H. francisci*, *Leporacanthicus*, *Loricariichthys*, *Megalancistrus*, some *Panaque*, *Peckoltia*, *Pseudacanthicus*, *Pseudancistrus barbatus* (Valenciennes), most *Pterygoplichthys*, and some *Spectracanthicus punctatissimus* (state 2).

Lateral line

92. Lateral line: (0) does not continue beyond hypural plate: (1) continues into the elongated plate covering base of the caudal rays. CI = 0.17.

In callichthyids, *Astroblepus*, and most loricariids, the lateral line does not continue beyond the hypural plate (state 0). In *Lithogenes*, *Acanthicus*, *Leporacanthicus*, the Loricariinae, most of the *H. emarginatus* group, and *Peckoltia ucayalensis*, the lateral line continues into the elongate plate posterior to the hypural plate, covering the insertion of the caudal-fin rays (state 1).

CRANIUM

Baudelot's ligament

93. Ridge formed by Baudelot's ligament: (0) does not form more than a slightly rounded ridge; (1) forms a shelf. CI = 0.33.

In most callichthyids, *Astroblepus, Lithogenes*, *Delturus*, *Lithoxus*, and *Upsilodus*, Baudelot's ligament forms a slight, rounded, ossified ridge (state 0). In most loricariids it forms a distinct wall that varies from short to very tall (state 1).

Frontal

94. Contact between frontal and orbit: (0) present; (1) absent. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the frontal forms the dorsal border of the orbit (state 0). In the Hypostomini, most *Lasiancistrus s.s.* (some *L. maracaiboensis* Schultz are polymorphic), *Panaque*, *Peckoltia*, the Pterygoplichthini, the Rhinelepini, and *Scobinancistrus*, the frontal is separated from the orbit by a small plate (state 1).

Lateral ethmoid

95. Shape of lateral ethmoid: (0) square to triangular; (1) triangular with ventrolateral corner greatly expanded. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the lateral ethmoid is roughly rectangular to triangular (state 0). In some hypoptopomatines, the posterolateral corner of the lateral ethmoid is greatly expanded (state 1).

96. Nasal capsule: (0) completely encased ventrally by the lateral ethmoid; (1) open ventrally; (2) anterior to the lateral ethmoid. CI = 0.67.

In callichthyids, *Lithogenes*, *Delturus*, the Hypostominae, the Loricariinae, *Neoplecostomus*, and *Upsilodus*, the nasal capsule is completely supported below by the lateral ethmoid (state 0; Fig. 20A, B, D). In the Hypoptopomatinae and most of the Neoplecostominae, the anterolateral part of the nasal capsule is not supported by the lateral ethmoid (state 1; Fig. 20C). In *Astroblepus* (and also most other catfishes), the naris is located anterior to the lateral ethmoid and the nasal capsule is formed by the palatine (state 2).

97. Ridge on lateral ethmoid: (0) absent; (1) rounded or moderately tall; (2) tall. CI = 0.09.

In callichthyids, *Astroblepus*, *Hypostomus emarginatus* 1, and *Otocinclus*, the lateral ethmoid lacks a ridge ventrally for contact with the metapterygoid (state 0). Basally in loricariids, the ridge is generally present as short to moderately tall (state 1). In *Lithogenes,* several taxa of the Ancistrini, some *Hypostomus*, loricariines, neoplecostomines, *Schizolecis*, and *Upsilodus*, it is very tall (state 2).

98. Pouch on ventral surface of lateral ethmoid: (0) absent; (1) present. CI = 0.09.

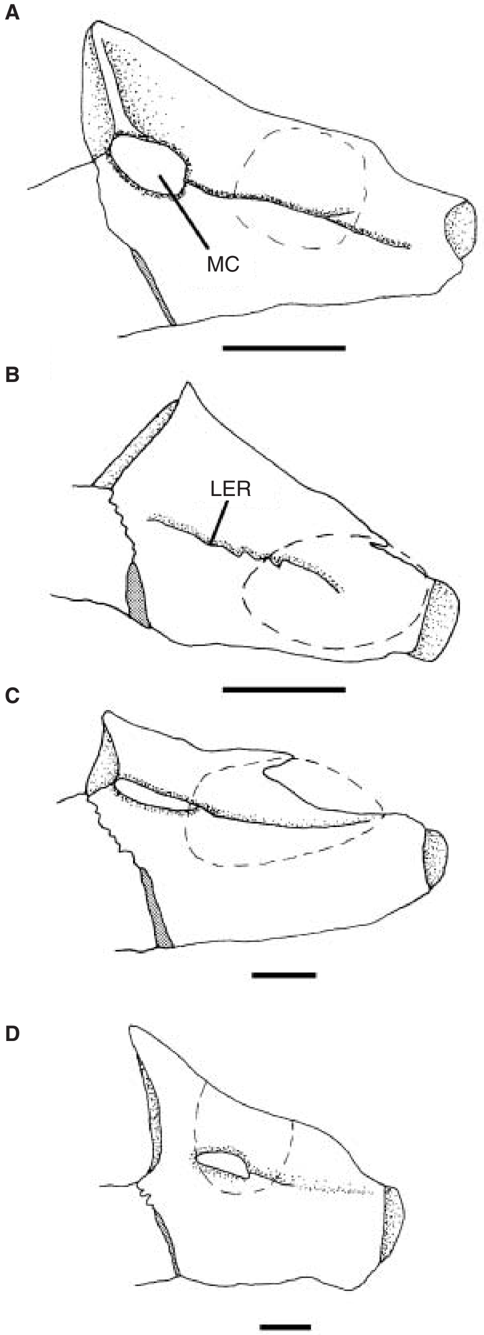

Figure 20. Lateral ethmoid, right side, ventral view. A, *Chaetostoma pearsei*, INHS 345889. B, *Delturus anguilicauda*, USNM 318209. C, *Hemipsilichthys* sp., USNM 320377. D, *Hypostomus unicolor*, USNM 319355. Scale bars = 1 mm. Shaded area is cartilage. Dashed line indicates the extent of the nasal capsule.

In callichthyids, *Astroblepus*, and most loricariids, the lateral ethmoid is flat posteriorly or else just slightly concave (state 0; Fig. 20B–D). In *Lithogenes,* several taxa of the Ancistrini, *Delturus*, some hypoptopomatines, *Hypostomus albopunctatus*, the Loricariini, neoplecostomines, and *Upsilodus*, the posterolateral corner of the lateral ethmoid is deeply concave such that the posterolateral edge appears as a ridge and a deep pouch is formed (state 1; Fig. 20A).

99. Posterior contact with metapterygoid: (0) contacting posterior margin of lateral ethmoid; (1) separated from posterior margin of lateral ethmoid. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there is either a condyle on the posterior margin of the lateral ethmoid connecting it to the metapterygoid, or the condyle is absent and they are aligned (state 0; Fig. 20A–C). In the *H. emarginatus* group, *Panaque*, *Pterygoplichthys multiradiatus*, *Peckoltia ucayalensis*, the Rhinelepini (except *Pseudorinelepis*), and *Scobinancistrus*, contact is shifted anteriorly (state 1; Fig. 20D).

Mesethmoid

100. Mesethmoid disk (ordered): (0) absent; (1) reduced; (2) developed. CI = 0.33.

In callichthyids, *Lithogenes,* and *Exastilithoxus*, the mesethmoid lacks a disk ventrally at its distal end (state 0). In *Astroblepus, Lithogenes*, *Crossoloricaria venezuelae*, and *Lithoxus*, the disk is present, but small (state 1); and in all other loricariids, the disk is large (state 2). It is hypothesized that the disk became larger through evolution; hence, this character is coded as ordered.

101. Mesethmoid disk, relative placement: (?) disk absent; (0) anterior to main body of mesethmoid; (1) extends beyond anterior margin of main body. CI = 0.20.

In *Astroblepus, Lithogenes* and most loricariids, the main body of the mesethmoid extends anterior to the mesethmoid disk (state 0). In *Ancistrus*, *Hemiancistrus megacephalus*, *Hypancistrus*, *Leporacanthicus*, *Lithoxus*, *Megalancistrus*, *Panaque*, *Parancistrus*, *Peckoltia*, *Pseudacanthicus* and *Spectracanthicus*, the mesethmoid disk extends beyond the anterior margin of the main body of the mesethmoid such that it is visible when viewed from above (state 1).

102. Mesethmoid flares anteriorly: (0) no; (1) yes. CI = 0.25.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the mesethmoid does not flare at its anterior edge (state 0). In the *Chaetostoma* group, *Dekeyseria scaphirhyncha*, *Hemipsilichthys nudulus*, and *H. splendens*, it flares widely anterior to the mesethmoid disk and the anterior margin of the disk does not contact the anterior margin of the main body of the mesethmoid (state 1) (see 103).

103. Mesethmoid anterior edge serrate: (0) absent; (1) present. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the anterior tip of the mesethmoid is smooth and either not widened or rounded anteriorly (state 0). In *Crossoloricaria*, *Harttia*, hypoptopomatines, and *Lamontichthys*, the mesethmoid flares out laterally at its tip, and the anterior edge is straight, but serrate (state 1).

104. Mesethmoid continued as a long blade anterior to disk (or well beyond the jaws in species without a disk): (0) no; (1) yes. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the tip of the mesethmoid does not form an elongate blade (state 0). In *Sturisoma* and *Sturisomatichthys*, the mesethmoid is greatly extended beyond the mesethmoid disk and forms a blade (state 1).

Nasal

105. Size of nasal: (0) very thin; (1) elongate but wide; (2) very large, almost square. CI = 0.22.

In callichthyids, *Astroblepus, Lithogenes*, *Acanthicus*, the *Chaetostoma* group, *Hemiancistrus megacephalus*, and *Pseudancistrus*, the nasal is very thin, not much wider than the segment of the latero-sensory canal passing through it (state 0). In most loricariids, the nasal is elongate, but it is widened such that it is wider than the canal (state 1). In *Ancistrus*, *Hypoptopoma*, *Nannoptopoma*, *Otocinclus*, some *Pterygoplichthys*, and the Rhinelepini, the nasal is very wide and almost square (state 2).

Parasphenoid

106. Parasphenoid on orbitosphenoid: (0) narrow, tall; (1) wide, slightly raised to flat. CI = 0.25.

In *Corydoras*, *Astroblepus, Lithogenes*, and most loricariids, the parasphenoid forms a narrow, tall ridge less than a fifth the width of the basioccipital. (state 0) (Armbruster, 1998c). In *Dianema*, *Hoplosternum*, *Lithoxus bovallii* (Regan), some loricariines, and the Rhinelepini, it is very wide, nearly half or greater than the width of the basioccipital, and is only slightly raised (state 1).

Pterotic-supracleithrum

107. Pterotic-supracleithrum expanded anteroposteriorly: (0) no; (1) yes. CI = 0.25.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the pterotic-supracleithrum is trapezoidal (108: 1) or oval with the anteroposterior axis shorter than the dorsoventral axis (state 0). In *Acanthicus*, *Panaque nigrolineatus*, and *Megalancistrus*, the pterotic-supracleithrum is oval with the anteroposterior axis longer than the dorsoventral axis (state 1).

108. Shape of pterotic-supracleithrum: (0) square to oval, widest medially; (1) trapezoidal, widest at ventral margin. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the pterotic-supracleithrum is oval to square and is widest medially (state 0). In the Loricariini it is roughly trapezoidal and widest ventrally (state 1).

109. Perforations in pterotic-supracleithrum: (0) many, small; (1) very large; (2) complex; (3) only a few, large perforations. CI = 0.60.

In most loricariids, the pterotic-supracleithrum is perforated with numerous small foramina (state 0). In *Acanthicus*, *Megalancistrus*, *Parancistrus*, and *Pseudacanthicus*, the perforations are very large (state 1). In most hypoptopomatines (except *Hypoptopoma*), the perforations are complex with the ventral foramina comparatively large and oval (state 2; see Schaefer, 1991). Callichthyids have only a few (1–4), large perforations (state 3).

110. Anterior process of pterotic-supracleithrum: (0) absent; (1) present. CI = 0.14.

In callichthyids, *Delturus*, some hypoptopomatines, *Ixinandria*, some neoplecostomines, *Rhinelepis*, *Rineloricaria*, and *Upsilodus*, the ventral margin of the pterotic-supracleithrum is straight and lacks an anterior process upon which the dilatator operculi muscle attaches (state 0). In *Lithogenes, Hemipsilichthys bahianus*, *Hemipsilichthys* sp., most of the Hypostominae (except *Rhinelepis*), *Kronichthys*, some of the Loricariinae, *Hisonotus*, *Parotocinclus*, and *Schizolecis*, there is a process extending anteroventrally from the pterotic-supracleithrum that is the origin of the dilatator operculi (state 1; Fig. 21). Schaefer & Lauder, 1986).

111. Anterior process of pterotic-supracleithrum separated mesially from main body, connected by a strut (ordered): (0) process absent to just slightly deflected; (1) process deflected with small gap; (2) gap large. CI = 0.13.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the anterior process of the pterotic-supracleithrum is (a) absent, (b) flush with the main body, or (c) slightly deflected mesially (state 0; Fig. 21A). In some of the Ancistrini, *Harttia*, most of the Hypostomini, most of the Pterygoplichthini, and *Schizolecis*, the process is deflected mesially such that there is a gap between the main body of the pterotic-supracleithrum and the process into which a sharp probe can be inserted (state 1; Fig. 21B). In most of the Ancistrini, the gap is very large with a strut between the process

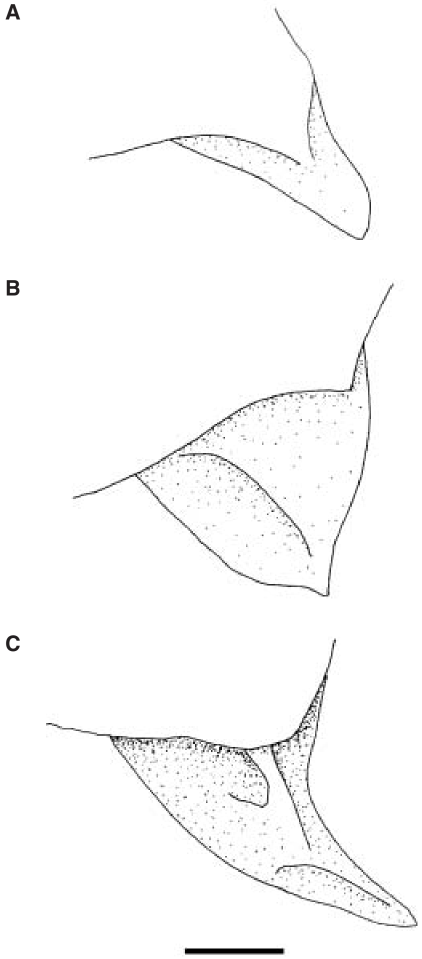

Figure 21. Anterior process of pterotic-supracleithrum, right side, dorsolateral view. A, *Hypostomus unicolor*, FMNH 101120. B, *Pseudacanthicus leopardus*, FMNH 95554. C, *Panaque maccus*, INHS 29906. Scale bar = 1 mm.

and the main body of the pterotic-supracleithrum and the dilatator operculi attaches laterally (state 2; Fig. 21C). This character appears to be related to an increase in evertibility of cheek odontodes. It is hypothesized that this character evolved by increasing the deflection of the process in response to increased reliance on the evertible cheek odontodes. By attaching the dilatator operculi laterally, the cheek plates could be better everted; hence, this character is coded as ordered. Schaefer & Lauder, 1986).

112. Forward extent of anterior process: (0) process absent or less than halfway through orbit; (1) halfway through the orbit or greater. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the anterior process of the pterotic-supracleithrum is either absent, or short (passing just anterior to the posterior margin of the orbit) (state 0). In several taxa of the Ancistrini, *Hypostomus*, and the *Hemiancistrus annectens* group, the process is longer and passes beyond halfway through the orbit (state 1).

113. Bifurcation of anterior process of pterotic-supracleithrum: (0) process absent or pointed; (1) present. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the anterior process of the pterotic-supracleithrum is either absent or pointed (state 0). In *Lasiancistrus* and *Parancistrus*, it bifurcates anteriorly such that it has two points (state 1).

114. Strut of the pterotic-supracleithrum directed ventrally so that it is visible from below: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the anterior process of the pterotic-supracleithrum is either absent or simple when viewed from below (state 0; Fig. 22A). In *Lasiancistrus s.s.* (*Lasiancistrus* sp. and *L. maracaiboensis*), there is a posteriorly directed strut leading from the process to the main body which is visible from below and which causes the dilatator operculi muscle chamber to be open posteriorly (state 1; Fig. 22B; PTS). Based on Schaefer (1986).

115. Dorsomesial process on pterotic-supracleithrum: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the pterotic-supracleithrum is fairly smooth mesially and does not have a dorsomesial process (state 0). In *Delturus* and *Upsilodus*, there is a long, thin, laminar process that attaches just ventral to where the hyomandibula contacts the pterotic-supracleithrum; the process runs along the anterior margin and ends well dorsal of the ventral margin; the dilatator operculi lies between the process and the main body (state 1). The process in *Delturus* and *Upsilodus* is in no way similar to that of 110: 1.

Sphenotic

116. Sphenotic: (0) with or without a thin ventral process; (1) ventral process wide, at least half as wide as main body of sphenotic. CI = 0.11.

In callichthyids, *Astroblepus*, and most loricariids, the sphenotic is either round, or round with a thin ventral process along the posterior margin of the orbit. The process is less than one quarter the width of the main body of the sphenotic (state 0; Fig. 23B, C). In *Lithogenes*, some *Ancistrus*, *Cordylancistrus*, *Crossoloricaria* sp., *Dolichancistrus* Isbrücker, *Leptoancistrus*, the *Lithoxus* group, *Loricariichthys*, *Parancistrus*, *Pterygoplichthys punctatus*, and *Neoplecostomus*, the process is at least half as wide (state 1; Fig. 23A).

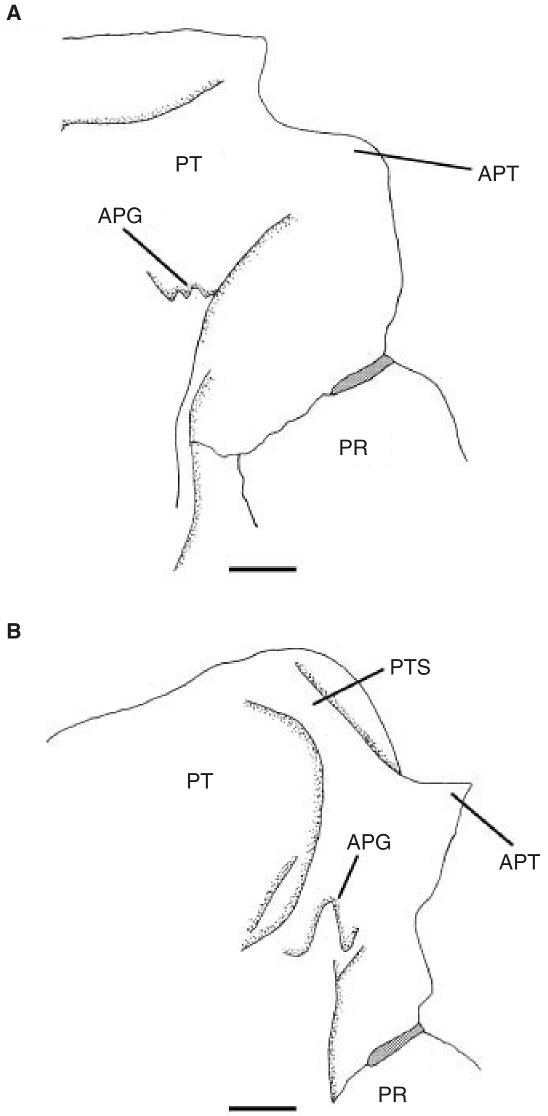

Figure 22. Anterior process of the pterotic-supracleithrum, right side, ventral view. A, *Ancistrus pirareta*, UMMZ 206085. B, *Lasiancistrus maracaiboensis*, INHS 60465. Scale bars = 1 mm. Shaded area is cartilage.

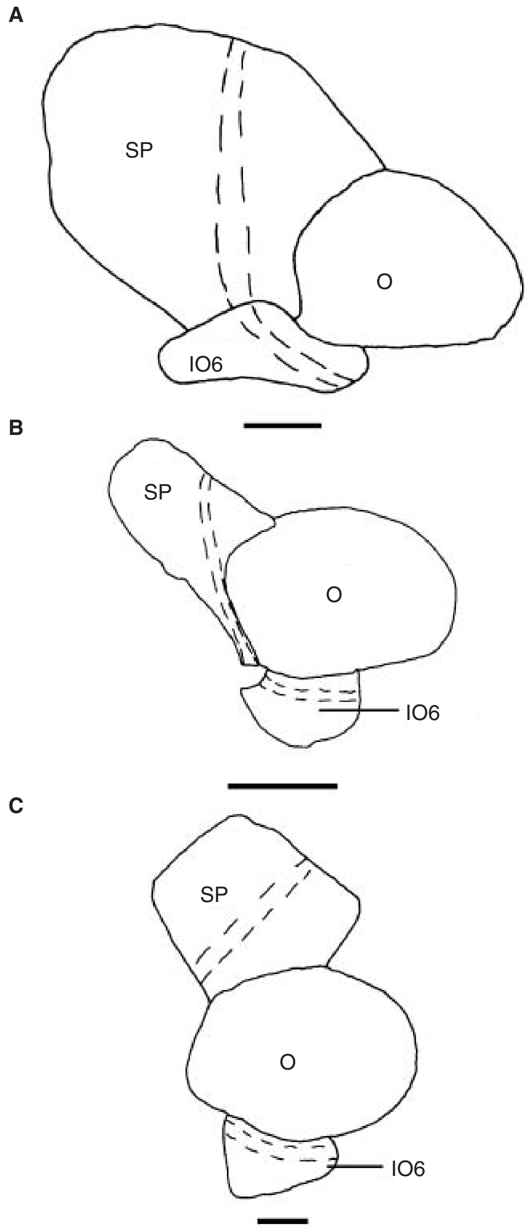

Figure 23. Sphenotic, right side, dorsolateral view. A, *Ancistrus pirareta*, UMMZ 206085. B, *Chaetostoma anomala*, INHS 69496. C, *Panaque albomaculatus*, FMNH 96951. Scale bars = 1 mm. Drawings sized such that the lengths of the orbits are the same.

117. Sphenotic, external contact with posteriormost infraorbital: (0) present; (1) absent. CI = 0.22.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the sphenotic has an external contact with the posteriormost infraorbital (state 0, Fig. 23A, B). In most *Kronichthys*, *Lasiancistrus s.s.*, *Lithoxancistrus*, *Megalancistrus*, *Panaque*, *Peckoltia* sp. 2, and *Pseudancistrus*, it does not (state 1, Fig. 23C).

Supraoccipital

118. Supraoccipital crest: (0) absent or broad and rounded; (1) tall and narrow. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there is either no crest on the supraoccipital or it is broad and rounded (state 0). In *Leporacanthicus, Pterygoplichthys gibbiceps* (Kner), and *P. lituratus* (Kner), the crest is tall and narrow (state 1; see Weber, 1992; Page, Armbruster & Sabaj, 1996).

VERTEBRAL COLUMN AND RIBS

Centra

119. Anteriorly directed transverse processes on eighth vertebra: (0) absent or short and broad; (1) long and pointed, passing between capitulum and tuberculum of rib of sixth vertebral centrum. CI = 0.17.

In *Corydoras*, *Astroblepus, Lithogenes*, and most loricariids, the eighth vertebral centrum either lacks anteriorly directed transverse processes or the transverse processes are short and broad (state 0). In all of the Hypostominae except *Acanthicus*, the *Chaetostoma* group, *Dekeyseria scaphirhyncha*, *Leporacanthicus*, and the *Lithoxus* group, the eighth vertebral centrum has long, pointed transverse processes that pass between the capitulum and tuberculum of the rib of the sixth vertebral centrum (state 1).

120. Number of vertebrae from first normal neural spine behind dorsal fin to spine under preadipose plate: (?) adipose fin and preadipose plate absent; (0) three to eight; (1) nine and above. CI = 0.67.

Species without adipose fins or preadipose plates are coded as unknown (?). The number of vertebrae between the dorsal and adipose fins is generally low in most loricariids (3–8; state 1). In callichthyids, *Astroblepus, Lithogenes*, some *Hypostomus*, and *Isbrueckerichthys duseni* (Miranda Ribeiro), there are more than nine vertebrae from the first normal neural spine posterior to the dorsal fin (loricariids and *Astroblepus, Lithogenes* have bifid neural spines below the dorsal fin) up to and including the vertebra with its neural spine below the preadipose plate (state 2). In *Astroblepus*, the adipose fin is long and fleshy, and an external view would suggest that there are no bony elements; however, some *Astroblepus* have a small, weak, V-shaped structure located posteriorly within the fleshy adipose fin that appears to be homologous to the adipose fin-spine in callichthyids and loricariids. The spine is not always present and counts were based on those individuals that possess it. In those species with more than one median, preadipose plate, counts were taken to the vertebra below the posteriormost plate. In callichthyids, bifid neural spines are absent, so counts were made from the first centrum posterior to the dorsal fin.

121. Number of vertebrae from first normal neural spine behind dorsal fin up to, but not including, hypural plate (ordered): (0) 16–20; (1) 12–15; (2) 8–11. CI = 0.28.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the number of vertebrae from the first normal neural spine behind dorsal fin up to, but not including, the hypural plate is variable. In *Astroblepus, Lithogenes*, some *Hypostomus*, *Isbrueckerichthys duseni*, loricariines, and *Upsilodus*, there are 16–20. In callichthyids and most loricariids, there are 12–15 (state 1). In most of the Ancistrini, *Delturus*, *Hemipsilichthys nudulus*, some *Hypostomus*, *Pseudorinelepis*, *Pterygoplichthys*, and *Rhinelepis*, there are 8–11. This character was coded as ordered.

Haemal spines

122. Bifid haemal spines: (0) absent; (1) present. CI = 0.25.

In callichthyids, *Delturus*, *Hemipsilichthys nudulus*, *H. splendens*, most hypostomines, and *Upsilodus*, there are no bifid haemal spines (state 0). In *Astroblepus, Lithogenes*, *Acanthicus*, *Corymbophanes*, *Dolichancistrus*, hypoptopomatines, the *Lithoxus* group, loricariines, most neoplecostomines, and *Pogonopoma*, there are one to several centra above (and sometimes behind) the anal fin with bifid haemal spines (state 1). Based on Schaefer (1986, 1987).

Hypurals

123. Hypurals: (0) two halves same length; (1) lower half longer than upper. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and loricariids, hypurals 1 & 2 and hypurals 3 & 4 are fused to one another, and the lower and upper halves are fused to the last vertebra and form the hypural plate (Schaefer, 1986, 1987). In callichthyids, *Astroblepus, Lithogenes*, *Delturus*, hypoptopomatines, loricariines, neoplecostomines, and *Upsilodus*, the upper and lower lobes of the hypural plate are of the same length (state 0; Fig. 24A). In hypostomines, the lower lobe is longer than the upper lobe (state 1; Fig. 24B). Based on Schaefer (1986, 1987).

124. Posterior margin of the hypural plate: (0) straight, or straight but offset; (1) a posteriorly directed point. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterior margin of the hypural plate is straight, or straight but offset as in 123-1 (state 0). In loricariines, the posterior margins of the upper and lower lobes of the hypural plate are angled such that they form a posteriorly directed point (state 1; Schaefer, 1986, 1987).

Neural spines

125. First neural spine, positioning: (0) below first dorsal-fin pterygiophore; (1) in front of first dorsal-fin pterygiophore. CI = 0.43.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there is an occasional, small anterior contact ventrally between the first neural spine and first dorsal-fin pterygiophore (state 0). In *Dolichancistrus*, *Dekeyseria*, hypoptopomatines, the *Lithoxus* group,

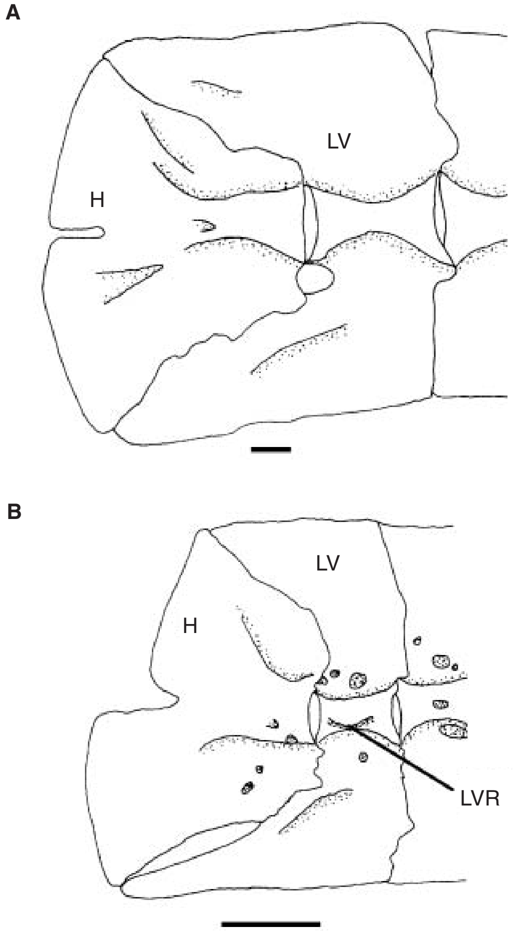

Figure 24. Posterior vertebrae and hypurals, right side, lateral view. A, *Neoplecostomus microps*, MNRJ 13555. B, *Pseudancistrus* sp., USNM 226181. Scale bars = 1 mm.

loricariines, neoplecostomines, some *Hypostomus panamensis*, and some *Panaque maccus* Schaefer and Stewart, the first neural spine is tall and located anterior to the first dorsal-fin pterygiophore, providing a large anterior contact between them (state 1).

126. Perforations in bifid neural spines: (0) absent; (1) present. CI = 0.20.

In callichthyids, *Astroblepus*, and most loricariids, the bifid neural spines under the dorsal fin are not perforated except at the level of the spinal cord (state 0). In *Lithogenes,* most hypoptopomatines, most neoplecostomines, some *Pseudancistrus*, *Scobinancistrus*, and *Upsilodus*, some of them are perforated above it (state 1).

127. Trifid neural spines posterior to dorsal fin: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no trifid neural spines posterior to the dorsal fin, or there may be one under the last dorsal-fin ray (state 0). In the Loricariinae, all of the centra posterior to the dorsal fin have lateral, accessory neural spines that are not as wide as the central spine, making the spines trifid (state 1).

Ribs

128. Distal margin of the rib of the sixth vertebral centrum: (0) about same width as rest of rib; (1) flared out distally so that the tip is much wider than the shaft. CI = 0.08.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the rib of the sixth vertebral centrum is of approximately equal width along its entire length, flaring slightly at the distal end (state 0; Fig. 25B–D). In *Acanthicus*, *Corymbophanes kaiei* Armbruster and Sabaj, *Delturus*, *Hemipsilichthys cameroni*, *Lasiancistrus s.s.*, *Lithoxus*, *Neblinichthys*, *Neoplecostomus*, *Otocinclus*, *Parotocinclus*, some *Pseudancistrus*, and *Upsilodus*, the distal tip of the rib is approximately 1.5 or more times wider than the shaft (state 1; Fig. 25A).

129. Ribs beyond enlarged rib of the sixth vertebral centrum: (0) thin; (1) absent; (2) thick. CI = 0.14.

In callichthyids and most loricariids, the ribs are present and very thin (state 0). In *Hypoptopoma* and the Rhinelepini, ribs are absent posterior to the enlarged rib of the sixth vertebral centrum (state 1; Armbruster, 1998b). In *Astroblepus, Lithogenes*, most of the Ancistrini, *Crossoloricaria*, *Delturus*, *Hemipsilichthys nudulus*, *Pterygoplichthys punctatus*, *Upsilodus* the ribs are considerably widened (state 2).

Weberian complex centrum

130. Weberian complex centrum: (0) relatively short, square; (1) elongated, rectangular. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the complex centrum is short and almost square (state 0; Fig. 25B–D). In *Acanthicus*, *Panaque nigrolineatus*, and *Megalancistrus*, it is elongated anteriorly to posteriorly and is at least twice as long as wide (state 1; Fig. 25A).

131. Distal margin of transverse process of Weberian complex centrum: (0) thin, about the same width distally as proximally or narrowing distally; (1) widened, flared distally. CI = 0.20.

In most callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the distal margin is either about the same width as the shaft or narrows to a point distally (state 0; Fig. 25B–D). In *Acanthicus*, most hypoptopomatines, *Megalancistrus*, and *Pogonopoma*, the distal margin is flared distally and much wider than the main shaft (state 1; Fig. 25A).

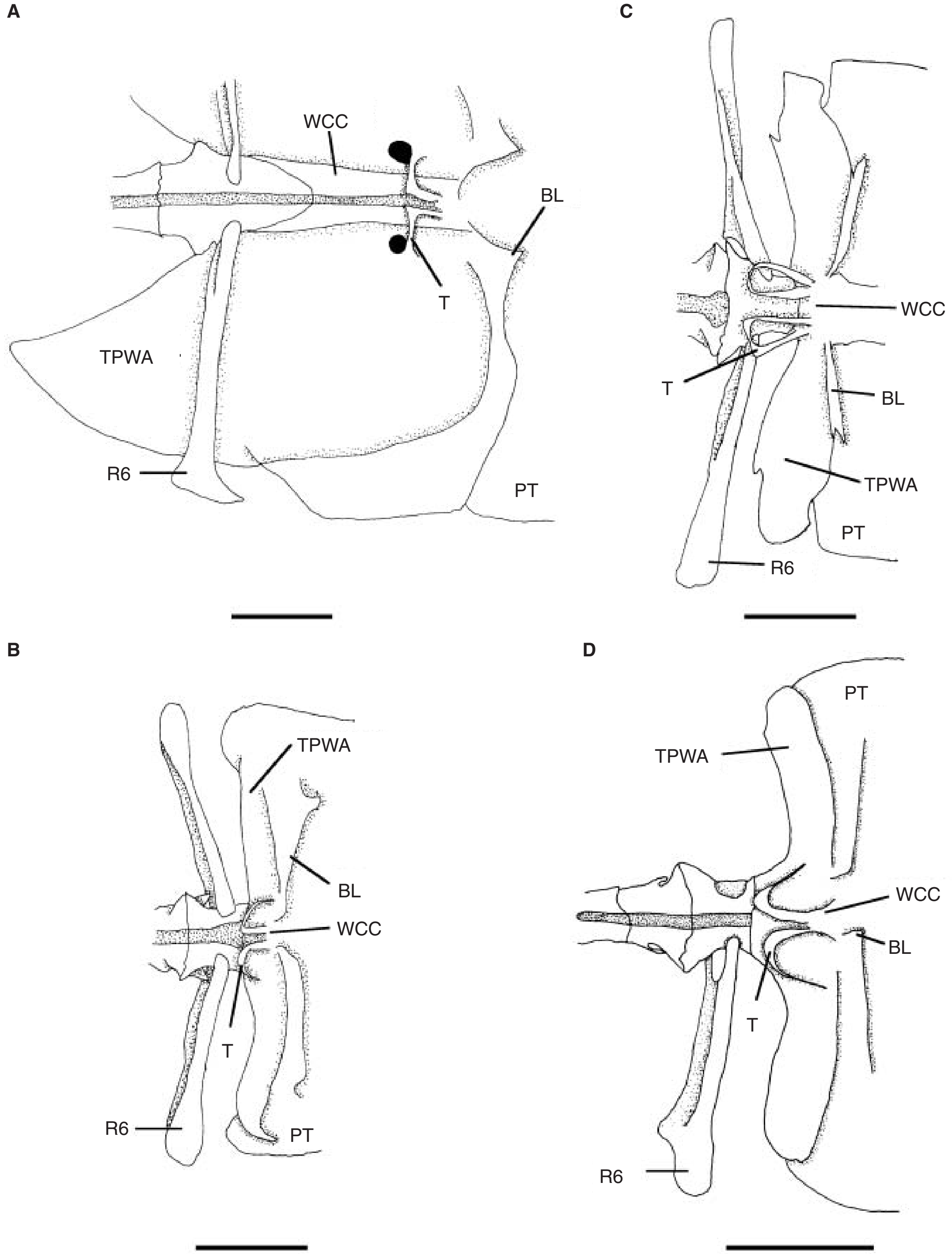

Figure 25. Weberian apparatus, ventral view. A, *Acanthicus hystrix* Spix and Agassiz, INHS 36803. B, *Hypostomus micromaculatus* Boeseman, ANSP 160774. C, *Pseudacanthicus leopardus*, FMNH 95554. D, *Hemiancistrus maracaiboensis*, EBRG 2855. Scale bars = 5 mm. In B, the transverse processes of the Weberian complex centrum (TPWA) appear to fuse into the pterotic-supracleithrum (PT) as is shown for the left (upper) side while the right (lower) side shows the TPWA as it appears after closer scrutiny.

132. Distal margin of transverse process of Weberian complex centrum: (0) wide or rounded; (1) pointed. CI = 0.23.

In callichthyids, *Astroblepus*, and most loricariids, the distal margin is wide or rounded (state 0; Fig. 25A, C, D). In *Lithogenes, Cordylancistrus*, most *Hypostomus*, *Loricariichthys*, most *Panaque*, some *Pterygoplichthys*, *Scobinancistrus*, some *Spectracanthicus punctatissimus*, *Sturisoma*, *Sturisomatichthys*, and *Upsilodus*, it is pointed (state 1; Fig. 25B).

133. Tip of transverse process of Weberian complex centrum: (0) clearly distinguishable from pterotic-supracleithrum: (1) anterior edge nearly indistinguishable from pterotic-supracleithrum. CI = 0.14.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the tip of the transverse process is clearly separated and distinguishable from the pterotic-supracleithrum (state 0; Fig. 25A, C, D). In most *Hypostomus*, *Peckoltia* sp. 1, *Peckoltia oligospila*, some of the *Hemiancistrus annectens* group, and *Pterygoplichthys etentaculatus* (Spix and Agassiz), the anterior edge of the tip is nearly indistinguishable from the pterotic-supracleithrum, with the two bones appearing to fuse (state 1; Fig. 25B). The appearance of fusion is caused by the presence of a ridge on the pterotic-supracleithrum. The anterior edge of the tip is flush with this ridge and tightly held to it, causing the two to be nearly indistinguishable. The only evidence of the separate nature of the two bones can be found in their quality: the transverse process is thin and laminar while the pterotic-supracleithrum is thick and more porous.

134. Transverse process of Weberian complex centrum: (0) not or only moderately perforated distally; (1) perforated distally with large foramina. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the transverse process is not or only moderately perforated distally (state 0). In some of the Ancistrini, most neoplecostomines, most hypoptopomatines, and some *Hypostomus*, the distal end is perforated with large foramina (state 1).

135. Tip of transverse processes of Weberian complex centrum: (0) at least partially contacting the pterotic-supracleithrum; (1) not contacting the pterotic-supracleithrum. CI = 0.21.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the distal tip at least partially contacts the pterotic-supracleithrum (state 0; Fig. 25B, D). In *Acanthicus*, *Chaetostoma sovichthys* Schultz, *Cordylancistrus*, *Corymbophanes andersoni* Eigenmann, some *Dekeyseria scaphirhyncha*, *Dolichancistrus*, *Delturus*, hypoptopomatines, *Leptoancistrus*, *Lithoxancistrus*, some loricariines, *Megalancistrus*, *Neblinichthys roraima*, neoplecostomines, *Pogonopoma*, *Pseudacanthicus*, *Rhinelepis*, and *Upsilodus*, the distal tip does not contact the pterotic-supracleithrum (state 1; Fig. 25A, C).

136. Lateral processes of tripus (LPT): (0) absent or short; (1) long. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the tripus of the Weberian apparatus forms an almost rectangular arch and may have short processes at the ventrolateral corners of the arch (state 0; Fig. 26A). In *Hypostomus cochliodon* Kner, *H. hondae*, and the *Panaque dentex* group, these lateral processes of the tripus are almost as long as the tripus is tall (Fig. 26B).

DORSAL AND ADIPOSE FINS

Adipose fin

137. Adipose fin: (0) present; (1) absent. CI = 0.09.

Presence or absence of the adipose fin is quite variable in loricarioids. In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, it is present (state 0). In *Acanthicus*, most hypoptopomatines, *Leptoancistrus*, loricariines, some neoplecostomines, and most of the Rhinelepini, it is absent (state 1).

138. Preadipose plates: (0) three or more; (1) 0–2. CI = 0.20.

In callichthyids, *Delturus*, *Hemipsilichthys nudulus*, *H. splendens*, *Leptoancistrus*, and *Upsilodus*, there are three or more median, unpaired plates (state 0, Fig. 27C). In loricariids, there is usually a single

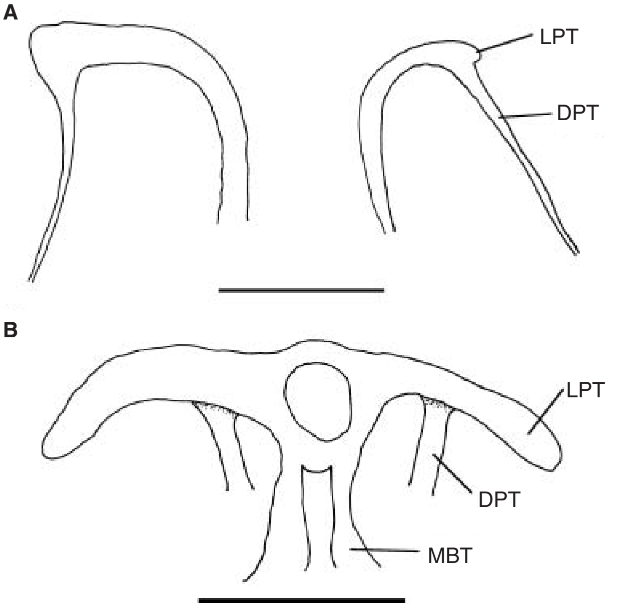

Figure 26. Tripus, antero-ventral view. A, *Hypostomus unicolor*, USNM 319355. B, *Panaque maccus*, INHS 29862. Scale bars = 1 mm.

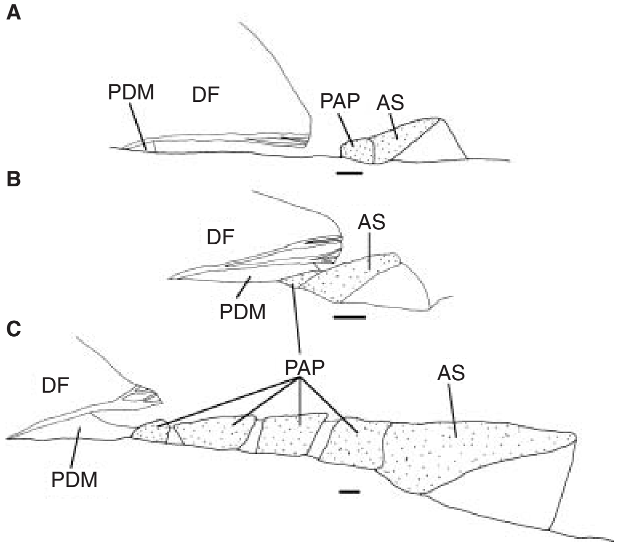

Figure 27. Adipose fin and preadipose plates, left side, lateral view. A, *Hypostomus panamensis*, INHS 36095. B, *Spectracanthicus murinus*, MZUSP 34279. C, *Delturus parahybae* Eigenmann and Eigenmann, FMNH 59734. Scale bars = 1 mm.

(rarely two) median, unpaired plate anterior to the adipose fin-spine or the plate is missing (state 1, Fig. 27A, B).

Connecting bone

139. Connecting bone: (0) absent; (1) a tendon; (2) ossified. CI = 1.00.

Most catfishes and *Hemipsilichthys nudulus* lack a bone or tendon attaching one of the anterior supporting bones of the dorsal fin to the large rib of the sixth vertebra (state 0). In callichthyids, there is a tendon that attaches the transverse process of the second dorsal-fin pterygiophore to the rib of the sixth vertebral centrum (state 1). In loricariids and *Astroblepus, Lithogenes* (and also in scoloplacids), the tendon is ossified and has been termed the 'connecting bone' by Bailey & Baskin (1976) (state 2; Fig. 28). In loricariids, the connecting bone may attach to either the second dorsal-fin pterygiophore or to the nuchal plate or to both (see 141).

140. Connecting bone/tendon: (?) absent; (0) flat; (1) cylindrical. CI = 1.00.

In callichthyids and most loricariids, the connecting bone or tendon is a flat, planar structure (state 0). In *Astroblepus, Lithogenes*, the connecting bone is cylindrical (state 1). Species without the connecting bone or tendon were coded as unknown (?).

141. Connecting bone, contact with nuchal plate: (0) none; (1) connects with the transverse process of the second dorsal-fin pterygiophore and/or the nuchal plate. CI = 0.17.

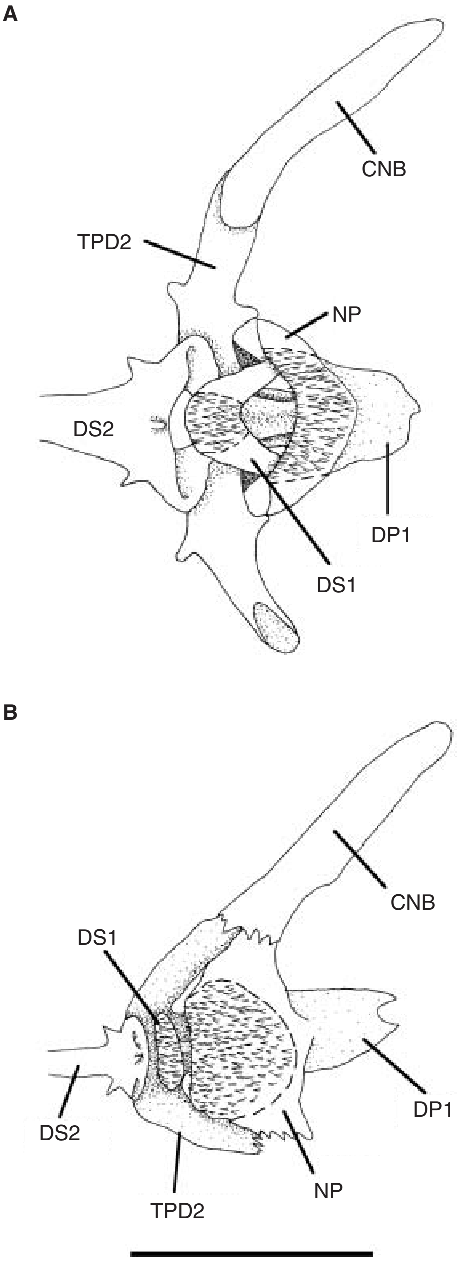

Figure 28. Locking mechanism of dorsal fin, dorsal view (left connecting bone shown). A, *Hypostomus unicolor*, USNM 319355. B, *Kronichthys* sp., MZUSP 27545. Scale bar = 5 mm. Dashed lines indicate the exposed areas of the dorsal-fin spinelet (DS1) and the nuchal plate (NP).

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the connecting bone or tendon originates at the transverse process of the second dorsal-fin pterygiophore (state 0; Fig. 28A). In some hypoptopomatines, most neoplecostomines, and some loricariines, the connecting bone has at least partial contact with the nuchal plate (state 1; Fig. 28B). Some loricariids, such as *Neoplecostomus*, lack contact of the connecting bone and the transverse process of the second dorsal-fin pterygiophore.

Dorsal fin

142. Number of dorsal-fin rays: (0) six or seven; (1) eight or more. CI = 0.25.

In most callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are either six or seven dorsal-fin rays (most loricariids have seven; state 0). An increase to eight or more has occurred several times, e.g. in the *Acanthicus* group, the *Chaetostoma* group, *Delturus*, and *Pterygoplichthys* (state 1).

143. Dorsal-fin membrane continues posteriorly: (0) for a short distance; (1) contacts the preadipose plate. CI = 0.25.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the dorsal-fin membrane continues for a short distance posterior to the base of the last dorsal-fin ray (state 0; Fig. 27A). In *Baryancistrus*, *Delturus*, *Parancistrus*, and *Spectracanthicus*, the membrane is expanded posteriorly and contacts the preadipose plate (state 1; Fig. 27B, C). In *Delturus*, the membrane contacts the anteriormost median preadipose plate only in adults.

Dorsal-fin pterygiophores

144. Chain-link of proximal dorsal spine to second dorsal-fin pterygiophore: (0) absent; (1) present. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the proximal end of the dorsal spine pivots on a dorsal condyle of the second dorsal-fin pterygiophore (state 0). In most of the Loricariinae examined (except *Harttia*), the second dorsal-fin pterygiophore forms a loop which passes through a foramen at the proximal end of the dorsal-fin spine linking the two structures together like a chain (state 1; Schaefer, 1986, 1987).

145. Number of dorsal-fin radial elements with transverse processes (ordered): (0) five to six; (1) one to four; (2) none. CI = 0.42.

In callichthyids, some hypoptopomatines, some *Kronichthys* sp. 1, most loricariines, and most *Pterygoplichthys*, there are five to six (state 0) dorsal-fin radial elements with transverse processes. In most loricariids there are one to four (state 1). In *Astroblepus, Lithogenes* and *Hemipsilichthys nudulus*, none of the radials have transverse processes (state 2). It is most parsimonious to assume that the number of radials with transverse processes decreased gradually; hence, this character is coded as ordered. Counts begin at the third radial. Based on Schaefer (1991).

Nuchal plate

146. Nuchal plate: (0) present; (1) absent. CI = 0.50.

In callichthyids and most loricariids, the nuchal plate is present and acts in the functioning of the dorsal-fin spine locking mechanism (state 0). In *Astroblepus, Lithogenes* and *Hemipsilichthys nudulus*, the nuchal plate has been lost (state 1).

147. Nuchal plate: (?) absent; (0) exposed; (1) covered entirely by skin or plates. CI = 0.25.

In callichthyids and most loricariids, the nuchal plate is exposed and supports odontodes (state 0; Fig. 28). In *Ancistrus* sp. 1, the *Chaetostoma* group, *Delturus*, *Exastilithoxus* sp., and *Upsilodus*, the nuchal plate is covered by lateral plates and thick skin and usually does not support odontodes except in some large adults (state 1). Species without nuchal plates are coded as unknown (?).

Spinelet

148. Spinelet: (0) V-shaped; (1) reduced and rectangular or absent. CI = 0.20.

In callichthyids and most loricariids (as well as most other catfishes), the first dorsal-fin spine is a short, V-shaped structure (often termed the spinelet, Fig. 28, DS1) in front of, and firmly attached to, the second, much longer, dorsal-fin spine (Fig. 28, DS2). The spinelet slips under the nuchal plate to lock the dorsal-fin spine in an upright position by friction (Alexander, 1962) (state 0; Fig. 28A). In some hypoptopomatines, many loricariines, most neoplecostomines, and *Upsilodus*, the spinelet is reduced to a rectangular, platelike structure and can no longer lock the spine into an upright position (Fig. 28B), and in *Astroblepus, Lithogenes*, some *Hemipsilichthys bahianus*, *Hemipsilichthys nudulus*, some hypoptopomatines, *Isbrueckerichthys*, and some loricariines, the spinelet is absent (state 1).

149. Spinelet: (?) absent; (0) exposed, covered with odontodes; (1) covered with skin. CI = 1.00.

In most loricariids and *Corydoras*, the spinelet is exposed and supports odontodes (state 0). In the *Chaetostoma* group, the spinelet is covered with skin and does not support odontodes or the odontodes do not pierce the skin except in the largest adults (state 1). Species without spinelets are coded as unknown (?).

Anal fin

150. Number of branched anal-fin rays (ordered): (0) six; (1) five; (2) four; (3) three; (4) zero. CI = 0.52.

In examined *Astroblepus* and *Lithogenes*, there are six branched anal-fin rays and one unbranched (state 0). Loricariids have a reduction in the number of branched rays with some of the Ancistrini, hypoptopomatines, loricariines, neoplecostomines, and the Rhinelepini having five (state 1), and most of the Hypostominae having four (state 2). In *Chaetostoma platyrhyncha* and *Spectracanthicus murinus*, there are three (state 3), and there are none in *Leptoancistrus* (state 4). Callichthyids, *Delturus*, and *Upsilodus* have five or six. *Hemipsilichthys nudulus* has three or four. It is most parsimonious to assume that the number of anal-fin rays has increased or decreased gradually; hence, this character is coded as ordered. *Leptoancistrus* retains two anal-fin pterygiophores, despite losing all anal-fin rays.

151. First anal-fin pterygiophore with a lateral ridge posterior to the widened anterior surface: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the first anal-fin pterygiophore has a wide anterior surface with a posterior pointing, flat blade (state 0; Fig. 29A). In *Neoplecostomus*, the blade has a strong, lateral ridge which forms a deep trough laterally (state 1; Fig. 29B).

PECTORAL GIRDLE

Adductor fossa

152. Adductor fossa: (0) incomplete; (1) complete. CI = 0.20.

In callichthyids, *Astroblepus, Lithogenes*, and loricariids, there is a fossa for the adductor ventralis muscle of the pectoral girdle that forms an oval ventrally. In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterior lip of the fossa terminates at the level of the contact between the coracoid and the cleithrum or just slightly anterior (state 0; Fig. 30B). In some *Hemipsilichthys*, *Isbrueckerichthys*, *Neoplecostomus*, *Pareiorhina* sp., *Schizolecis*, and *Upsilodus*, the posterior lip abuts the anterior lip, giving the impression of the fossa being displaced laterally (state 1; Fig. 30A).

153. Adductor fossa: (0) deep to midline; (1) nearly flat anteromesially. CI = 0.17.

In *Dianema*, *Hoplosternum*, and most loricariids, the adductor fossa of the pectoral girdle forms a cup and is deep to the midline (state 0). In *Corydoras*, *Astroblepus, Lithogenes*, *Lithoxus*, some loricariines, *Pareiorhina* sp., and *Rhinelepis*, the fossa is nearly flat anteromesially (state 1). Based on Armbruster (1998b).

154. Adductor fossa, exposure (ordered): (0) exposed; (1) only partially exposed; (2) completely covered in bone. CI = 0.67.

In *Astroblepus, Lithogenes*, and most loricariids, the adductor fossa of the pectoral girdle is exposed ventrally (state 0). In callichthyids and *Schizolecis* it is partially covered by bone, leaving only a small part exposed (state 1). In most of the Hypoptopomatinae it is completely encased in bone (state 2). It is hypothesized that this character evolved by the successive increase in the size of the shelf; hence, this

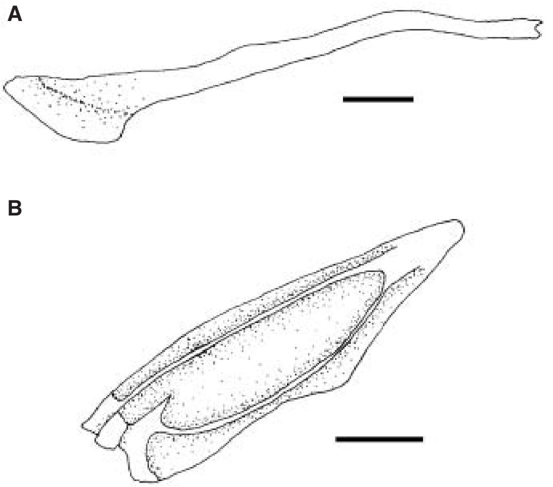

Figure 29. First anal-fin pterygiophore, right side, lateral view. A, *Hypostomus unicolor*, USNM 319355. B, *Neoplecostomus microps*, MNRJ 13555. Scale bars = 1 mm.

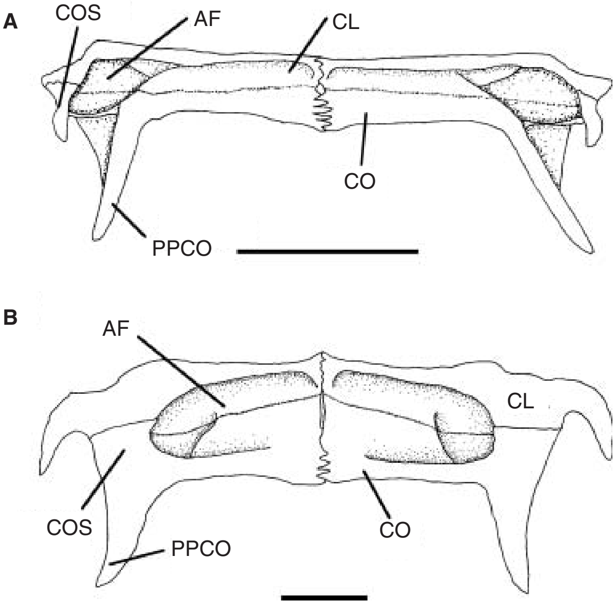

Figure 30. Pectoral girdle. ventral view. A, *Isbrueckerichthys duseni*, UMMZ 215262. B, *Pseudorinelepis genibarbis*, INHS 36938. Scale bars = 5 mm.

character is coded as ordered. Based on Schaefer (1991).

Cleithrum

155. Shape of cleithrum: (0) rectangular; (1) trapezoidal. CI = 0.25.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the cleithrum is roughly rectangular (state 0). In *Dekeyseria*, *Lithoxus*, the Loricariini, and *Rhinelepis*, the anterolateral margins of the cleithrum are angled mesially, making the cleithrum appear roughly trapezoidal (state 1) Based on Armbruster (1998b).

156. Shape of posterior margin of the exposed cleithrum: (0) mostly straight and tall; (1) tapers posteriorly to a point. CI = 0.06.

In callichthyids and most loricariids, the cleithrum has an exposed process that passes posterodorsally to the pectoral-fin insertion; it is nearly straight posteriorly and tall, roughly forming a rectangle (*Astroblepus, Lithogenes* are similar except that the process is not exposed; state 0). In several loricariids (most notably *Hypostomus*), the process is pointed posteriorly (state 1).

157. Shape of exposed cleithral process: (0) large; (1) reduced. CI = 0.13.

In callichthyids and most loricariids, the cleithral process described in 156 is exposed and the exposed part is large (state 0). In *Astroblepus, Lithogenes*, *Chaetostoma anomala* Regan, *Crossoloricaria* sp., *Dolichancistrus*, *Leptoancistrus*, the *Lithoxus* group, *Isbrueckerichthys*, *Neoplecostomus*, *Pareiorhina* sp., and *Upsilodus*, the exposed part is much reduced (state 1).

Coracoid

158. Posterior process of coracoid: (0) distal end much wider than shaft; (1) distal end about as wide as shaft; (2) elongated, thin, pointed. CI = 0.16.

The shape of the posterior process of the coracoid is variable in loricariids. In callichthyids, some hypoptopomatines, some *Hypostomus*, *Panaque*, *Parancistrus*, *Peckoltia*, the Pterygoplichthini, and *Sturisoma* the distal end is much wider than the shaft (state 0; Fig. 31C). In some of the Ancistrini, some *Hypostomus*, *Parotocinclus*, *Pogonopoma*, and *Rhinelepis*, it is about the same width (state 1; Fig. 31B). In *Astroblepus, Lithogenes*, most of the Ancistrini, *Delturus*, most loricariines, neoplecostomines, *Rhinelepis*, *Schizolecis*, and *Upsilodus*, the posterior process is pointed distally (state 2; Fig. 31A).

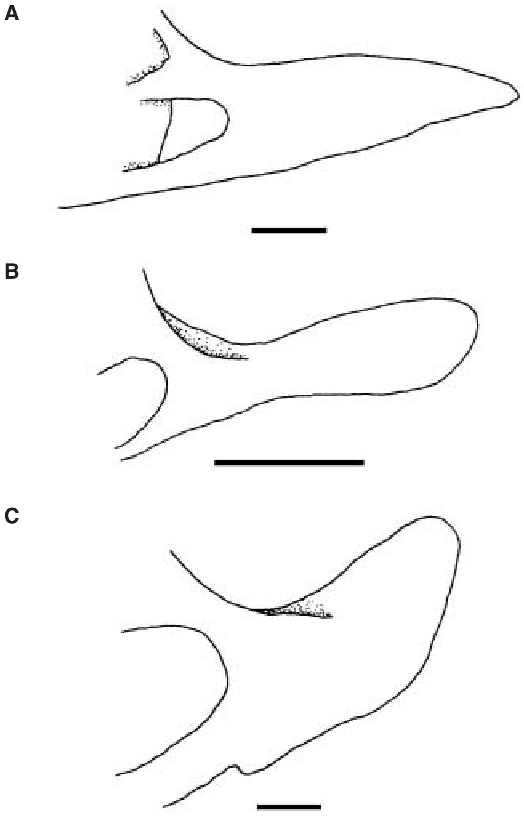

Figure 31. Posterior process of coracoid, right side, mesial view. A, *Lasiancistrus maracaiboensis*, INHS 60465. B, *Hypostomus cordovae*, UF 82322. C, *Hypostomus* cf. *plecostomus*, UF 77909. Scale bars = 1 mm.

159. Posterior process of coracoid: (0) short; (1) very elongate. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the posterior process is not particularly elongate (state 0). In *Acanthicus*, *Harttia*, and *Otocinclus*, it is extremely elongate (state 1).

160. Posterior section of coracoid: (0) angled upwards mesially, tall; (1) straight, short. CI = 0.17.

In callichthyids, and most loricariids, the coracoid forms part of the posterior wall of the pectoral girdle posteriorly and the contact between the coracoid and the cleithrum is angled dorsomesially and tall (state 0). In *Astroblepus, Lithogenes*, several Ancistrini, *Delturus*, most loricariines, neoplecostomines, *Pterygoplichthys punctatus*, *Rhinelepis*, *Schizolecis*, and *Upsilodus*, the posterior section of the coracoid is reduced with the contact with the cleithrum, being low and almost parallel with the ventral margin of the pectoral girdle (state 1).

161. Lateral strut of coracoid: (0) thin; (1) wide. CI = 0.13.

In *Corydoras*, *Astroblepus, Lithogenes*, and most loricariids, there is a thin, lateral strut on the ventral surface of the coracoid ventral to which the arrector ventralis runs (state 0; Fig. 30A). In *Dianema*, *Hoplosternum*, *Hemipsilichthys bahianus*, *Hemipsilichthys*?, hypoptopomatines, most loricariines, *Pogonopoma parahybae*, and *Pseudorinelepis* the coracoid strut is wide (state 1; Fig. 30B). Based on Armbruster (1998b).

162. Lateral strut of coracoid: (0) at least partially exposed, bearing odontodes; (1) covered in skin or plates, does not bear odontodes. CI = 0.10.

In most callichthyids, hypoptopomatines, some *Hypostomus*, some loricariines, *Peckoltia ucayalensis*, most *Pterygoplichthys*, and the Rhinelepini, the lateral strut supports at least some odontodes directly (state 0). In *Astroblepus, Lithogenes* and most loricariids, the lateral strut of the coracoid does not support odontodes and is covered either by skin or by bony plates (state 1). Based on Armbruster (1998b).

163. Passage of arrector ventralis through a channel: (0) present; (1) absent. CI = 0.13.

In callichthyids, *Lithogenes, Hemipsilichthys bahianus*, *Hemipsilichthys*?, hypoptopomatines, most loricariines, *Pogonopoma parahybae*, and *Pseudorinelepis*, the arrector ventralis passes through a channel in the coracoid strut (state 0; Fig. 32A). In *Astroblepus* and most loricariids, the arrector ventralis passes ventral to the coracoid strut and attaches onto the posterior condyle of the pectoral-fin spine (state 1; Fig. 32B, C). Based on Schaefer (1987, 1991) and Armbruster (1998b).

164. Space between posterior process of coracoid strut and posterior process of coracoid: (0) large; (1) absent to small. CI = 0.13.

In callichthyids, the *Chaetostoma* group, *Crossoloricaria*, *Delturus*, *Hemipsilichthys cameroni*, *Isbrueckerichthys*, *Lithoxancistrus*, the *Lithoxus* group, *Loricaria*, *Neoplecostomus*, *Sturisoma*, and *Upsilodus*, the space between the coracoid strut and the posterior process of the coracoid is much greater than the width of the strut (state 1; Fig. 32C). In *Astroblepus, Lithogenes* and most loricariids, the strut has a posterior nub that fuses with, touches, or is only slightly separated (less than the width of the strut) from the posterior process (state 0; Fig. 32A, B).

General

165. Suture of pectoral girdle: (0) strong; (1) weak or absent. CI = 0.33.

In callichthyids and most loricariids, the suture between the two halves of the pectoral girdle is very strong (state 0). In *Astroblepus, Lithogenes*, *Delturus*,

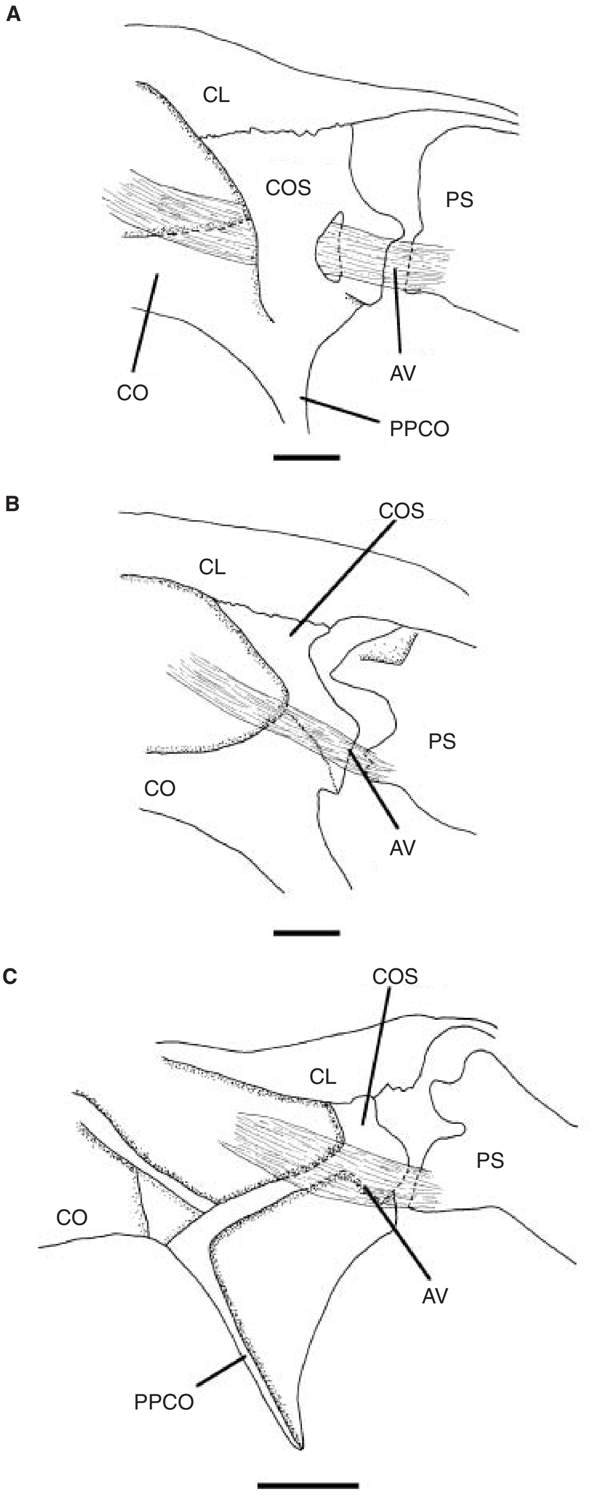

Figure 32. Coracoid strut, left side, ventral view. A, *Hemipsilichthys bahianus*, USNM 318203. B, *Hypostomus unicolor*, USNM 319355. C, *Neoplecostomus microps*, MNRJ 12802. Scale bars = 1 mm.

Pareiorhina sp., and *Upsilodus*, it is either weak or absent (state 1).

166. Pectoral-fin spines greatly elongated in males: (0) no; (1) yes. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the pectoral-fin spines are either not greatly elongated or are elongated in both sexes (state 0). In *Dolichancistrus* they are greatly elongated in males only (state 1; Schaefer, 1986).

PELVIC GIRDLE

The pelvic basipterygium normally consists of an anterolateral process (ALP), an anteromesial process (AMP), and a posterior process (PPP) on each side (Fig. 33).

Basipterygium: anterolateral processes

167. Anterolateral processes: (0) curved such that they meet or nearly meet at the midline. (1) slightly angled, do not converge at midline; (2) straight. CI = 0.11.

The shape of the anterolateral processes is variable. In callichthyids, *Lithogenes*, most of the Ancistrini, *Corymbophanes kaiei*, hypoptopomatines, some loricariines, most neoplecostomines, they are curved such that they meet or almost meet at the midline (state 0; Fig. 33D, E). In *Astroblepus*, some of the Ancistrini, *Corymbophanes andersoni*, *Delturus*, *Hemipsilichthys nudulus*, the Hypostomini, some loricariines, *Pseudorinelepis*, the Pterygoplichthini, *Rhinelepis*, and *Upsilodus*, they are slightly angled but do not converge at the midline (state 1; Fig. 33A, C, F). In *Cordylancistrus*, *Dekeyseria*, some loricariines, *Pogonopoma*, and *Pseudancistrus* sp., the processes are straight (state 2; Fig. 33B). In some groups, they are probably fused to the anteromesial processes and are coded as state 0 (see 168).

168. Anterolateral processes fused to anteromesial processes: (0) yes; (1) no. CI = 0.13.

In callichthyids, *Exastilithoxus*, some hypoptopomatines, *Kronichthys*, some loricariines, and *Pareiorhina* sp., the anterolateral processes are fused to the anteromesial processes (state 0; Fig. 33D). In *Astroblepus, Lithogenes* and most loricariids, they are not (state 1; Fig. 33A–C, E, F). It is hypothesized that any apparent absence of anterolateral processes is due to fusion rather than loss of either type of process. This is based on some anomalous specimens where the fusion is not complete on one side and both the anterolateral and anteromesial processes are visible.

169. Anterolateral process of the basipterygium: (0) thin; (1) wide through entire length. CI = 0.07.

In callichthyids, *Astroblepus*, and most loricariids, the anterolateral process is thin or tapers to a point (state 0; Fig. 33A–E). In *Lithogenes,* some of the Ancistrini, *Hemipsilichthys* sp., *Hypostomus albopunctatus*, *Isbrueckerichthys alipionis*, *Neoplecostomus*, and the Rhinelepini, it is widened along its entire length (state 1; Fig. 33F). Some hypostomines have a widening at the base of the process, but it tapers to a point distally and these species are considered to have state 0. Those species where the anterolateral processes are fused to the anteromesial processes (except *Exastilithoxus*) are coded as having state 0 based on specimens where the fusion is not complete. In *Exastilithoxus*, the anterolateral process clearly contributes more to the fused anterior process than the anteromesial process, and is hence coded as state 1.

Basipterygium: anteromesial processes

170. Anteromesial processes: (0) present; (1) absent. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the anteromesial processes are present (state 0; Fig. 33A, C–F); in *Delturus* and *Upsilodus* they are absent (state 1; Fig. 33B).

Basipterygium: main body

171. Fenestra present anterior to cartilaginous section: (0) absent; (1) present. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the basipterygium has a cartilaginous connection posteriorly and lacks a large, mesial fenestra anteriorly (state 0; Fig. 33A, B, D). In some loricariines and all hypostomines except *Exastilithoxus*, there is a large, medial, round to oval fenestra on the basipterygium anterior to the cartilaginous section (state 1; Fig. 33C, E, F; PF).

172. Ventral ridge of the basipterygium: (0) tall; (1) short to absent. CI = 0.09.

In most callichthyids and most loricariids, there is a tall ridge anteroventrally on the basipterygium (state 0; Fig. 33C, E; VRPB). In *Astroblepus, Lithogenes*, *Dekeyseria pulcher*, *Delturus*, most neoplecostomines, *Otocinclus*, *Pareiorhina*, *Pogonopoma*, some *Pseudancistrus*, *Pseudorinelepis*, *Pterygoplichthys lituratus*, and *Schizolecis*, this ridge is slight and rounded or is absent (state 1; Fig. 33A, B, D, F).

173. Posteroventral ridge of the basipterygium: (0) absent; (1) present. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, *Delturus*, hypoptopomatines, the *Lithoxus* group, most loricariines, most neoplecostomines, and *Upsilodus*, the basipterygium lacks a ridge at the posteroventral margin of the cartilaginous section (state 0; Fig. 33A,

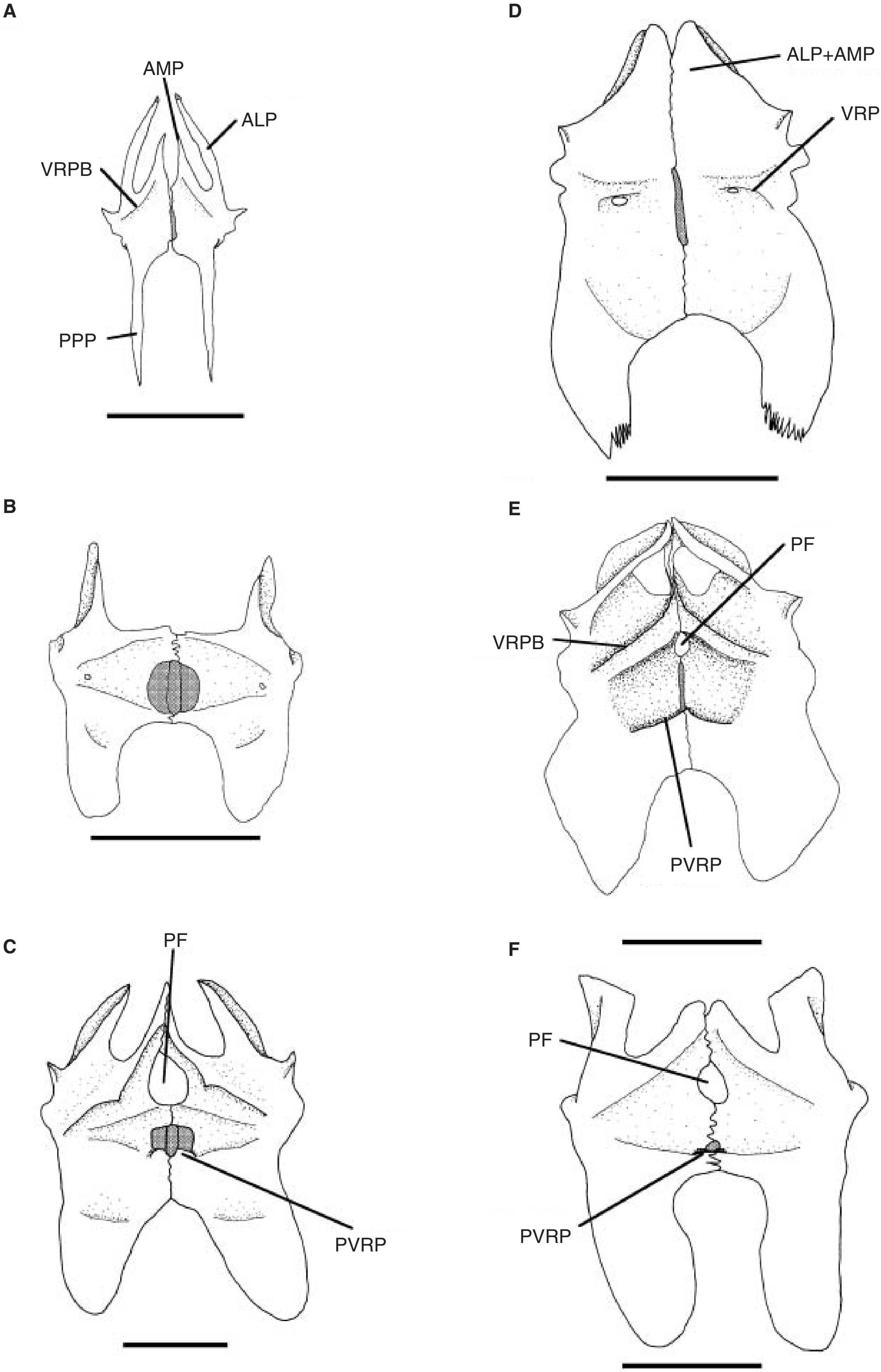

Figure 33. Pelvic basipterygium, ventral view. A, *Astroblepus* sp., USNM 318209. B, *Delturus anguilicauda*, USNM 318209. C, *Hypostomus plecostomus*, ZMA 105.306. D, *Kronichthys* sp., MZUSP 27545. E, *Peckoltia ucayalensis*, INHS 40916. F, *Pseudorinelepis genibarbis*, INHS 39730. Scale bars = 5 mm.

B, D). In *Hemipsilichthys nudulus*, most hypostomines, *Loricariichthys*, *Neoplecostomus*, *Sturisoma*, and *Sturisomatichthys*, there is a short, rounded ridge (state 1, Fig. 33C, E, F; PVRP).

Basipterygium: posterior processes

174. Posterior process of the basipterygium (Armbruster, 1998b): (0) rounded; (1) pointed. CI = 0.33.

In callichthyids, *Lithogenes*, and most loricariids, the posterior processes of the basipterygium are rounded posteriorly (state 0; Fig. 33B–F). In *Astroblepus*, *Nannoptopoma*, and *Pogonopoma*, they are pointed posteriorly (state 1; Fig. 33A).

Lateropterygium

175. Lateropterygium of pelvic girdle: (0) absent; (1) wedge-shaped; (2) thin; (3) triangular with ventral part widest; (4) disk-shaped. CI = 0.57.

The lateropterygium – a unique bone of the pelvic girdle – is absent in callichthyids, *Crossoloricaria* and *Loricariichthys* (state 0). In *Astroblepus, Lithogenes* and most loricariids, it is located at the anterolateral corner of the basipterygium, articulating with the base of the anterolateral process. In *Neoplecostomus* the lateropterygium is wedge-shaped and widest dorsally (state 1). In most loricariids it is thin and rod-shaped (state 2). In *Ixinandria*, *Loricaria, Rineloricaria*, and *Sturisoma*, it is triangular with the ventral part widest (state 3). In *Astroblepus* it is disk-shaped and widest in the middle (state 4). Regan (1904) suggested that the widening seen in the lateropterygium of *Astroblepus* and *Neoplecostomus* is homologous; however, as their shapes represent two different states, this is not the case.

First pelvic-fin ray

176. Two rows of the first pelvic-fin ray: (0) fused; (1) separated. CI = 1.00.

The first pelvic-fin ray is composed of two rows of segmented lepidotrichia, anterior and posterior. In callichthyids and loricariids, the rows are held tightly together and generally fuse distally (state 0). In *Astroblepus* and *Lithogenes*, they are completely and widely separated, making it appear as if there are two separate rays (state 1).

177. First pelvic-fin rays greatly widened in adults: (0) absent; (1) present. CI = 0.17.

In callichthyids and most loricariids, the first pelvic-fin ray is fairly thin (state 0). In most of the *Chaetostoma* group, most neoplecostomines, and *Peckoltia ucayalensis*, it is greatly widened in adults (state 1). *Astroblepus* and *Lithogenes* were coded as state 0 as the widening observed is due to separation, rather than widening, of the two rows of lepidotrichia (176–1).

EXTERNAL ANATOMY

Buccal papillae and barbels

178. Central buccal papilla: (0) absent or small; (1) large. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there is either no central buccal papilla behind the upper jaw or else it is small (state 0). In the *H. emarginatus* group, there is at least a central papilla and it is large (state 1; see photo in Armbruster & Page, 1996).

179. Buccal papillae: (0) not numerous; (1) numerous, present behind upper jaw. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are papillae on either side of the centra papilla (178: 0), but they are not numerous. In *Crossoloricaria*, the *Hypostomus unicolor* group, and *Loricaria*, there are numerous papillae in the buccal cavity surrounding the central papilla (178: 1). See Isbrücker & Nijssen (1982) and Armbruster & Page (1996) for photographs of state 1.

180. Single papilla located behind each dentary: (0) absent; (1) present. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no large papillae behind the dentary teeth (state 0). In most *Chaetostoma* and *Lithoxancistrus*, each dentary has a single large papilla just behind the teeth (state 1). See Isbrücker *et al.* (1988) for a photograph of state 1.

181. Barbel: (0) free; (1) adnate. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the maxillary barbel has at least a small section free from the lip (state 0). In some *Hemipsilichthys*, *Isbrueckerichthys*, *Neoplecostomus*, and *Pareiorhina* sp., the barbel has no free section and is completely attached to the lower lip (adnate; state 1).

182. Number of barbels: (0) two to three; (1) one. CI = 1.00.

In callichthyids, there are two to three barbels surrounding the mouth (state 0). In *Astroblepus, Lithogenes*, and loricariids, there is only a single barbel, the maxillary barbel (state 1).

Cheek and side of snout

183. Hypertrophied odontodes on cheeks: (0) absent; (1) present in nuptial males; (2) present regardless of season or sex. CI = 0.18.

In most callichthyids, astroblepids, and most loricariids, there are no hypertrophied odontodes on the cheek (state 0; Fig. 34A). They develop in males of *Delturus*, *Hemipsilichthys*, *Isbrueckerichthys*, *Hypostomus spinosissimus*, and several loricariines during the breeding season (state 1). In most of the Ancistrini, *Pogonopoma*, *Pseudorinelepis*, and most of the Pterygoplichthini, they develop in both males and females and the odontodes are not restricted to the breeding season (they may be better developed in nuptial males; state 2; Fig. 34B). Isbrücker & Nijssen (1992) provide an excellent set of photographs of the various modifications of cheek armature in loricariids.

184. Evertible cheek plates (ordered): (0) absent; (1) slightly evertible; (2) fully evertible. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the cheek plates are either absent or secured tightly to the preopercle (state 0; Fig. 34A). Evertible cheek odontodes are generally referred to as evertible interopercular spines. Alternatively, the Ancistrini are referred to as having an evertible interopercular area. However, because loricariids lack interopercles (Schaefer, 1987, 1988) it is incorrect to dub the cheek as being the interopercular area. In addition, referring to evertible cheek odontodes is not precise. The evertible structures are in fact the plates that support the odontodes, and these may be evertible while lacking odontodes. I therefore prefer to use the term 'evertible cheek plates' and separate the condition of having hypertrophied odontodes on the cheek (183: 1/2) from having evertible cheek plates.

Recent authors (Isbrücker, 1980; Schaefer, 1987; Burgess, 1989) usually refer to members of the Ancistrini and the *Hemiancistrus annectens* group as having evertible cheek plates; however, earlier authors (for example, Regan, 1904) also recognized *Pterygoplichthys* as having evertible cheek plates. Weber (1991) also suggests that some *Pterygoplichthys* have evertible cheek plates. Problems in observing the evertibility of cheek plates in some species of *Pterygoplichthys* (the *P. multiradiatus* group) occur because the plates do not support hypertrophied odontodes. However, in life, the evertibility of the cheek plates of the *P. multiradiatus* group can be readily observed and there is no difference in this ability between species of the *P. multiradiatus* group and other members of *Pterygoplichthys* (Regan, 1904; pers. observ.). Clearly, there is some variability in the ability to evert the cheek plates in the Hypostominae that has been causing problems for researchers. Examination of the cheek plates of all of the loricariids in this study sug-

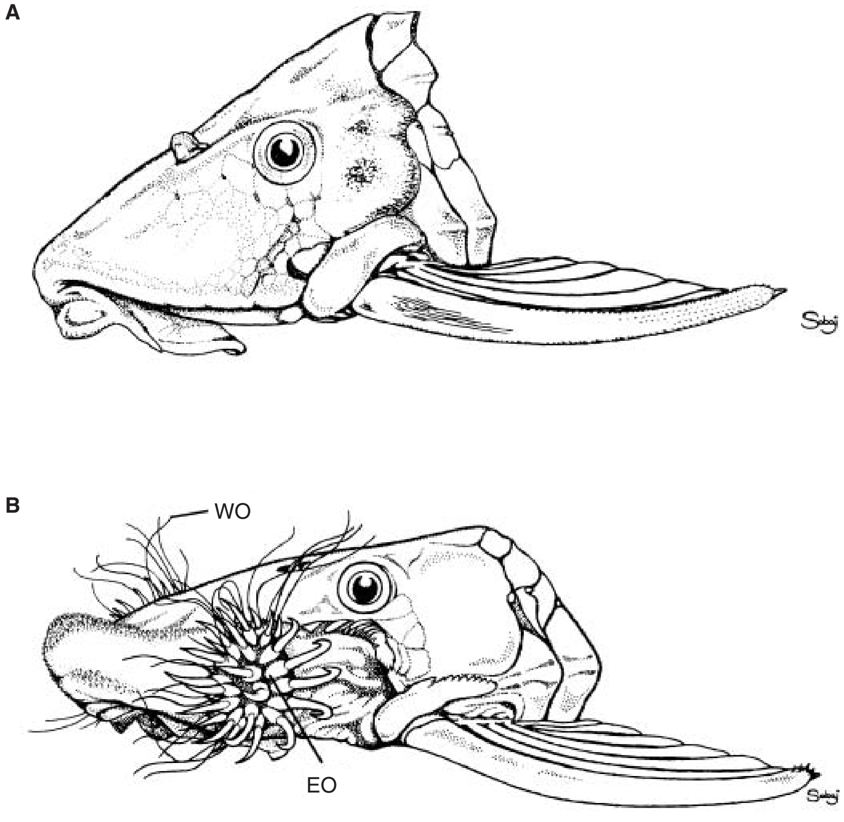

Figure 34. Head, left side, lateral view. A, *Hypostomus plecostomoides*, INHS 31837, 120.1 mm SL. B, *Lasiancistrus* sp., INHS 28650, 109.0 mm SL. Drawings by M.H. Sabaj.

gests that there are two relatively distinct states of evertibility of the cheek plates based on the angle they can be everted from the head.

Hypostomus is intermediate in the ability to evert the cheek plates between non-everters such as the Rhinelepini and everters of the Pterygoplichthini + Ancistrini. In *Hypostomus*, *Pseudancistrus*, and *Spectracanthicus murinus*, the cheek plates are slightly loosened from the preopercle posteriorly (connected only by loose connective tissue and muscle) and can be everted up to *c.* 30 ° from the head (state 1); the states in *Pseudancistrus* and *Spectracanthicus murinus* represent reversals. In the remainder of the Ancistrini and the Pterygoplichthini, the posterior cheek plates are only loosely connected to the preopercle by connective tissue and muscle and can be everted more than 75 ° from the head (state 2; Fig. 34B). Although there is wide variation in the ability of species with state 2 to evert the cheek plates, all species of *Pterygoplichthys* can evert them at least as well as *Chaetostoma*, *Spectracanthicus punctatissimus*, and *Leporacanthicus*. This character was coded as ordered because state 1 is clearly intermediate in the ability to evert the cheek plates.

185. One or two extremely hypertrophied odontodes on cheek: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, hypertrophied odontodes are either absent, the odontodes are fairly short, or there are many more than one or two (state 1). In *Dolichancistrus* and *Leptoancistrus*, the evertible cheek plates usually have only one (occasionally two) extremely hypertrophied odontodes about as long as or longer than the head (state 1). *Dolichancistrus* and *Leptoancistrus* appear to occasionally shed their odontodes, so it is fairly common to encounter specimens in which they are either absent or still in a state of growth.

186. Whiskerlike odontodes: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no whiskerlike odontodes on the cheek (state 0; Fig. 34A). In *Lasiancistrus s.s.*, there are some extremely long and thin odontodes on the cheek plates that resemble whiskers among the stout, evertible cheek odontodes (state 1; Fig. 34B; WO); whiskerlike odontodes can also be found along the snout in some species. They appear to be best developed in nuptial males, but are also present in females and juveniles.

187. Fleshy pad covering odontodes on cheeks of nuptial males: (0) absent; (1) present. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no hypertrophied odontodes embedded in thick skin on the side of the snout (state 0). Normally in loricariids, hypertrophied odontodes appear to be correlated with a thickening of the skin of the plates supporting the odontodes. In nuptial males of *Hemipsilichthys* and *Isbrueckerichthys* this swelling reaches an extreme and usually forms a thick fold of skin around the snout (state 1). The posterior process of the cleithrum also develops a thick layer of skin in fishes with state 1.

188. Hypertrophied odontodes along snout margin anterior to cheek spines: (0) absent; (1) present. CI = 0.08.

In most callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no hypertrophied odontodes along the snout margin (state 0). In the *Acanthicus* group, *Dekeyseria*, *Delturus*, *Dolichancistrus*, most *Hemipsilichthys*, *Hypostomus spinosissimus*, *Isbrueckerichthys*, *Ixinandria*, *Lasiancistrus*, *Leptoancistrus*, *Neblinichthys*, *Pogonopoma*, *Pseudancistrus*, *Pseudorinelepis*, *Rineloricaria*, *Sturisoma*, *Sturisomatichthys*, and *Upsilodus*, there are hypertrophied odontodes anterior to the cheek along the snout margin in at least nuptial males (state 1). Size of the snout odontodes is variable, reaching an extreme in some *Hemipsilichthys* and in *Pseudancistrus*. *Pseudancistrus* and *Pseudolithoxus* are notable because females also possess hypertrophied odontodes along the snout. See Isbrücker & Nijssen (1992) for photographs.

General

189. Optic notch: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the sphenotic posterior to the orbit does not develop a concavity (state 0). In the Loricariini there is a distinct notch posterior to the eye, referred to as an optic notch (state 1).

190. Position of pectoral fins in relation to first pelvic-fin ray when depressed parallel to body axis: (0) above and separated from ray; (1) even with or resting on top of ray. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, *Corymbophanes*, *Delturus*, *Exastilithoxus fimbriatus*, hypoptopomatines, loricariines, neoplecostomines, most of the Rhinelepini, and *Upsilodus*, when the pectoral fin is adpressed parallel to the body axis, it rests above and does not contact the first pelvic-fin ray (state 0). In most of the Ancistrini, the Hypostomini, *Pogonopoma*, and the Pterygoplichthini, the pectoral fins insert on the same plane as the pelvic fins so that when adpressed, the pectoral-fin spine rests on top of the first pelvic-fin ray and there is no space between the two (state 1). In some fishes the pectoral fin is angled slightly dorsally, so it is necessary to lower the spine so that it is parallel to the main axis of the body to examine this characteristic.

191. Number of caudal-fin rays: (0) 10 or 12; (1) 14. CI = 0.33.

In callichthyids, *Astroblepus,* and loricariines, there are either ten or 12 principal caudal-fin rays (state 0). In *Lithogenes* and most loricariids, there are 14 (state 1).

192. Postdorsal ridge: (0) absent; (1) present. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the dorsum lacks a ridge posterior to the dorsal fin (state 0; Fig. 27A, B). In *Delturus*, *Leptoancistrus*, and *Upsilodus*, a ridge consisting of raised, median plates is present posterior to the dorsal fin, referred to as a postdorsal ridge (state 1; Fig. 27C).

193. Lips forming suckerlike disk: (0) absent; (1) present. CI = 1.00.

In callichthyids and most other catfishes, the lips do not form a suckerlike disk (state 0). In *Astroblepus, Lithogenes* and loricariids, the lips are expanded into a suckerlike disk (state 1).

Plates

194. Numerous small plates behind pterotic-supracleithrum: (0) no; (1) yes. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are either just a few small plates (1–3), a naked area, or a medium-sized plate posterior to the pterotic-supracleithrum at the level of the lateral line (state 0). In *Isbrueckerichthys*, *Neoplecostomus paranensis*, *Pareiorhina*, *Pogonopoma*, and *Rhinelepis*, there is a patch of numerous small plates just posterior to the pterotic-supracleithrum (state 1; Armbruster, 1998b).

195. Contact between plates prior to anal fin: (0) present; (1) absent. CI = 0.25.

In callichthyids, hypoptopomatines, loricariines, and *Pterygoplichthys zuliaensis* Weber, at least one pair of lateral plates contact one another externally along the ventral midline between the anus and the anal fin (state 0). In most loricariids, the lateral plates do not meet along the midline (state 1).

196. Number of plate rows at thinnest part of caudal peduncle: (0) none; (1) two; (2) three; (3) five or more. CI = 0.33.

Astroblepus has no plates (state 0). There are two rows of lateral plates in callichthyids (state 1). In *Lithogenes*, *Ancistrus*, *Lasiancistrus*, *Dekeyseria*, the *Lithoxus* group, loricariines, hypoptopomatines, and most neoplecostomines, there is at least one transverse column of three rows of plates on the thinnest part of the caudal peduncle (state 2). In the remainder of the Loricariidae, there are usually five, rarely more (*Isbrueckerichthys duseni* often has more than five), transverse rows of plates on the caudal peduncle (state 3).

197. Number of predorsal plates: (0) none; (1) two to three; (2) four or more. CI = 0.14.

Establishing the number of predorsal plates involves counting the median plates between the supraoccipital and nuchal plate (when present). The nuchal plate is also included in those species where it is covered in skin or lateral plates (147: 1). In *Astroblepus, Lithogenes* and *Hemipsilichthys nudulus*, there are no predorsal plates (state 0). In callichthyids, most of the Ancistrini, most of the Hypostomini, some loricariines, *Hisonotus*, the Pterygoplichthini, and the Rhinelepini, there are two to three (state 1). In *Ancistrus*, the *Chaetostoma* group, *Corymbophanes*, *Delturus*, most hypoptopomatines, *Hypostomus albomaculatus*, *Lasiancistrus s.s.*, *Leporacanthicus*, *Lithoxancistrus*, the *Lithoxus* group, some loricariines, *Neblinichthys*, most neoplecostomines, *Spectracanthicus murinus*, and *Upsilodus*, there are four or more.

198. Keeling of plates: (0) plates absent or unkeeled to moderately keeled; (1) very well-developed keel. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are either no lateral plates, the plates are smooth, or the plates do not develop extremely strong keels of bone and odontodes (state 0). In the *Acanthicus* group, *Dekeyseria*, and *Pterygoplichthys punctatus*, the keels are particularly well developed and the odontodes forming them are long, stout, and sharp (state 1).

199. Hypertrophied odontodes on bodies of nuptial males: (0) absent; (1) present. CI = 0.17.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no hypertrophied odontodes on the sides of nuptial males (state 0). In the *H. emarginatus* group, *Neblinichthys*, *Panaque albomaculatus*, *P. maccus*, *Parancistrus*, and *Peckoltia*, males develop hypertrophied odontodes on the lateral plates during the breeding season (Isbrücker & Nijssen, 1992; Armbruster & Page, 1996; state 1). Some of the species with state 1 appear to develop hypertrophied odontodes only during the breeding season, and lose them after it (Armbruster & Page, 1996).

200. Extremely elongated odontodes on top of the snout: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the snout lacks hypertrophied odontodes dorsally (state 0). In *Neblinichthys*, nuptial males develop extremely hypertrophied odontodes on the snout that are orientated anteriorly (state 1; Ferraris, Isbrücker & Nijssen *et al.*, 1986).

201. Snout: (0) naked from just anterior to nares down to lip; (1) covered with plates. CI = 0.25.

In *Astroblepus, Lithogenes*, callichthyids, *Ancistrus*, and most *Chaetostoma*, there are no odontode-bearing plates on the snout (state 0). In most loricariids, the entire margin of the snout is covered in plates (state 1). In *Ancistrus* there are small, weak ossifications at the bases of each of the large tentacles, although these do not support odontodes.

202. Snout: (0) naked or with many plates; (1) one or two solid plates. CI = 1.00.

In *Astroblepus, Lithogenes*, callichthyids, and most loricariids, there are either no odontode-bearing plates on the snout or they are numerous and small (state 0). In *Hypoptopoma*, *Hisonotus*, *Nannoptopoma*, and *Otocinclus*, the snout margin consists of one or two solid plates (state 1; Schaefer, 1991).

203. Abdominal plating: (0) absent; (1) present. CI = 0.14.

Callichthyids, *Astroblepus, Lithogenes*, *Ancistrus*, *Baryancistrus*, the *Chaetostoma* group, *Corymbophanes*, *Delturus*, *Dekeyseria*, *Hemiancistrus megacephalus*, most *Lasiancistrus*, *Leporacanthicus*, the *Lithoxus* group, *Neblinichthys*, most neoplecostomines, *Spectracanthicus murinus*, and *Upsilodus*, completely lack plates on the abdomen (state 0). Most of the *Acanthicus* group, most *Hemiancistrus* Bleeker, *Hypancistrus*, the Hypostomini, *Isbrueckerichthys*, most loricariines, *Panaque*, *Parancistrus*, *Peckoltia*, the Pterygoplichthini, and the Rhinelepini, *Scobinancistrus*, and *Spectracanthicus punctatissimus*, have at least some small plates on the abdomen (state 1).

Teeth

204. Teeth in nuptial males: (0) bicuspid or unicuspid in all individuals; (1) unicuspid and elongated only in nuptial males. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the teeth are either unicuspid or bicuspid in all individuals (state 0). In members of the *Hypostomus unicolor* group, females, non-nuptial males, and juveniles have bicuspid teeth, while nuptial males develop elongated, unicuspid teeth, particularly mesially (state 1). See Armbruster & Page (1996).

205. Teeth: (0) viliform; (1) spoon-shaped; (2) large, but not spoon-shaped. CI = 0.29.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the teeth are viliform (threadlike) (state 0; Fig. 35A, B). In the *H. cochliodon group* and *Panaque*, the teeth – used to scrape off small bits of wood which are then consumed – are enlarged and spoon-shaped and the lateral cusp is absent or reduced (state 1; Fig. 35C. See Schaefer & Stewart, 1993). In *Leporacanthicus*, the *Lithoxus* group, *Hypancistrus*, *Megalancistrus*, *Pseudacanthicus*, *Scobinancistrus*, and *Spectracanthicus*, the teeth are wide and long, but are not spoon-shaped (state 2; Fig. 35D). *Hypostomus hemicochliodon* has teeth that approach the spoon-shaped teeth of the *H. cochliodon* group, but are not coded as state 1 (Fig. 35B); its diet consists mostly of wood, although the percentage of wood is not as high as in the *H. cochliodon* group or *Panaque*.

Tentacles

206. Fleshy appendages around both jaws: (0) absent; (1) present. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no fleshy appendages (often referred to as barbels) around the jaws (state 0). In *Crossoloricaria* and *Loricaria*, the entire mouth is surrounded by long, thin, barbel-like structures (state 1).

207. Lower lip fimbriate: (0) no; (1) yes. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the lower lip is either smooth or with numerous barbel-like structures (state 0). In *Exastilithoxus*, the posterior margin of the lower lip has elongate, fleshy extensions (fimbriae; state 1).

208. Fleshy tentacles on snout (ordered): (0) absent; (1) sheath partially detached from odontode; (2) sheath long and well separated from odontode; (3) very long, odontodes missing. CI = 0.75.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no fleshy tentacles on the snout. Primitively, there is a sheath which may be responsible for the growth of the odontode; it normally surrounds the odontode equally on all sides (state 0). In *Dekeyseria*, *Pseudolithoxus*, *Neblinichthys*, and *Pseu-*

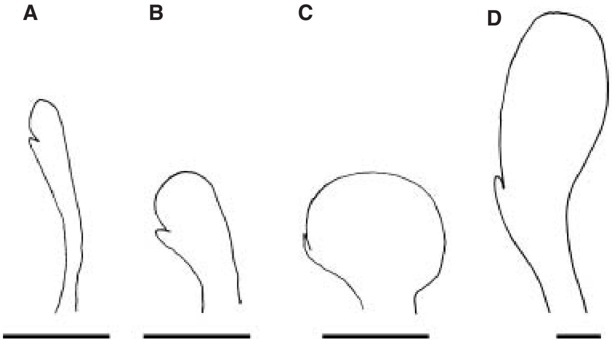

Figure 35. Inner dentary teeth, right side, ventral view. A, *Hypostomus plecostomus* 3, INHS 28903. B, *Hypostomus hemicochliodon,* FMNH 97010. C, *Hypostomus plecostomoides* (*H. cochliodon* group), INHS 59831. D, *Scobinancistrus pariolispos* Isbrücker and Nijssen, ZMA uncatalogued. Scale bars = 0.5 mm.

dancistrus, the sheath has become partially detached from the odontode and exists as a 'tentacule' (tentacule is the term introduced by Sabaj, Armbruster & Page, 1999 to describe a small tentacle associated with an odontode; state 1). In *Lasiancistrus s.s.*, the tentacule is long, sometimes branched, and longer than the supporting odontode (state 2). *Ancistrus* has lost the odontodes and well-developed snout plates and the tentacles develop without odontodes (state 3).

It is hypothesized that the tentacules were initially formed by the odontodes erupting from the side rather than the middle of the sheaths. Because most of the skin of loricariids contains taste buds, the formation of small tentacules probably increased the efficiency of the skin's ability to taste particles. In some groups, the increased sensitivity led to an increase in the size and complexity of the tentacules such that they became branched and longer than the associated odontodes. In *Ancistrus*, the tentacules became even larger (tentacles) and the supporting odontodes were lost. Sharp odontodes, useful for fighting, may be a liability to male loricariids when they are tending eggs within nest cavities. Tentacules may therefore have a secondary function of blunting the points of the odontodes.

Ancistrus has small ossifications at the bases of most of the tentacles – very thin, weak plates that do not support odontodes. Plates are found nowhere else along the snout of *Ancistrus*. This character is coded as ordered because it is most parsimonious to assume that tentacles increased in size in order to provide: (1) an increase in surface area for taste and (2) potential for using as larval mimics, as suggested by Sabaj *et al.* (1999).

209. Tentacules on pectoral fins (ordered): (0) absent; (1) small, partially detached from odontodes; (2) large, free from odontodes and longer than them. CI = 0.40.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, there are no tentacules on the pectoral-fin spine (state 0). *Chaetostoma platyrhyncha*, *Dekeyseria*, *Lithoxancistrus*, *Pseudolithoxus*, *Neblinichthys*, *Parancistrus*, develop short tentacules partially detached from the odontodes (see 208: 1). *Lasiancistrus s.s.* and *Ancistrus* have large tentacules free from the odontodes and longer than them (state 2). This character is coded as ordered. See Sabaj *et al.* (1999) for more detail.

GASTROINTESTINAL SYSTEM

Oesophagus

210. Oesophagus: (0) bent; (1) straight. CI = 0.33.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the oesophagus bends to the right upon entering the visceral cavity (state 0). In *Lithoxus*, the Rhinelepini, and *Otocinclus*, it passes straight to the stomach (state 1). See Armbruster (1998b) for more detail.

211. U-shaped diverticulum (ordered): (0) absent; (1) expandable, loosely attached to abdominal wall; (2) expandable, firmly attached to abdominal wall; (3) retroperitoneal, swim bladder-like. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the digestive tract lacks a diverticulum that holds air or else the diverticulum is not U-shaped (state 0). The Rhinelepini is diagnosed by a large, two part, U-shaped diverticulum at the level where the oesophagus and the stomach meet. In *Pseudorinelepis*, the diverticulum is loosely attached to the abdominal wall and is intraperitoneal (state 1). In *Rhinelepis*, it is still intraperitoneal, but is firmly attached to the abdominal wall (state 2). In *Pogonopoma*, it is much wider, is retroperitoneal, and has a reduced first section (state 3). It is hypothesized that the diverticulum evolved first as an intraperitoneal organ, became firmly attached to the abdominal wall and then became retroperitoneal. Because the digestive tract is intraperitoneal, it is unlikely that the diverticulum would first evolve as a retroperitoneal organ and then move back inside the peritoneum; hence, this character is coded as ordered. See Armbruster (1998c) for more detail.

In 1998 I tested the ordering of this character by removing it; the resultant tree was the same as with the character added, thereby supporting the ordering (Armbruster, 1998b). In the same paper I also suggested that *Pogonopoma parahybae* is unique among the Rhinelepini in lacking the initial, short, anteriorly directed section of the second part of the diverticulum. However, after further scrutiny, this characteristic is more variable in the Rhinelepini than I initially believed.

212. Diverticulum nearly completing a ring: (0) absent; (1) present. CI = 1.00.

In callichthyids, astroblepids, and most loricariids, the digestive tract lacks a diverticulum that holds air or else the diverticulum is not shaped like a ring (state 0). In *Otocinclus* there is a ringlike diverticulum that begins on the right side of the body, passes anteriorly, runs down the left side of the body, passes through the peritoneum, and terminates at about the same level it started (state 1) (see Schaefer, 1997; Armbruster, 1998c).

Stomach

213. Stomach greatly expanded and connected to the abdominal wall by a connective tissue sheet: (0) no; (1) yes. CI = 1.00.

In many loricariids, the stomach may be expanded to hold air or is not expanded, as in *Astroblepus,* *Lithogenes* and callichthyids (state 0). In the Pterygoplichthini, the stomach is greatly expanded, highly vascularized, and is covered ventrally with a connective tissue sheet made up of numerous interconnecting and overlapping bands that attach the stomach to the abdominal wall (state 1). See Armbruster (1998c) for more detail.

214. Stomach expanded such that it extends anteriorly to the pectoral girdle and intestine exits dorsally from expanded region: (0) no; (1) yes. CI = 1.00.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the stomach is not expanded to the pectoral girdle, so that the intestine exits dorsally (state 0). In *Lithoxus*, the stomach is expanded such that the anterior margin is just posterior to the pectoral girdle; the stomach narrows prior to the pylorus, which is located dorsal to it (state 1). See Armbruster (1998c) for more detail.

Swim bladder

215. Swim bladder: (0) restricted to a small area anterior to the rib of the sixth vertebral centrum; (1) extremely large, extending as far as or beyond the rib of the sixth vertebral centrum. CI = 0.50.

In callichthyids, *Astroblepus, Lithogenes*, and most loricariids, the swim bladder is reduced and restricted to an encapsulated region anterior to the rib of the sixth vertebral centrum (state 0; Fig. 25B–D). In *Acanthicus*, *Panaque nigrolineatus*, and *Megalancistrus*, the swim bladder is greatly expanded and extends as far as or beyond the rib (state 1; Fig. 25A). In at least *Megalancistrus* and *P. nigrolineatus*, the size of the swim bladder increases with body size. *Acanthicus* has the most extreme development of the swim bladder and the rib of the sixth vertebral centrum fits into a groove ventral to the swim bladder capsule (Fig. 25A).

RESULTS AND DISCUSSION

Phylogenetic analysis with just the callichthyids as the outgroup resulted in 5098 trees of 1328 steps, CI = 0.203, RI = 0.759 (Figs 36–38). It is readily apparent from the phylogeny that the taxonomy of the Loricariidae as expressed by Isbrücker (1980), Schaefer (1986, 1987), and Burgess (1989) needs modification. No characteristics are found to support a monophyletic Hypostominae that excludes the Ancistrinae or to place the putatively basal members (*Delturus*, *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Pareiorhina*, and *Upsilodus*) with the remainder of Hypostominae in a monophyletic group. In addition, the placement of some of the genera precludes keeping the current subfamilial taxonomy. A new subfamily must be described for *Delturus* and *Upsilodus*. *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, and *Pareiorhina* are best placed temporarily in the Neoplecostominae (Fig. 36) until further phylogenetic analysis can ascertain relationships. The Ancistrinae should be returned to the synonymy of the Hypostominae (Fig. 37). In addition, the generic level taxonomy is in need of revision. New genera to be described and genera that are synonymized are discussed below. In order to examine character state changes, a single, fully resolved tree (the first of the 5098) was chosen arbitrarily. Character state changes presented in Appendix 3 are only for those clades supported in the strict consensus tree. Clade numbers are given in Figures 36–38. In addition to clades, character states are provided in Appendix 3 for those genera represented by single species in the analysis (except those in the Hypoptopomatinae and the Loricariinae).

The unordered analysis with just the callichthyids as the outgroup resulted in 3941 trees of 1322 steps, CI = 0.204, RI = 0.752. The strict consensus tree differed in only one respect from the strict consensus in the ordered analysis: *Chaetostoma platyrhynchus* was sister to all other *Chaetostoma* as opposed to being in a polytomy with the other species of *Chaetostoma*. The congruence between the ordered and unordered analyses suggests that the ordering of the characters indicated in the character descriptions was satisfactory.

A final analysis with *Scoloplax* included in the outgroup and characters ordered resulted in 639 trees of 1401 steps, CI = 0.194, RI = 0.753. The ingroup phylogeny in this analysis is identical to that in the ordered analysis.

The strict consensus tree (Figs 36–38) differs in many respects from the taxonomy suggested by previous workers. Required taxonomic changes in subfamilies, tribes, and genera are discussed beginning with Figure 36.

New subfamily

Delturus + *Upsilodus* is supported as a monophyletic group by two unique synapomorphies: dorsomesial process on pterotic-supracleithrum present (115: 1) and loss of the anteromesial processes of the basipterygium (170: 1). In addition, the branch leading to *Delturus* + *Upsilodus* is supported by 17 steps, making it the second longest branch in the phylogeny and the decay index is very high (DI = 14; Fig. 36). Additional characteristics that support *Delturus* + *Upsilodus* can be found in Appendix 3, clade 3. *Delturus* + *Upsilodus* lack several synapomorphies that diagnose the remainder of the Loricariidae: posterior shelf on the fourth epibranchial (17: 1), lateral wall of the pterygoid channel (52: 2; Fig. 15B–F, H, I), a metapterygoid condyle on the lateral ethmoid (57: 1 and 2; Fig. 15B,

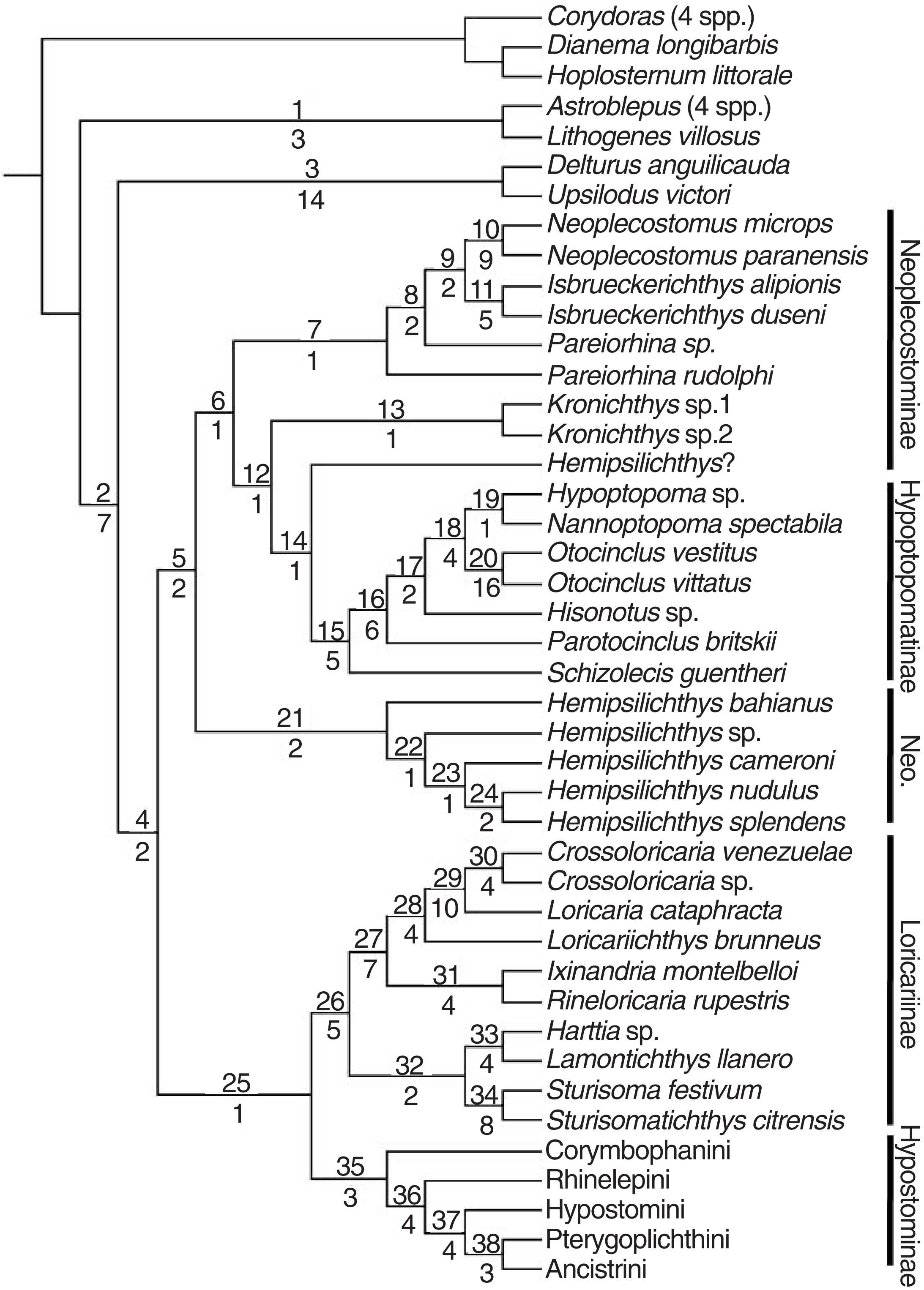

Figure 36. Relationships of *Astroblepus, Lithogenes*, hypostomine tribes, and the nonhypostomine loricariids based on the ordered analysis. This is part of the strict consensus of 5098 most parsimonious trees of trees of 1328 steps, CI = 0.203, remainder of the consensus tree is in Figs 37 and 38. Numbers above the branches are clade numbers, numbers below are decay indices.

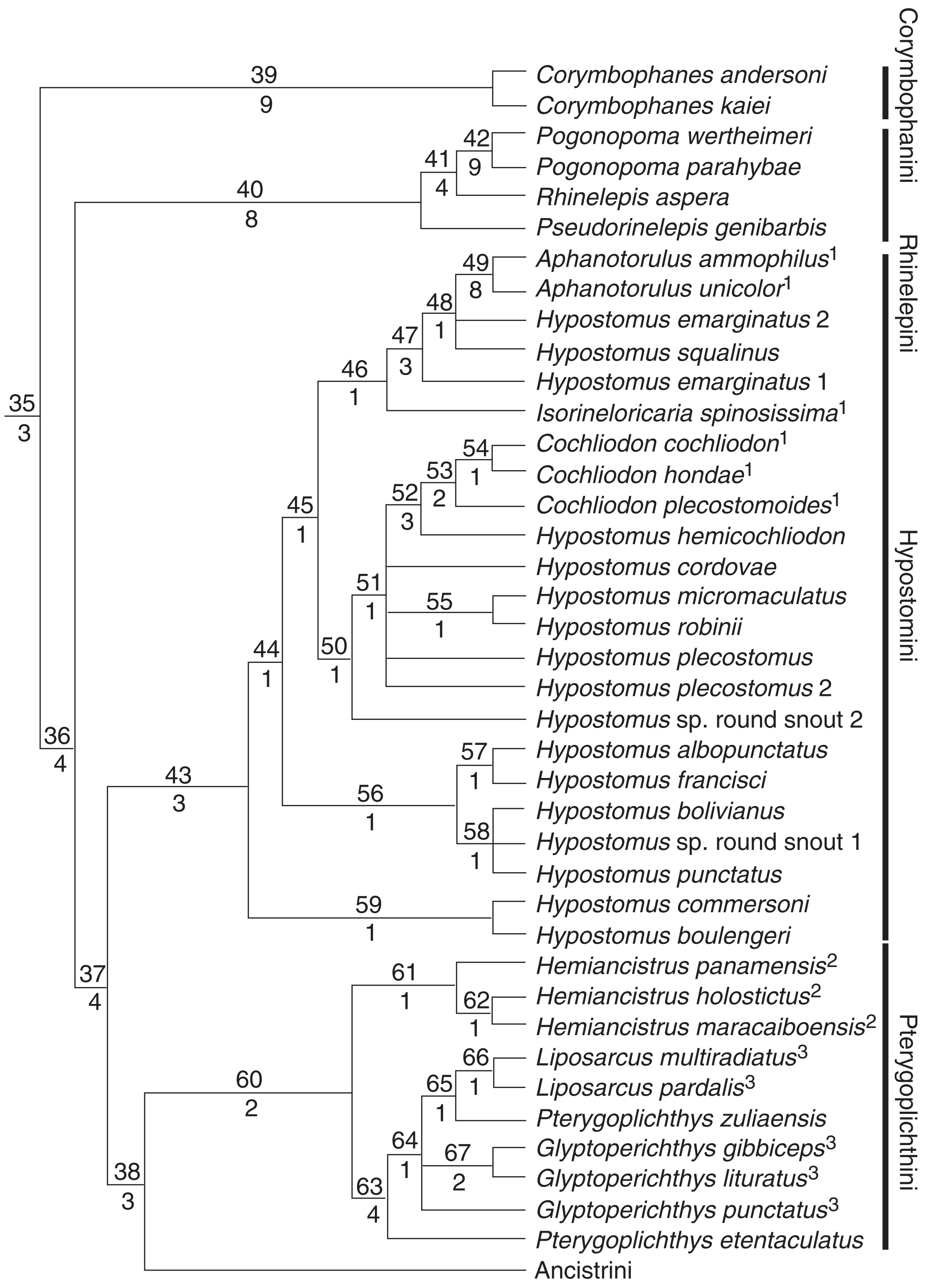

Figure 37. Relationships of the hypostomine tribes and taxa within the Corymbophanini, the Rhinelepini, the Hypostomini, and the Pterygoplichthini based on the ordered analysis. This is part of the strict consensus of 5098 most parsimonious trees of trees of 1328 steps, CI = 0.203, remainder of the strict consensus tree is in Figs 36 and 38. Numbers above the branches are clade numbers, numbers below are decay indices. [1]*Aphanotorulus, Cochliodon,* and *Isorineloricaria* are placed in *Hypostomus*. [2]The *Hemiancistrus annectens* group represents an undescribed genus, *Hypostomus panamensis* is now placed in *Hemiancistrus*. [3]*Glyptoperichthys* and *Liposarcus* are placed in *Pterygoplichthys*.

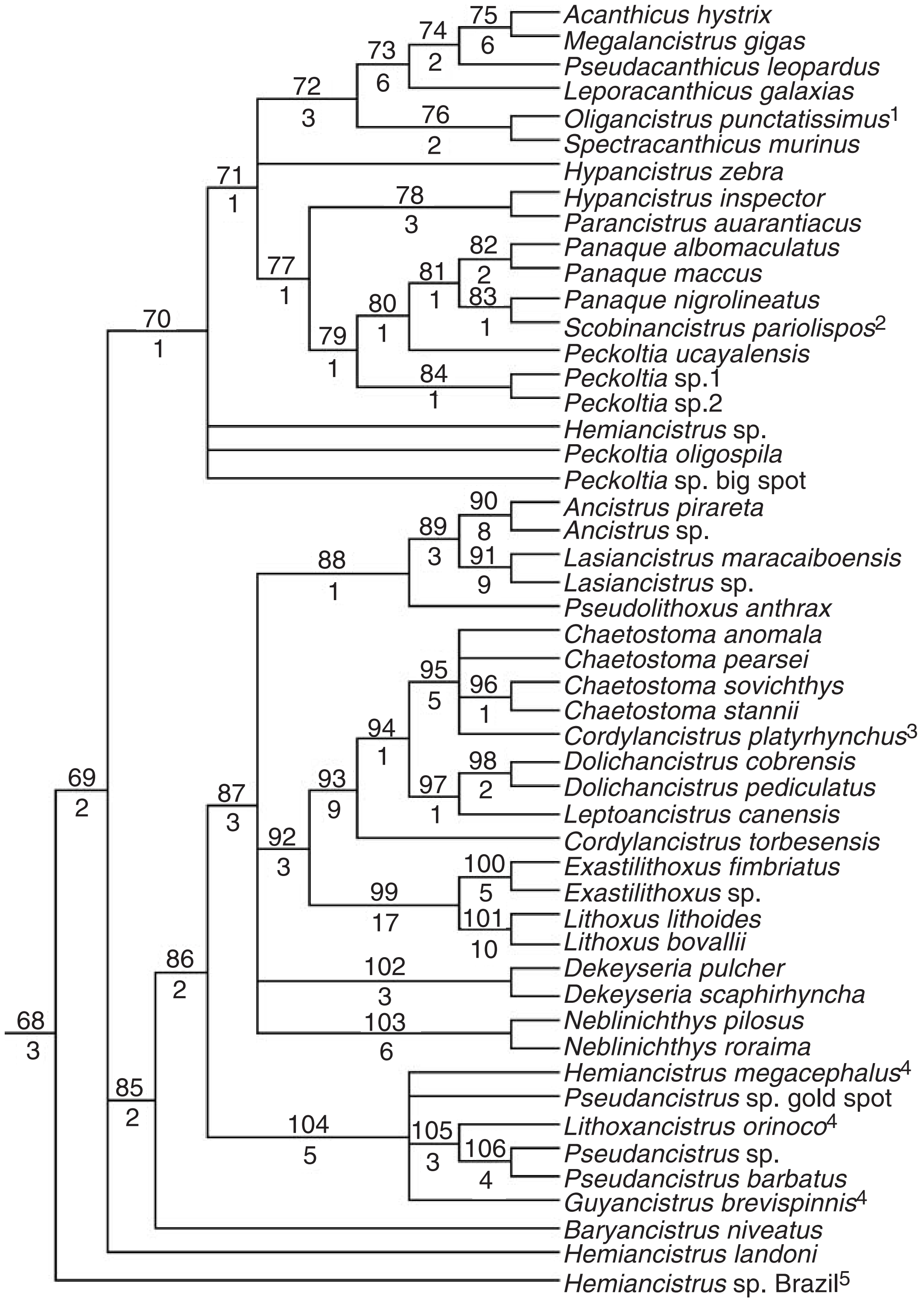

Figure 38. Relationships of the taxa within the Ancistrini based on the ordered analysis. This is part of the strict consensus of 5098 most parsimonious trees of trees of 1328 steps, CI = 0.203, remainder of the strict consensus tree is in Figs 36 and 37. Numbers above the branches are clade numbers, numbers below are decay indices. [1]*Hemiancistrus landoni* represents an undescribed genus. [2]*Oligancistrus* is placed in *Spectracanthicus*. [3]*Lithoxancistrus* is transferred to *Pseudancistrus*. [4]*Cordylancistrus platyrhynchus* is transferred to *Chaetostoma*.

D–I), a canal plate (84: 0), Baudelot's ligament forming at least a short shelf (93: 1), an anterior process of the pterotic-supracleithrum (110: 1; Fig. 22), and abdominal plating (203: 1). Interestingly, the position of *Upsilodus victori* (which is probably a synonym of *Hemipsilichthys gobio*; R. E. Reis and E. Pereira, pers. comm.) was found by Montoya-Burgos *et al.* (1998) to also be at the base of all other loricariids based on DNA sequence data. *Delturus* and *Upsilodus* are currently under study by myself, Roberto Reis, and Edson Pereira: a new subfamily will be described in a future publication. Armbruster (1997) has *Upsilodus* listed; however, the specimens examined are actually juvenile *Delturus*.

NEOPLECOSTOMINAE

I am recognizing an expanded Neoplecostominae that includes *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Neoplecostomus,* and *Pareiorhina* despite the fact that these genera did not form a monophyletic group in this analysis. *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, and *Pareiorhina* were placed in the Neoplecostominae by Gosline (1947), but have been placed in the Hypostominae since Isbrücker (1980). As the dataset presented herein evolved, the relationships of the genera of the Neoplecostominae were in flux because so few characteristics were found to help resolve them. In this final analysis, some of the genera (*Isbrueckerichthys* and *Pareiorhina*) formed a monophyletic group with *Neoplecostomus*, while *Kronichthys* and an undescribed genus (*Hemipsilichthys*?) formed a monophyletic group with the Hypoptopomatinae. *Hemipsilichthys* was sister to the remainder of the Neoplecostominae and Hypoptopomatinae. Montoya-Burgos *et al.* (1998) found support for a monophyletic Neoplecostominae minus *Pareiorhina*.

I have no confidence in the relationship of the genera of the Neoplecostominae and Hypoptopomatinae. Based on Gosline (1947) and Montoya-Burgos *et al.* (1998), and the fact that *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Neoplecostomus,* and *Pareiorhina* definitely do not belong in the Hypostominae, the most conservative act is to place *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, and *Pareiorhina* in the Neoplecostominae and await a study that will examine the relationships of these genera to each other and to the Hypoptopomatinae. The Neoplecostominae is currently being studied by Pereira and Reis.

Corymbophanes bahianus and typical *Corymbophanes* (*C. andersoni* and *C. kaiei*) are unrelated (Armbruster *et al.*, 2000). Based on the phylogeny presented herein, *C. bahianus* is related to *Hemipsilichthys* while *C. andersoni* and *C. kaiei* are sisters to all other hypostomines. *C. bahianus* was transferred to *Hemipsilichthys* by Armbruster *et al.* (2000)

Despite the contention of Regan (1904) and Schaefer (1987), there is no support for *Neoplecostomus* as a basal hypostomine. Regan (1904) suggests that *Neoplecostomus* was close to *Arges* (= *Astroblepus*) based on the presence of a plate-like lateropterygium (see 175); however, as mentioned in the character description above, the lateropterygium is shaped differently in *Neoplecostomus* and *Astroblepus* and the widened morphology is not likely to be homologous. Schaefer (1987) suggests one character that is synapomorphic for all loricariids minus *Neoplecostomus* – slender secondary radial elements in the pectoral-fin ray. However, the radial elements in callichthyids are also slender, and several loricariids have much wider elements than *Astroblepus*, suggesting that widened pectoral radial elements have evolved multiple times. Widened pectoral radial elements were not found to be useful in reconstructing the phylogeny of loricariids in this study.

Schaefer (1987) also suggests that *Neoplecostomus* lacks the characteristics he uses to diagnose all other loricariids; however, he states that a test of the phylogenetic position awaits examination of skeletal material. *Neoplecostomus* does have the characteristics Schaefer (1987: 21, fig. 15) provides as synapomorphies for Hypoptopomatinae + Loricariinae + Hypostominae + Ancistrinae.

Of the Neoplcostominae, Schaefer (1986) examined only *Kronichthys*, which he found to be the sister to *Schizolecis* (and incorrectly referred to as *Pogonopomoides*) and this clade as sister to all other Hypostominae + Ancistrinae. In this study and in Schaefer (1991) *Schizolecis* is clearly a hypoptopomatine; a relationship between *Kronichthys* and the Hypoptopomatinae is certainly possible, given the results presented here. *Kronichthys* is also listed as examined in Schaefer (1987) and is considered to be a hypostomine; however, in the preparation of this study, the characteristics of Schaefer (1987) were re-examined in several taxa and *Kronichthys* has none of the characteristics that Schaefer used to diagnose the clade of Hypostominae + Ancistrinae.

Support for Neoplecostominae + Hypoptopomatinae (Fig. 36) is moderately strong based on several synapomorphies, including (1) long anterior process of the fourth epibranchial (16: 1; Fig. 12B), (2) a preopercular latero-sensory canal that proceeds posteriorly from the preopercle for a great distance (63: 1), and (3) a nasal capsule not completely supported ventrally (96: 1; Fig. 20C; reversed in *Neoplecostomus*). The most useful of these are 2 and 3 – characteristics possessed by no other loricariid examined.

There is congruence between this study and Montoya-Burgos *et al.* (1998) in the placement of *Hemip-*

silichthys, *Kronichthys*, and *Isbrueckerichthys* with *Neoplecostomus* and the Hypoptopomatinae. In some analyses, Montoya-Burgos *et al.* obtain a monophyletic Neoplecostominae (minus *Pareiorhina*); in all analyses they obtain a clade consisting of all of the genera of the Neoplecostominae and the Hypoptopomatinae.

LORICARIINAE

Schaefer (1987) suggests that the Loricariinae is the sister to Hypostominae + Ancistrinae (= Hypostominae; Fig. 2), based on the presence of eight or more bifid neural spines and 30 or more preural vertebrae; however, these characteristics appear to be incorrect. In the Loricariinae, there are usually only about five bifid neural spines; Schaefer had probably included the trifid spines (see 127: 1) in his count for the Loricariinae. These trifid spines are a feature unique to the Loricariinae and occur posterior to the dorsal fin. The bifid neural spines are restricted to a region ventral to the dorsal fin. Also, members of the Rhinelepini have less than 30 preural centra. Schaefer also includes two other characters (arrector ventralis of the pectoral girdle passing through a channel, see 163: 0; and presence of the lower lobe of the hypural plate longer than the upper, see 123: 1) as synapomorphies of his Loricariinae + Hypostominae + Ancistrinae; however, passage of the arrector ventralis through a channel is not found in most hypostomines and a longer lower lobe of the hypural plate is not found in the Loricariinae.

Montoya-Burgos *et al.* (1998) suggest that the Loricariinae is both closely related to, and derived from within, the Hypostominae, and that *Pseudorinelepis* is the sister to the Loricariinae. There is no morphological support for *Pseudorinelepis* as the sister to the Loricariinae; Montoya-Burgos *et al.* suggest that there is a phenetic similarity between them, although the taxa share very little other than the loss of the adipose fin in common (a very homoplasious characteristic, CI = 0.09).

In this analysis, the Loricariinae was found to be the sister to the Hypostominae based on the following characteristics: loss of adipose fin (137-1, this is secondarily reversed in most of the Hypostominae), anterolateral processes of basipterygium slightly angled, do not converge at midline (167: 1), and ventral ridge on basipterygium tall (172: 0). However, as this dataset evolved, the relationships of the Loricariinae were not stable, and these characteristics vary widely among the Hypostominae and Loricariinae; hence, I have no confidence in the relationship of the Hypostominae to the Loricariinae. None of the characteristics found as synapomorphies are particularly compelling reasons to accept the monophyly of Loricariinae + Hypostominae, the decay index for the node is low (DI = 1), and more research is needed. No attempt was made to ascertain the relationships of the genera of the Loricariinae. For a more complete treatment of the Loricariinae, see Rapp Py-Daniel (1997).

HYPOSTOMINAE

Isbrücker (1980), Nijssen & Isbrücker (1986), and Isbrücker & Nijssen (1989) broke the Ancistrinae into an array of tribes and subtribes based on few or no characters. Their system is found not to reflect phylogeny and is here abandoned. It is almost impossible to compare the morphological phylogeny presented here (Figs 36–38) with that of Montoya-Burgos *et al.* (1998), so mainly instances of similarity are mentioned.

The Hypostominae is broken into five tribes, three of them new: Corymbophanini new tribe, Rhinelepini new tribe, Hypostomini, Pterygoplichthini new tribe, and Ancistrini (Figs 36–38). An interesting finding is the sister-group relationship of the Pterygoplichthini and the Ancistrini (Figs 36, 37). Schaefer (1986) has the Ancistrini placed within a polytomy consisting of various genera or species now placed in *Hypostomus* and *Pterygoplichthys* as sister to *Hypostomus* + Ancistrinae (Fig. 4). However, recognition of a relationship between the Pterygoplichthini and Ancistrini has precedent. Prior to this study, most of the species of the *Hemiancistrus annectens* group were referred to the Ancistrinae, and several of the species now placed in *Pterygoplichthys* had been considered to be *Ancistrus* or *Chaetostoma* (genera that are essentially synonymous with the Ancistrini in many early works) by early workers (i.e. Kner, 1853; Regan, 1904). In this study, the sister-group relationship of the Pterygoplichthini and the Ancistrini is supported by five or more plates between the opercle and canal plate (88: 3) and hypertrophied odontodes present regardless of season or sex on evertible cheek plates (183: 2 and 184: 2).

CORYMBOPHANINI

In this analysis, *Corymbophanes* is sister to all the other Hypostominae (Fig. 37) and a monogeneric tribe, Corymbophanini, is described below. *Corymbophanes* is described in detail in Armbruster *et al.* (2000). *Corymbophanes* is known only from the Potaro River above Kaieteur Falls in western Guyana, and Armbruster *et al.* (2000) contend that it is a relict. *Corymbophanes* would likely be in direct competition with morphologically similar species of the Ancistrini, although no species of the latter are known from above Kaieteur Falls. Based on its range and phylogenetic position, it would be logical to speculate that *Corymbophanes* once had a larger range that has become restricted to the Upper Potaro, and that it persists there because there are no sympatric species of the Ancistrini.

Corymbophanes bahianus Gosline from Bahia, Brazil is actually *Hemipsilichthys* (see above). Schultz (1944) describes *C. venezuelae* from the Lago Maracaibo basin of Venezuela, although it is a species of *Chaetostoma* (Isbrücker, 1980; Armbruster *et al.*, 2000). Schaefer (1986) includes what he calls *Corymbophanes* in his analysis and he determines that it is amongst a polytomy with *Hypostomus*, *Isorineloricaria*, and the Ancistrini. I have examined the specimens he used and have found that they belong to *Hypostomus*. Schaefer (1987) also refers to these specimens of *Hypostomus* as *Corymbophanes*.

RHINELEPINI

The Rhinelepini represents a group of three genera: *Pogonopoma*, *Pseudorinelepis*, and *Rhinelepis*. It is one of the best-diagnosed groups in the Loricariidae and is supported by such unique characteristics as a lateral shelf on the upper pharyngeal tooth plate and a large, U-shaped diverticulum of the oesophagus (Armbruster, 1998c). Its position as sister to the remainder of the Hypostominae (Fig. 37) is identical in this study to Schaefer (1986). For further detail, see Armbruster (1998b) and Quevedo & Reis (2002).

HYPOSTOMINI

Within the Hypostomini, *Hypostomus* is a paraphyletic assemblage whose members are sisters to *Aphanotorulus*, *Isorineloricaria*, and *Cochliodon* (Fig. 37). Armbruster & Page (1996) and Armbruster (1998a) provide evidence that suggests that *Aphanotorulus*, *Isorineloricaria*, *H. emarginatus*, and *H. squalinus* form a monophyletic group (the *H. emarginatus* group).

Analysis including the characteristics suggested in the previous studies provides several potential synapomorphies for the *H. emarginatus* group: elongated first hypobranchial (23: 1), seven or more infraorbital plates (91: 2), contact between metapterygoid and lateral ethmoid shifted anteriorly (99: 1; Fig. 20D), an enlarged central papilla in the buccal cavity (178: 1), and hypertrophied odontodes on the bodies of breeding males (199: 1; Fig. 39A). The unique coloration of these species (white to tan ground colour with black spots; Figs 39A, 40A) makes them readily identifiable from most other *Hypostomus*. In this analysis, a monophyletic *H. emarginatus* group was found in most of the most parsimonious trees; however, *Isorineloricaria* was restricted from the group in the strict consensus tree (Fig. 37). Montoya-Burgos *et al.* (1998) also suggest that *Aphanotorulus* and *H. emarginatus* are sisters; however, *Isorineloricaria* is the sister to *Parancistrus* (Ancistrini) in their analysis. A monophyletic group of *Isorineloricaria* and *Parancistrus* is not supported by any morphological evidence. *Squaliforma* was described in Isbrücker *et al.* (2001); however, no evidence was found to support *Squaliforma* Isbrücker, which consists of species of the *H. emarginatus* group minus *Aphanotorulus* and *Isorineloricaria*.

Cochliodon also appears to be a well-diagnosed group supported by the following synapomorphies: loss of the notch between the metapterygoid and hyomandibula (36: 0; Fig. 15A, H, I), a strongly curved maxilla (70: 1; Fig. 17C), and spoon-shaped teeth (205: 1; Fig. 35C). Evidence that *Cochliodon* is not as unique as taxonomy suggests is provided by *Hypostomus hemicochliodon* (Fig. 37). This species shares several synapomorphies with *Cochliodon*: preoperculo-hyomandibular ridge deflected posteriorly such that it is visible mesially (46: 1; Fig. 15D, I), a longitudinal ridge on the quadrate (68: 1; Fig. 15H, I; reversed in *C. cochliodon*), dentaries forming an angle averaging less than or equal to 80° (69: 1), and two plates between the suprapreopercle and exposed opercle (81: 2; reversed in *C. cochliodon*). However, *H. hemicochliodon* has teeth that, though tending towards the spoon-shaped teeth characteristic of *Cochliodon*, are not spoon-shaped (Fig. 35B). *Cochliodon* uses its spoon-shaped teeth as chisels to remove small chips of wood from submerged logs (Schaefer & Stewart, 1993; pers. observ.), and the vast majority of material in the intestine consists of small flakes of wood (pers. observ.). *H. hemicochliodon* predominantly has wood in the digestive tract, but has much more algae and detritus than typical *Cochliodon*. The placement of *H. hemicochliodon* in the phylogeny suggests that *Cochliodon* has evolved from algivorous *Hypostomus*.

Although the *H. emarginatus* group and *Cochliodon* (with the addition of *H. hemicochliodon*) are probably monophyletic entities within the Hypostomini, there are no general trends in the relationships of the remainder of the species. There is very limited osteological differentiation among the various species of *Hypostomus*, and there are currently no characters that would allow one to break the Hypostomini into meaningful monophyletic groups. The Hypostomini is supported by the following synapomorphies: a hatchet-shaped opercle (78: 1; Fig. 19B), the anterior process of the pterotic-supracleithrum passing halfway through the orbit (112: 1), and a pointed cleithral process (156: 1). The decay index for the Hypostomini is fair (DI = 3) and equal to the decay index of many other similar groups). Because there is support for the Hypostomini as monophyletic, and because there is no information to suggest how to break the Hypostomini into smaller monophyletic entities, only *Hypostomus* is recognized, with *Aphanotorulus*, *Cochliodon*, *Isorineloricaria, Squaliforma*, and *Watawata* as synonyms. In the future, it would probably be useful to

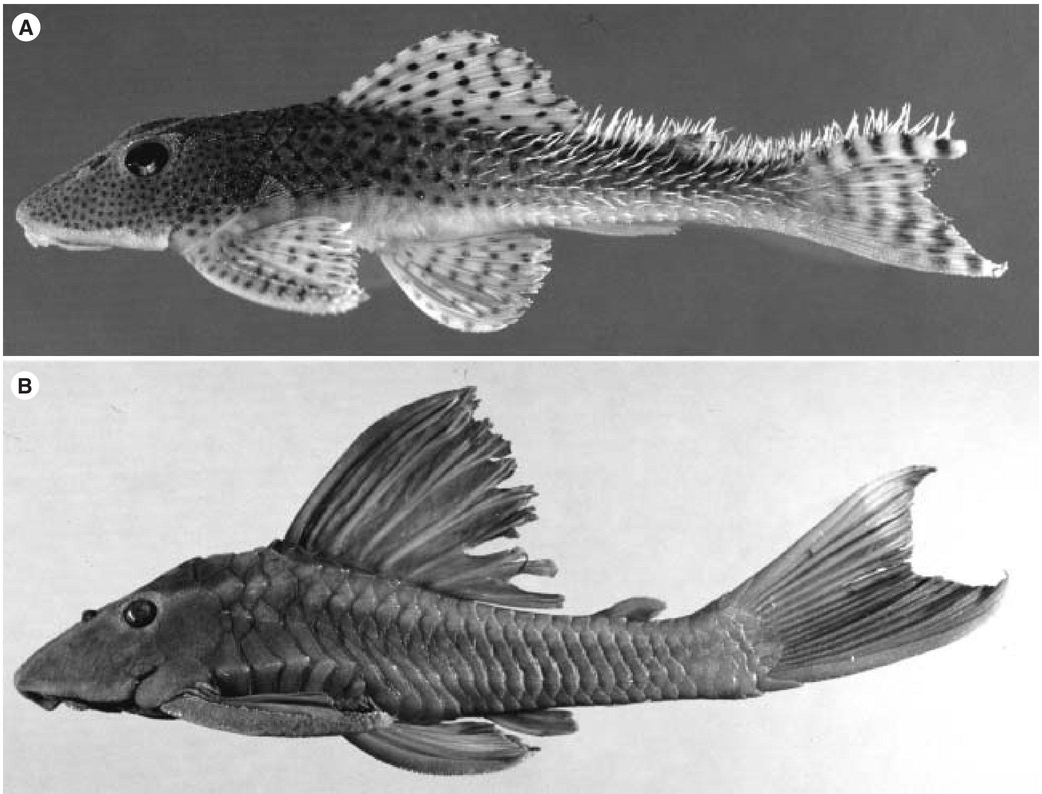

Figure 39. Examples of the Hypostomini. A, *Hypostomus ammophilus* (holotype), INHS 32035, 86.0 mm SL. B, *Hypostomus cochliodon*, UMMZ 206338, 139.8 mm SL. Photographs by K. S. Cummings.

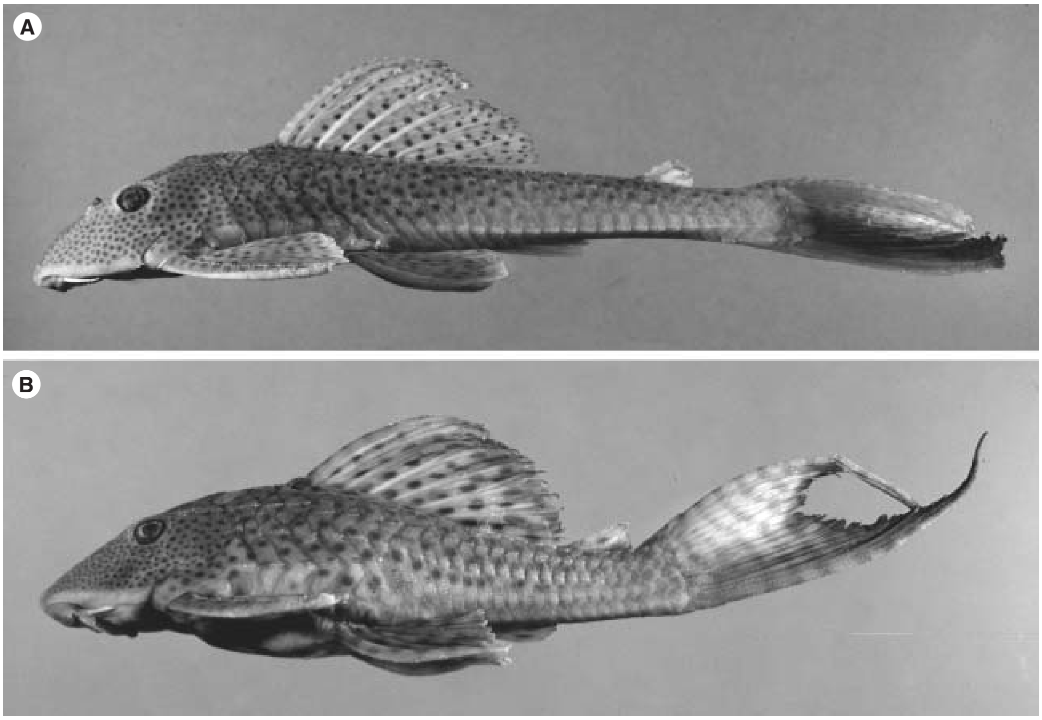

Figure 40. Examples of the Hypostomini. A, *Hypostomus emarginatus* 2, INHS 29085; 196.4 mm SL. B, *Hypostomus plecostomus* (type species of genus), ZMA 105.306, 111.2 mm SL. Photographs by K. S. Cummings.

Table 1. The tribes and genera of the Hypostominae and their synonyms

Tribe	Genus
Ancistrini	
	Acanthicus
	Acanthodemus (syn. *Parancistrus*)
	Ancistomus (syn. *Hemiancistrus*)
	Ancistrus
	Baryancistrus
	Chaetostoma
	Cordylancistrus
	Dekeyseria
	Dolichancistrus
	Exastilithoxus
	Guyanancistrus (syn. *Pseudancistrus*)
	Hemiancistrus
	Hemiancistrus landoni
	Hopliancistrus
	Hypancistrus
	Hypocolpterus (syn. *Chaetostoma*)
	Lasiancistrus
	Leporacanthicus
	Leptoancistrus
	Lipopterichthys (syn. *Chaetostoma*)
	Lithoxancistrus (syn. *Pseudancistrus*)
	Lithoxus
	Megalancistrus
	Neblinichthys
	Oligancistrus (syn. *Spectracanthicus*)
	Panaquolus (syn. *Panaque*)
	Panaque
	Paralithoxus (syn. *Lithoxus*)
	Parancistrus
	Peckoltia
	Peckoltichthys (syn. *Peckoltia*)
	Pristiancistrus (syn. *Ancistrus*)
	Pseudacanthicus
	Pseudancistrus
	Pseudolithoxus
	Scobinancistrus (syn. *Panaque*)
	Sophiancistrus (syn. *Peckoltia*)
	Spectracanthicus
	Stoniella (syn. *Pseudacanthicus*)
	Thysanocara (syn. *Ancistrus*)
	Xenocara (syn. *Ancistrus*)
	Zonancistrus (syn. *Dekeyseria*)
Corymbophanini	
	Corymbophanes
Hypostomini	
	Aphanotorulus (syn. *Hypostomus*)
	Cheiridodus (syn. *Hypostomus*)
	Cochliodon (syn. *Hypostomus*)
	Hypostomus
	Isorineloricaria (syn. *Hypostomus*)
	Squaliforma (syn. *Hypostomus*)
	Watawata (syn. *Hypostomus*)
Pterygoplichthini	
	Glyptoperichthys (syn. *Pterygoplichthys*)
	Hemiancistrus annectens group
	Liposarcus (syn. *Pterygoplichthys*)
	Pterygoplichthys
Rhinelepini	
	Canthopomus (syn. *Pseudorinelepis*)
	Monistiancistrus (syn. *Pseudorinelepis*)
	Pogonopoma
	Pogonopomoides (syn. *Pogonopoma*)
	Pseudorinelepis
	Rhinelepis

break *Hypostomus* into subgenera, doing so is beyond the scope of the present study.

PTERYGOPLICHTHINI

Several problems are evident in Weber's (1991, 1992) treatment of the species of *Pterygoplichthys s.l.* The first is that the phylogeny given is not the single shortest tree. Given the data, a second most parsimonious tree could be constructed with the positions of *Pterygoplichthys* and *Glyptoperichthys* switched, and the tree should have more properly included a trichotomy of *Pterygoplichthys*, *Glyptoperichthys*, and *Megalancistrus*. Second, a close relationship of *Pterygoplichthys* and *Megalancistrus* would suggest that the distinct alteration to the opercle in the Ancistrinae (Schaefer, 1986, 1987) had to evolve twice (see character 75: 1; Fig. 19C, D). Third, none of the genera are uniquely diagnosed. *Glyptoperichthys* with the inclusion of *G. punctatus* Natterer has no unique synapomorphies, although a particular pattern of plates between the dorsal-fin spine and the head putatively diagnoses both *Glyptoperichthys* and *Liposarcus* (Weber, 1992). The pattern is also present in many other loricariids and seems of little phylogenetic usefulness (pers. observ.). The other characteristic that is listed as synapomorphic for *Liposarcus*, thin anterolateral processes of the basipterygium, is polymorphic within the genus (pers. observ.). Finally, it appears that Weber lumps the species of his *Pterygoplichthys* together based on the putatively plesiomorphic condition of the postdorsal plates mentioned above. Two of the species retained in *Pterygoplichthys* (*P. undecimalis* (Steindachner) and *P. zuliaensis* Weber) occur to the west of the Andes in the Río Magdalena and Lago Maracaibo basins, respectively, and the other species (*P. etentaculatus*) occurs on the opposite side of South America in the Rio São Francisco. Although not impossible, the range suggested by Weber (1991, 1992) is unlikely.

The monophyly of *Glyptoperichthys* + *Liposarcus* + *Pterygoplichthys* (Fig. 37) is supported by several characteristics: a diminutive or absent interhyal located posteriorly (26: 0, 27: 2), 8–11 postdorsal vertebrae (121: 2), and eight or more dorsal-fin rays (142: 0). The decay index is fairly high (DI = 4). Of the three genera recognized by Weber, only *Liposarcus* is monophyletic in this analysis, and support is weak (DI = 1, Fig. 36). If monophyly is forced upon both *Glyptoperichthys* and *Pterygoplichthys sensu* Weber (1991, 1992), there are no characteristics that would be synapomorphic for either genus. Thus, in order to retain *Liposarcus* and *Glyptoperichthys* as valid taxa, a new genus would have to be described for *P. zuliaensis* + *P. undecimalis* (these two taxa are most likely to be sisters; Weber, 1992), and a second would have to be described for *G. punctatus*. Given that the species of *Pterygoplichthys*, *Glyptoperichthys*, and *Liposarcus* form a well-diagnosed clade and the fact that they are all readily identifiable from most other species of the Loricariidae by their high number of dorsal-fin rays (ten or more, rarely 9 vs. 7), it is more practical to refer the species to a single genus (*Pterygoplichthys*) and to place *Liposarcus* and *Glyptoperichthys* in the synonymy of *Pterygoplichthys*.

Weber (1992) contends that *Megalancistrus* is most closely related to some *Pterygoplichthys* (Fig. 5). In this study, based on specimens examined, the type species *M. gigas* (Boulenger) shares numerous synapomorphies with *Acanthicus* (most notably an enlarged swimbladder capsule), does not possess a modified stomach, and is clearly not related to *Pterygoplichthys*. At MNRJ I examined some uncatalogued specimens from the Rio São Francisco basin identified as *M. barrae* and which conform to the original description of the species by Steindachner (1910). These are clearly different from, and almost certainly not related to, *M. gigas*, although they are very similar to *Pterygoplichthys*. Because I have not examined the type of *M. barrae* or examined the stomachs of the MNRJ specimens, I defer transferring *M. barrae* to *Pterygoplichthys*.

Based on a unique modification of the stomach (213: 1), I have already suggested (Armbruster, 1998c) that *Pterygoplichthys*, *Glyptoperichthys*, and *Liposarcus* represent a monophyletic group sister to the *Hemiancistrus annectens* group, which consists of several species formerly placed in *Hemiancistrus* (represented in this analysis by *H. holostictus, H. maracaiboensis,* and *H. panamensis*). The results of this study support the conclusion of the earlier one, and the Pterygoplichthini is supported both by the modified stomach and the presence of 2–3 plates between the suprapreopercle and the exposed opercle (81: 2).

The support for the *H. annectens* group is provided by three characters, all of which are also found in some *Hypostomus*: an invagination in the fifth ceratobranchial (11: 1), presence of an interoperculo-mandibular ligament (74: 0), and the anterior process of the pterotic-supracleithrum extending at least midway through the eye (112: 1). However, the *H. annectens* group does not form a monophyletic group with *Hypostomus* in the phylogeny because of the shared presence of a modified stomach with *Pterygoplichthys* and the presence of evertible cheek plates. The connective tissue sheet found in the Pterygoplichthini is a complex characteristic found in no other loricariids. Despite the fact that many *Hypostomus* live in waters at least as hypoxic as those where *Pterygoplichthys* and the *H. annectens* group occur, they never develop a connective tissue sheet. Because there is support for the monophyly of the *H. annectens* group and because it is not closely related to *Hypostomus* in the phylogenetic analyses, a new genus for the *H. annectens* group should be described. This genus will be described in a future manuscript detailing the Pterygoplichthini.

ANCISTRINI

Isbrücker (1980) and Schaefer (1986, 1987) diagnosed the Ancistrini (then the Ancistrinae) on the basis of the presence of evertible cheek odontodes and/or characteristics associated with them; however, as mentioned above, evertible cheek odontodes are also found in the Pterygoplichthini and support the sister-group relationship of the Ancistrini and Pterygoplichthini. Schaefer (1986, 1987) further diagnoses the Ancistrini by the presence of a derived opercle (75: 1/2); however, *Hemiancistrus* sp. Brazil that is the sister to all other members of the Ancistrini has an unmodified opercle (75: 0). With evertible cheek plates and modified opercles no longer able to diagnose the Ancistrini, the Ancistrini is left with no significant synapomorphies (Appendix 3) and it is appropriate to place Ancistrinae into the synonymy of Hypostominae.

Within the Ancistrini, several taxonomic problems are inherent. No characteristics are found to suggest that *Cordylancistrus* is monophyletic (Fig. 38). The basic difference between species of *Chaetostoma*, *Cordylancistrus*, *Dolichancistrus*, and *Leptoancistrus* is the lack of plates along the snout of *Chaetostoma*; otherwise, the species are similar. Given the phylogeny, there are several possibilities of how to make the taxonomy reflect phylogeny, including describing a new genus for *Cordylancistrus platyrhynchus* (Fowler), placing it in *Chaetostoma*, or placing *Cordylancistrus*, *Dolichancistrus*, and *Leptoancistrus* into the synonymy of *Chaetostoma*. I act conservatively and place *C. platyrhynchus* in *Chaetostoma* with the genus diagnosed by the following characteristics: loss of suture between the pterotic-supracleithrum and hyomandibula (34: 0), loss of the hyomandibula angled mesially so that the opercle is held almost perpendicular to the main body axis (42: 0), the anterior process of the pterotic-supracleithrum is slightly deflected mesially (111: 0), reversal to narrow ventral process of sphenotic (116: 0), and tip of transverse process of the complex centrum of the Weberian apparatus not contacting the pterotic-supracleithrum (135: 1).

Although I have not examined *Lipopterichthys* osteologically, the genus is virtually indistinguishable from *Chaetostoma* except for the lack of adipose and anal fins (one species of *Chaetostoma*, *C. venezuelae* Schultz, shares the loss of the adipose fin). There are several specimens of *Chaetostoma* at the Auburn University Museum from near the type locality of *Lipopterichthys carrioni* (AUM 28213, 28215, 28222, and 28227). These are variable in the presence of the adipose fin and some have very reduced anal fins. It is probable that the type of *Lipopterichthys* is simply a morphotype of this variable species of *Chaetostoma*; therefore, *Lipopterichthys* is recognized as a synonym of *Chaetostoma*.

Of the genera of the Hypostominae described in Isbrücker *et al.* (2001), the only one that can be adequately supported as a genus is *Pseudolithoxus* Isbrücker and Werner. *Pseudolithoxus* was described as the *Lasiancistrus anthrax* group of Armbruster & Provenzano (2000), although they provided little diagnostic information. Isbrücker *et al.* (2001) only repeat Armbruster and Provenzano's diagnosis. *Pseudolithoxus anthrax* lacks most of the synapomorphies for *Lasiancistrus* and shares with other *Lasiancistrus* only the derived presence of a bifurcated anterior process of the pterotic-supracleithrum (113: 1). In addition, *P. anthrax* lacks synapomorphies of *Lasiancistrus* + *Ancistrus*, including the presence of tentacules on the snout larger than the supporting odontodes and tentacules on the pectoral-fin spines (Sabaj *et al.*, 1999). *Pseudolithoxus* shares with *Pseudancistrus* the trait of both males and females developing hypertrophied odontodes along the snout anterior to the cheek. Both males and females also develop extremely hypertrophied but flexible odontodes on the pectoral-fin spine of a type seen elsewhere only in *Lithoxus*. Given the phylogeny, hypertrophied odontodes along the snout in males and females and extremely hypertrophied odontodes on the pectoral-fin spines could be used as synapomorphies for *Pseudolithoxus*; however, there are no other characteristics that serve to diagnose the genus.

Lasiancistrus is almost certainly a polyphyletic genus. Heitmans, Nijssen & Isbrücker (1983) describe several species that appear to be unrelated to the type species of *Lasiancistrus* [*L. heteracanthus* (Günther)]. In addition, an examination of type specimens of the species of *Lasiancistrus sensu* Isbrücker (1980) reveals several that more properly should be placed in other genera (including *Chaetostoma*, *Hemiancistrus*, *Peckoltia*, and Pseudancistrus). *Lasiancistrus* should be restricted to those species with three rows of plates on the caudal peduncle and the presence of whisker-like odontodes on the evertible cheek plates. *Lasiancistrus* will be detailed in a future publication on the Ancistrini, and the species that do not belong in *Lasiancistrus* will be discussed then.

Hemiancistrus sensu Isbrücker (1980) is polyphyletic with several species representing the sister to *Pterygoplichthys* as mentioned above, and the remainder in several clades of the Ancistrini (Fig. 38). The type species of *Hemiancistrus*, *H. medians*, is clearly a member of the Ancistrini, although no specimens are available for osteological examination. Based on superficial examination it appears that *H. medians* is closely related to *Peckoltia*. Three taxa clearly unrelated to *Hemiancistrus s.s.* are *Hemiancistrus* sp. Brazil, *H. landoni*, and *H. megacephalus*. *Hemiancistrus* sp. Brazil lacks the modified opercle diagnostic for the remainder of the Ancistrini. It is likely that a new genus needs to be described for *Hemiancistrus* sp. Brazil and possibly other south-eastern Brazilian *Hemiancistrus* (see Cardoso & Malabarba, 1999). The distribution of *H. landoni* is restricted to the Gulf of Guayaquil drainage of western Ecuador. No other *Hemiancistrus* (*H. hammarlundi* is also described from west of the Andes, but is a synonym of *H. landoni*, pers. observ.) or the phenetically similar *Peckoltia* occur to the west of the Andes. *H. megacephalus* was well-supported as sister to *Pseudancistrus* and is transferred to *Pseudancistrus*.

Peckoltia is very problematic and is polyphyletic in this analysis (Fig. 38). In addition, it is likely that the type species of *Hemiancistrus* (*H. medians*) is related to *Peckoltia*. Because the relationships of *Peckoltia* are not resolved and because there is the potential that some species of *Hemiancistrus* may be congeneric with species of *Peckoltia*, no changes to the taxonomy are made. Before the taxonomic problems inherent in *Peckoltia* and *Hemiancistrus* can be solved, *Peckoltia* and *Hemiancistrus* must first be revised. Isbrücker *et al.* (2001) describe *Sophiancistrus* for *P. ucayalensis*; however, this study is not conclusive on the relationships of *P. ucayalensis*. Until such time as a future study can conclusively determine whether *Sophiancistrus* should be recognized, I recognize *Sophiancistrus* as a synonym of *Peckoltia*.

Armbruster (2002) recognized a new species of *Hypancistrus* and suggested that *Hypancistrus* could be diagnosed by bent adductor palatini crest and loss of the anterior contact of the metapterygoid and lateral ethmoid. In this study, *Hypancistrus* was not recovered as monophyletic; however, there is little support for relationships of species closely allied with *Peckoltia* (such as those of *Hypancistrus* and *Parancistrus*) in the analysis and there is no justification for splitting *Hypancistrus* at this time.

Schaefer & Stewart (1993) provide compelling evidence that *Panaque* is monophyletic, although they did not examine *Scobinancistrus* which was found to be the sister to *P. nigrolineatus* in this analysis (Fig. 38). *Scobinancistrus* shares with *Panaque* the presence of tall ridges on the hyomandibula and preopercle, a characteristic they listed as a synapomorphy for *Panaque*. This ridge is much taller in *Panaque* and *Scobinancistrus* than in most other loricariids (44), but I considered it too subjective to include an additional state of the levator arcus palatini crest in this analysis. Schaefer and Stewart also list the presence of an elongate, narrow metapterygoid channel as a synapomorphy for *Panaque*. *Scobinancistrus* lacks the lateral wall of the pterygoid channel and, hence, the state cannot be homologized with that seen in

Panaque. The third synapomorphy for *Panaque* (hypertrophied muscles between the jaw rami) was not examined in *Scobinancistrus* due to lack of materials. *Scobinancistrus* differs from *Panaque* mainly in the lack of true spoon-shaped teeth; however, the teeth in *Scobinancistrus* appear as if they might be elongated spoon-shaped teeth (Fig. 35D vs. C).

Isbrücker *et al.* (2001) describe *Panaquolus* as a new genus for the small members of *Panaque* (such as *P. maccus* and *P. albomaculatus* in this study); however, Chockley & Armbruster (2002) placed *Panaquolus* in the synonymy of *Panaque*, stating that there was no reason to accept *Panaquolus* as valid. In order for the taxonomy to reflect phylogeny, either *Panaquolus* must be recognized or *Scobinancistrus* placed into the synonymy of *Panaque*. In order to make the taxonomy reflect phylogeny more effectively it is better to recognize larger genera and to break them down into subgenera; thus, I retain *Panaquolus* as a synonym of *Panaque,* place *Scobinancistrus* into the synonymy of *Panaque*, and recognize three subgenera (*Panaque, Panaquolus*, and *Scobinancistrus*) in *Panaque*.

Oligancistrus Rapp Py-Daniel and *Spectracanthicus* are supported as sister taxa (Fig. 38) by the mesial wall of the metapterygoid being much taller than the lateral wall (55: 1), a spoon-shaped anterior process of the metapterygoid (58: 1; Fig. 15D), a deep pouch on the lateral ethmoid (98: 1; Fig. 20A), and expansion of the dorsal-fin membrane such that it contacts the preadipose plate (143: 1; Fig. 27B). The main difference between the two genera is that *Spectracanthicus* has lost evertible cheek plates and the modified opercle diagnostic of the Ancistrini. *Oligancistrus* appears to be in the process of losing evertibility of the cheek plates (they are only weakly evertible when compared to those of other members of the Ancistrini) and the opercle is intermediate between that of closely related Ancistrini and *Spectracanthicus*.

Given the many reversals associated with the cheek, *Spectracanthicus* is a very well-diagnosed genus as it now stands. *Oligancistrus*, however, is not. Given the strong support for *Spectracanthicus* + *Oligancistrus* as monophyletic (*Oligancistrus* shows trends towards losing the cheek armature and is not-well diagnosed; the two genera are currently monotypic and monotypic genera cannot express phylogeny), *Oligancistrus* is recognized as a synonym of *Spectracanthicus*.

Pseudancistrus has traditionally been identified by the presence of hypertrophied odontodes along the snout in both males and females and by an inability to evert the cheek plates. Among other Ancistrini, only *Pseudolithoxus, Lithoxancistrus,* and some members of *Guyancistrus* share the presence of hypertrophied snout odontodes in males and females with *Pseudancistrus*. It is clearly not closely related to *Pseudolithoxus*, although it shares numerous synapomorphies with *Lithoxancistrus* and *Guyancistrus*. A monophyletic group consisting of *Hemiancistrus megacephalus, Guyancistrus, Lithoxancistrus,* and *Pseudancistrus* is well supported with a decay index value of five and the following synapomorphies: loss of a suture between the pterotic-supracleithrum and hyomandibula (34: 0), loss of contact between the hyomandibula and prootic (35: 1), a spoon-shaped anterior process of the metapterygoid (58: 1), a thin nasal bone (105: 0), a sphenotic that does not contact the posteriormost infraorbital (117: 1), and a short ventral ridge of the basipterygium (172: 1). To rectify the paraphyly and retain *Guyancistrus* and *Lithoxancistrus* as valid genera, it is likely that several more poorly diagnosed genera would have to be described; thus, the best solution is to place *Guyancistrus* and *Lithoxancistrus* in the synonymy of *Pseudancistrus* and to transfer *H. megacephalus* to *Pseudancistrus*.

Rapp Py-Daniel (1985) describes *Dekeyseria* for two species (*D. amazona* and *D. scaphirhyncha*). In addition, she suggests that *Peckoltia brachyura*, *P. picta*, and *P. pulcher* are also *Dekeyseria*, but does not formally place the species in *Dekeyseria*. Schaefer (1986) does place the species in *Dekeyseria*, but Burgess (1989) and Burgess & Finley (1996) retain them in *Peckoltia*. All the species mentioned are unique among the Ancistrini for a combination of the presence of highly keeled lateral plates (198: 1), three rows of plates along the caudal peduncle, and several additional synapomorphies: reversal to posteriorly placed interhyal (26: 0; Fig. 13B), an enlarged neural arch anterior to the first dorsal-fin pterygiophore (125: 1), a reversal to thin ribs (129: 0), a trapezoidal cleithrum (155: 1), and a straight anterolateral process of the basipterygium (167: 2; Fig. 33B). Schaefer (1986) is correct in placing the species in *Dekeyseria* (Fig. 38). In addition, *Plecostomus niveatus* La Monte has highly keeled lateral plates and three rows of plates on the caudal peduncle (pers. observ.), and is recognized here as *Dekeyseria niveata*. Isbrücker *et al.* (2001) recognize *Zonancistrus* for some species of *Dekeyseria* based on coloration (alternating brown and tan bands in *Zonancistrus* and grey in *Dekeyseria*). However, there is no reason to recognize *Zonancistrus* as distinct based simply on colour differences, and I recognize it as a synonym of *Dekeyseria*.

The relationships of the genera of the Ancistrini in Schaefer's (1986) study and this study (Fig. 38) differ in many respects. The greatest similarities are the recognition of *Chaetostoma*, *Dolichancistrus*, and *Leptoancistrus* as a clade and this group plus *Ancistrus*, *Exastilithoxus*, *Lasiancistrus*, and *Lithoxus* as a clade. In this study, *Lasiancistrus s.s.* is found to be the sister of *Ancistrus* instead of *Chaetostoma* as determined by Schaefer (1986). Support for a clade of *Ancistrus* + *Lasiancistrus* comes mainly from the recognition of the presence of snout tentacles/tentacules in *Lasiancistrus* (208: 1/2). *Ancistrus* has long been diagnosed by the presence of elongate fleshy structures (tentacles, 208: 2) on the top of the snout in males. Although *Lasiancistrus* does not have tentacles as long as those in *Ancistrus*, short tentacules are present on the snout plates (208: 1; Sabaj *et al.*, 1999). Several other characteristics corroborate the evolution of these snout tentacles: a spindle-shaped hypohyal (21: 1), a slender quadrate (64: 0) and tentacules on the pectoral-fin spine that are larger than their supporting odontodes (209: 2).

The placement of *Lasiancistrus* as sister to *Chaetostoma* by Schaefer (1986) is based on three putative synapomorphies. The first is an extension of the quadrate for articulation with the canal plate (65: 1; Fig. 13B, D) which is found in this study to have evolved independently in several lineages. The second is a sculpturing of the anterior edge of the anterohyal; however, the states seen in *Lasiancistrus* and *Chaetostoma* are not homologous (see Fig. 8B vs. D). The last, a mesial process on the second branchiostegal (6: 1), is not present in the *Lasiancistrus* I examined.

Another major difference between this study and that of Schaefer (1986) is the placement of *Pseudacanthicus*. In this study it is part of a large clade with the rest of the *Acanthicus* group, *Hypancistrus*, *Parancistrus*, *Panaque*, and *Peckoltia* (referred to below as the *Panaque* clade). In all of the *Panaque* clade except *Acanthicus* and *Peckoltia oligospila*, the dentaries form an angle averaging less than or equal to 80° (69: 1) and the mesethmoid disk extends anterior to the main body of the mesethmoid (101: 1). In addition, all except *P. oligospila* have a longitudinal ridge on the quadrate (68: 1; Fig. 15H, I). Support in Schaefer (1986) for the placement of *Pseudacanthicus* with *Hemiancistrus* (the latter is a combination of several unrelated taxa in his analysis), *Ancistrus*, the *Lithoxus* group, *Lasiancistrus*, and *Chaetostoma* is based on the attachment of the canal plate to the suspensorium (which I found in nearly all the Ancistrini) and a ridge (or process) ventrally on the suspensorium for the attachment of the canal plate. The process contacted by the canal plate is on the preopercle in *Pseudacanthicus* while it is on the quadrate in the other taxa (when present), and I did not consider the two processes to be homologous.

The only described genus of the Ancistrini that was not examined for this study is *Hopliancistrus* Isbrücker and Nijssen. It is difficult to speculate on the phylogenetic position of *Hopliancistrus* based on the specimens I have examined. It appears to be very similar to *Lasiancistrus*, but lacks whiskerlike odontodes. It shares with *Ancistrus* and *Lasiancistrus* the presence of very strongly evertible cheek plates and very strong hypertrophied odontodes associated with them, and probably belongs along the branch that includes *Ancistrus* and *Lasiancistrus*; however, *Hopliancistrus* must be examined in detail before its relationships can be determined.

LITHOGENES

In the analysis, *Lithogenes* grouped with *Astroblepus* and not the Loricariidae. *Lithogenes* and *Astroblepus* are diagnosed by two unique characteristics: a cylindrical connecting bone (140: 1) and a first pelvic-fin ray that is completely split in two (176: 1). In addition, there is one other characteristic synapomorphic for *Astroblepus* + *Lithogenes* that is shared only with *Hemipsilichthys nudulus*, loss of the nuchal plate (146: 0), and several other characteristics with a low CI (see Appendix 3). However, other morphological data (S. A. Schaefer, pers. comm.) seem to suggest that *Lithogenes* is sister to all other loricariids. More information needs to be obtained to fully resolve the conflict of the relationships of *Lithogenes*, which is left in the Loricariidae until further evidence becomes available.

ADDITIONAL INFORMATION

For keys, more detailed information on some genera and species, photographs, and lists of taxa in each genus, please visit the following website: http://george.cosam.auburn.edu/usr/key_to_loricariidae/lorhome/lorhome.html.

DESCRIPTIONS

The following descriptions are of the loricariid subfamilies Neoplecostominae and Hypostominae and the tribes of the Hypostominae. The Loricariinae was examined by Rapp Py-Daniel (1997) (who is currently involved in a further study of the subfamily) and the Hypoptopomatinae by Schaefer (1991, 1998) and Reis & Schaefer (1998). Limited information is presented for the Corymbophanini (Armbruster *et al.*, 2000) and the Rhinelepini, which have already been examined in depth (Armbruster, 1998b; Quevedo & Reis, 2002). The Ancistrini and the Pterygoplichthini are only briefly diagnosed and will be the subjects of future study. A new subfamily for *Delturus* and *Upsilodus* will also be described at a later date.

SUBFAMILY NEOPLECOSTOMINAE REGAN, 1904

Includes:
Hemipsilichthys Eigenmann & Eigenmann, 1889
Isbrueckerichthys Derjist, 1996
Kronichthys Miranda Ribeiro, 1908

Neoplecostomus Eigenmann & Eigenmann, 1888
Pareiorhina Gosline, 1947

Type genus: Neoplecostomus Eigenmann & Eigenmann, 1888: 170–171

Diagnosis: The Neoplecostominae is not diagnosed by any unique characteristic and was not monophyletic in this analysis. The genera are clearly not in the Hypostominae and the most conservative act is to recognize them in the Neoplecostominae until more information becomes available.

Description: Species of the Neoplecostominae are convergent with *Chaetostoma* with which they share a high-montane, swift-flowing river habitat. Colour pattern typically dark brown and mottled or with dorsal saddles. Abdomen usually unplated although some deeply embedded plates present in *Isbrueckerichthys* and *Neoplecostomus*. Four or more predorsal plates. Spinelet a small, square ossification or absent. Generally at least one column of plates, consisting of three rows, on caudal peduncle (except *Isbrueckerichthys* and *Hemipsilichthys nudulus*, which have five or more rows).

Comparisons: The Neoplecostominae is very similar to the *Chaetostoma* group of the Ancistrini; however, members of the Neoplecostominae lack evertible cheek plates, the spinelet (covered with skin in the *Chaetostoma* group) usually supports odontodes or is absent, and the nuchal plate is exposed (vs. covered by plates). Also, the *Chaetostoma* group is restricted to the Andes and some of the Tipuis of the Guiana Shield, while the Neoplecostominae is found in south-eastern Brazil. The Neoplecostominae differs from *Lithogenes* by being completely plated laterally and dorsally [*Hemipsilichthys nudulus* is incompletely plated and can be distinguished from *Lithogenes* by its having (1) hypertrophied odontodes on the leading edge of the pectoral fins and along the snout in nuptial males, and (2) plates anterior to the dorsal fin]; from *Delturus* + *Upsilodus* by its lack of a postdorsal ridge of several median preadipose plates (*H. nudulus* has numerous, median, preadipose plates, but they are not raised and the adipose fin is absent); from the Hypoptopomatinae by having, maximally, only a small part of the coracoid strut of the pectoral girdle exposed ventrally (vs. all or most of the girdle exposed and supporting odontodes) and by lacking a bony covering over the adductor fossa of the pelvic girdle; from the Loricariinae by having a round to oval (vs. a compressed, rectangular) caudal peduncle; from most of the Hypostominae by having a square (vs. triangular) dorsal-fin spinelet or lacking the spinelet; and from the *Chaetostoma* group as above.

SUBFAMILY HYPOSTOMINAE KNER,1853

Synonyms:
Ancistri Kner, 1853
Hypostomiden Kner, 1853
Lictores Kner, 1853
Plecostomiformes Bleeker, 1862
Chaetostomidi Fowler, 1958

Includes:
Ancistrini Kner, 1853
Corymbophanini new tribe
Hypostomini Kner, 1853
Pterygoplichthini new tribe
Rhinelepini new tribe

Type genus: Hypostomus Lacépède, 1808.

Diagnosis: The Hypostominae is diagnosed by a unique characteristic: the lower lobe of the hypural plate longer than the upper (123: 1; Fig. 24B). Other characteristics considered synapomorphic for Hypostominae are: a long accessory process on the first ceratobranchial (7: 2; Fig. 9E; reversed in some groups), a small canal plate (83: 1), a V-shaped spinelet (148: 0), and a posteroventral ridge on the basipterygium (173: 1; Fig. 33C, E, F).

Description: With the inclusion of the Ancistrinae (and exclusion of some genera formerly within it) the Hypostominae becomes the largest of the loricariid subfamilies in number of species (366 currently valid). Size is incredibly variable within the subfamily, which includes small genera such as *Lithoxus* (50 mm) and the largest of all loricariids, *Acanthicus* (maximum size probably around 1 m). Hypostomines are typically bulkier than other loricariids and generally have thicker plates than neoplecostomines. The tribe and generic descriptions below provide more information on the diversity of forms.

Comparisons: The best character to distinguish the Hypostominae from most other loricariids is the development of the spinelet. In all the Hypostominae, the spinelet is large and V-shaped and clearly slides under the nuchal plate, whereas it is square or absent in most other loricariids and, when present, does not slide under the nuchal plate. Some hypoptopomatines have a triangular spinelet, but these species can be distinguished from the Hypostominae by a completely or nearly completely exposed pectoral girdle (vs. at most some odontodes supported by the coracoid strut), the adductor fossa of the pectoral girdle covered by bone (vs. wholly exposed), and by having the fenestrae of the pterotic-supracleithrum larger ventrally than dorsally (vs. all fenestrae of about equal size). *Delturus* also has a triangular spinelet but can be distinguished by the presence of an adipose fin with a postdorsal ridge (all hypostomines with a postdorsal ridge lack an adipose fin). The *Chaetostoma* group and some *Ancistrus* have the spinelet covered in skin; these species can be distinguished from the other loricariid subfamilies by the presence of evertible cheek plates with hypertrophied odontodes. The Hypostominae further differs from the Loricariinae by having a round, oval, or triangular cross-section of the caudal peduncle (vs. rectangular and depressed).

TRIBE ANCISTRINI KNER, 1853

Includes:
Acanthicus Agassiz, 1829
Acanthodemus Marschall, 1873 (synonym of *Parancistrus*)
Ancistomus Isbrücker and Seidel (synonym of *Hemiancistrus*)
Ancistrus Kner, 1854
Baryancistrus Rapp Py-Daniel, 1989
Chaetostoma Tschudi, 1845
Cordylancistrus Isbrücker, 1980
Dekeyseria Rapp Py-Daniel, 1985
Dolichancistrus Isbrücker, 1980
Exastilithoxus Isbrücker & Nijssen, 1979
Guyancistrus Isbrücker, 2001 (synonym of *Pseudancistrus*)
Hemiancistrus Bleeker, 1862
Hopliancistrus Isbrücker & Nijssen, 1989
Hypancistrus Isbrücker & Nijssen, 1991
Hypocolpterus Fowler, 1943 (synonym of *Chaetostoma*)
Lasiancistrus Regan, 1904
Leporacanthicus Isbrücker & Nijssen, 1989
Lipopterichthys Norman, 1935 (synonym of *Chaetostoma*)
Lithoxancistrus Isbrücker, Nijssen & Cala, 1988 (synonym of *Pseudancistrus*)
Lithoxus Eigenmann, 1909
Megalancistrus Isbrücker, 1980
Oligancistrus Rapp Py-Daniel, 1989 (synonym of *Spectracanthicus*)
Panaque Eigenmann & Eigenmann, 1889
Panaquolus Isbrücker & Schraml, 2001 (synonym of *Panaque*)
Paralithoxus Boeseman ,1982 (synonym of *Lithoxus*)
Peckoltia Miranda Ribeiro, 1912
Parancistrus Castelnau, 1855
Pristiancistrus Fowler, 1945 (synonym of *Ancistrus*)
Pseudacanthicus Bleeker, 1862
Pseudancistrus Bleeker, 1862
Pseudolithoxus Isbrücker & Werner, 2001
Neblinichthys Ferraris Isbrücker & Nijssen 1986
Scobinancistrus Isbrücker & Nijssen, 1989
Sophiancistrus Isbrücker & Seidel, 2001 (synonym of *Peckoltia*)
Spectracanthicus Nijssen & Isbrücker, 1986
Stoniella Fowler, 1914 (synonym of *Pseudacanthicus*)
Thysanocara Regan, 1906 (synonym of *Ancistrus*)
Xenocara Regan, 1904 (synonym of *Ancistrus*)
Zonancistrus Isbrücker, 2001 (synonym of *Dekeyseria*)

Synonyms:
Acanthicini Bleeker, 1862
Hopliancistrini Isbrücker & Nijssen, 1989
Lithoxina Isbrücker, 1980
Pseudacanthicini Isbrücker, 1980
Pseudacanthicina Isbrücker, 1980
Spectracanthicina Nijssen & Isbrücker, 1989

Type genus: Ancistrus Kner, 1854

Diagnosis: The Ancistrini is not diagnosed by any unique characteristics. Those considered synapomorphic but which may be lost in some taxa are: a tall levator arcus palatini crest (44: 2), a vertically orientated preopercle (61: 1), and contact of the frontal with the orbit (94: 0). The majority of species of the Ancistrini (except *Hemiancistrus* sp. Brazil) are supported by a unique synapomorphy: a modification of the opercle into a bar or sickle-shaped structure (75: 1/2; Fig. 19C, D; lost in *Spectracanthicus*; Fig. 19A, B, D). More information on the Ancistrini will be presented in a future publication.

Comparisons: The Ancistrini (except some *Pseudancistrus* and *Spectracanthicus*) can be distinguished from all other loricariids except the Pterygoplichthini by the presence of evertible cheek plates with hypertrophied odontodes. It can be distinguished from the Pterygoplichthini (see the Pterygoplichthini description below). *Spectracanthicus* can be distinguished from all other non-Ancistrini loricariids except *Delturus* by having the dorsal-fin membrane contacting the preadipose plate; and from *Delturus* by having only one preadipose plate (vs. 3+) and by having highly angled jaws (dentary angle less than 80° vs. greater than 90°). *Pseudancistrus* without evertible cheek plates can be distinguished from most of the Hypostomini, *Pogonopoma parahybae*, and *Rhinelepis* by having hypertrophied odontodes along the snout anterior of the cheek; from the Rhinelepini by having a dorsal flap of the iris present so that the eye appears bilobed (vs. dorsal flap absent, iris round); and from most of the Hypostomini, the Pterygoplichthini, and the Rhinelepini by lacking plates on the abdomen (vs. plates present).

CORYMBOPHANINI NEW TRIBE

Type genus: Corymbophanes (only genus)

GENUS *CORYMBOPHANES* EIGENMANN, 1909

Type species: Corymbophanes andersoni Eigenmann, 1909

Includes:
Corymbophanes andersoni Eigenmann, 1909
Corymbophanes kaiei Armbruster & Sabaj, 2000 (in Armbruster *et al.*, 2000)

Diagnosis: Corymbophanes is not diagnosed by any unique characteristics. Those considered synapomorphic are: mesial surface of first epibranchial forming a blade (15: 1), anterior-facing process on the fourth epibranchial very long (16: 1; Fig. 12B), upper pharyngeal tooth plate round, teeth uniformly distributed (30: 0), hyomandibula deflected beyond posterior margin (46: 1), anterior process of metapterygoid spoon-shaped (58: 1), exit of preopercular latero-sensory canal anterior to posteroventral edge of quadrate (62: 1), preopercular latero-sensory canal extended posteriorly (63: 1), contact of canal plate with suspensorium present (85: 1), three or more preadipose plates (138: 0), and a postdorsal ridge of median unpaired plates (192: 1). See description and diagnosis of *Corymbophanes* in Armbruster *et al.* (2000).

Comparisons: Corymbophanes can be distinguished from all loricariids except some *Chaetostoma*, *Leptoancistrus*, and *Hemipsilichthys nudulus* by the presence of a postdorsal ridge made up of several median, unpaired plates and a lack of an adipose-fin membrane. *Corymbophanes* can be distinguished from *Chaetostoma* and *H. nudulus* by the presence of plates on the snout, from *Chaetostoma* and *Leptoancistrus* by the lack of evertible plates on the cheek and three (vs. five) rows of plates on the caudal peduncle, and from *H. nudulus* by having the sides and back completely plated (vs. partially unplated).

TRIBE HYPOSTOMINI KNER, 1853

Type genus: Hypostomus (only genus)

GENUS *HYPOSTOMUS* LACÉPÈDE, 1803 (FIGS 39, 40)

Type species: Acipenser plecostomus Linnaeus, 1758

Synonyms:
Aphanotorulus Isbrücker & Nijssen, 1982
Cheiridodus Eigenmann, 1922
Cochliodon Heckel, 1854
Isorineloricaria Isbrücker, 1980
Plecostomus Gronovius, 1754
Squaliforma Isbrücker & Michels, 2001
Watawata Isbrücker & Michels, 2001

Includes:
See Appendix 4.

Diagnosis: Hypostomus is not diagnosed by any unique characteristics. Characteristics considered synapomorphic for *Hypostomus* are: a hatchet-shaped opercle (78: 1; Fig. 19B), the anterior process of the pterotic-supracleithrum passing halfway through the orbit (112: 1), and a pointed cleithral process (156: 1). In addition, in several trees, the bulk of *Hypostomus* [except *H. commersoni* Valenciennes and *H. boulengeri* (Eigenmann and Kennedy)] are supported by a pointed transverse process of the Weberian apparatus that is fused to the pterotic-supracleithrum (132: 1, 133: 1; Fig. 25B).

Description: Small to large loricariids that defy a unifying description. Colour pattern varies from having a white ground colour and black spots, to brown and spotted, to black with red, gold, or white spots. Abdomen also varies in colour from white to black and may be spotted or not. Abdomen ranges from naked to completely plated (usually with plates). Caudal fin forked with the lower lobe longer than upper. Two or three predorsal plates. Five rows of plates on caudal peduncle (except *H. dlouhyi* Weber which has three). Body typically stout, but *H. emarginatus* group, *H. cordovae* (Günther), *H. spiniger* (Hensel), and *H. spinosissimus* with elongated bodies. Lateral plates keeled or not. Cheek plates evertible to *c.* 30°.

Comparisons: Hypostomus is most similar to the *Hemiancistrus annectens* group. Externally, it is very difficult to separate from the *H. annectens* group, differing mainly in the lack of highly evertible cheek plates with hypertrophied odontodes in adults (cheek odontodes are present in *H. spinosissimus*, but they are present only in nuptial males, are not highly evertible, and are accompanied by a lengthening of nearly all of the odontodes on the body) and by usually having only one (occasionally two) row of plates between the suprapreopercle and the exposed opercle (vs. three, occasionally two). The only species of *Hypostomus* sympatric or potentially sympatric with the *H. annectens* group are members of the *H. cochliodon* group which have wide, spoon-shaped teeth (vs. viliform teeth) and *H. spinosissimus*, *H. tenuicauda* and *H. villarsi* which have a white or tan ground colour (vs. dark brown) and are elongate (vs. short); thus, most *Hypostomus* can be distinguished from the *H. annectens* group by having a distribution east of the Andes (vs. west).

Hypostomus can be distinguished from most *Pterygoplichthys* by the same characters as for the *H. annectens* group with the addition of having only seven (vs. 9–14) dorsal-fin rays; most species from all *Pogonopoma* and *Rhinelepis* by having a single, medium-sized plate posterior to the pterotic-supracleithrum (vs. many small plates); from *Pseudorinelepis* and *Rhinelepis* by usually having an adipose fin (adipose fin is also missing in *H. levis* of the *H. cochliodon* group); from all the Rhinelepini by generally having one unbranched and four branched anal-fin rays (vs.

one unbranched and five branched rays) and a dorsal flap of the iris making the eye appear bilobed (vs. iris round, without flap); and from most of the Ancistrini by a lack of highly evertible cheek plates with hypertrophied odontodes (*Spectracanthicus* lacks evertible cheek plates with hypertrophied odontodes and can be distinguished by having the dorsal-fin membrane attached to the preadipose plate; some *Pseudancistrus* lack evertible cheek plates and can be distinguished by a combination of the presence of hypertrophied odontodes along the snout and on the cheek and no plates on the abdomen).

Sexual dimorphism: Most males develop hypertrophied odontodes on the leading edge of the pectoral-fin spine and the distal tip of the spine may become swollen. Additionally, in members of the *H. emarginatus* clade, males develop hypertrophied odontodes on the body during the breeding season (Armbruster & Page, 1996); these odontodes are normally best developed on the posterolateral plates, the caudal-fin spines, and the adipose-fin spine. In addition, *H. spinosissimus* develops hypertrophied odontodes over the entire lateral and dorsal surfaces of the body including the cheeks (Armbruster & Page, 1996). Nuptial males of some species of the *H. cochliodon* group develop wider, more widely spaced odontodes on the lateral plates (the odontodes are not longer in nuptial males).

Ecology: Hypostomus are essentially ubiquitous across their range. Most species are lowland, sluggish stream- and lake-dwellers usually found associated with submerged wood; however, many species may be found among rocks in piedmont to mountain streams with moderate to swift flow. *Hypostomus* may be found above substrates ranging from mud and detritus, to gravel and cobbles and boulders, to sand. Many spawn in hollows dug into mud banks or within hollow logs (Burgess, 1989).

Range: Throughout most of the range of loricariids except for drainages west of the Río Atrato.

PTERYGOPLICHTHINI NEW TRIBE

Type genus: Pterygoplichthys Gill, 1858

Includes:
Glyptoperichthys Weber, 1991 (synonym of *Pterygoplichthys*)
The *Hemiancistrus annectens* group (undescribed genus)
Liposarcus Günther, 1864 (synonym of *Pterygoplichthys*)
Pterygoplichthys Gill, 1858

Diagnosis: The Pterygoplichthini is diagnosed by a unique characteristic: the presence of an enlarged stomach that is attached to the dorsal abdominal wall by a connective tissue sheet (213: 1; Armbruster, 1998c). One other characteristic is considered synapomorphic for the Pterygoplichthini: 2–3 rows of plates between the suprapreopercle and exposed opercle (81: 2). More information on the Pterygoplichthini will be presented in a future publication.

Comparisons: The Pterygoplichthini differs from the Rhinelepini and the Hypostomini by having evertible cheek plates. It is difficult to separate the Pterygoplichthini from the Ancistrini except by examining the stomach for the presence of a connective tissue sheet (213: 1). *Pterygoplichthys* differs from all the Ancistrini except the *Acanthicus* group and the *Chaetostoma* group by having more than seven dorsal-fin rays; from the *Chaetostoma* group by having plates on the abdomen; from *Acanthicus* by having an adipose fin present (vs. absent) and by having the pterotic-supracleithrum taller than long (vs. longer than tall); and from *Leporacanthicus*, *Megalancistrus*, and *Pseudacanthicus* by having the dentaries meet at an angle greater than 80° (vs. less than 80°).

The *H. annectens* group differs from the *Acanthicus* and *Chaetostoma* groups by having seven dorsal-fin rays (vs. eight or more); from *Ancistrus*, the *Chaetostoma* group, *Dekeyseria*, most *Lasiancistrus*, *Leporacanthicus*, the *Lithoxus* group, *Hemiancistrus megacephalus*, *Neblinichthys*, *Pseudancistrus*, and *Spectracanthicus* by having plates on the abdomen (vs. abdomen naked, an undescribed species of the *H. annectens* group from western Panama and southern Costa Rica also lacks plates on the abdomen, but it is not sympatric to any other species of the Hypostominae); from *Hypancistrus*, *Panaque*, *Parancistrus*, and most *Peckoltia* by having the dentaries meet at an angle greater than 80 ° (vs. less than or equal to 80 °); from all but *Acanthicus*, *Dekeyseria*, *Cordylancistrus platycephalus*, *Hemiancistrus landoni*, *Panaque*, and *Peckoltia* by having keeled lateral plates (vs. unkeeled); and from *H. landoni* by having less than ten hypertrophied cheek odontodes (vs. 10 +). See Hypostomini for more detail.

RHINELEPINI NEW TRIBE

Includes:
Canthopomus Eigenmann, 1910 (synonym of *Pseudorinelepis*)
Monistiancistrus Fowler, 1939 (synonym of *Pseudorinelepis*)
Pogonopoma Regan, 1904
Pogonopomoides Gosline, 1947 (synonym of *Pogonopoma*)
Pseudorinelepis Bleeker, 1862
Rhinelepis Valenciennes, 1829

Diagnosis: The Rhinelepini is diagnosed by two unique characteristics: an upper pharyngeal tooth plate with a lateral shelf (31: 1) and a large, U-shaped, two-part diverticulum of the digestive tract (211: 1–3). Other characteristics considered synapomorphic for the Rhinelepini are: loss of the second basibranchial (3: 2), interhyal not contacting the cartilaginous section between the hyomandibula and quadrate (26: 0), a long ventromesial process of the palatine (59: 1), a very large, almost square nasal (105: 2), a flattened and widened parasphenoid (106: 1), a loss of ribs behind the enlarged rib of the sixth vertebral centrum (129: 1), at least a partial exposure of the coracoid strut (162: 0), circular (vs. bilobed) pupils, and a straight oesophagus to which the intestine does not pass dorsally (210: 1). See description and diagnosis of the Rhinelepini in Armbruster (1998b) and Quevedo & Reis (2002).

Comparisons: The Rhinelepini can be distinguished from *Corymbophanes* by the lack of a postdorsal ridge of three or more median preadipose plates, and by having five (vs. three) rows of plates on the caudal peduncle, from the Hypostomini and the Pterygoplichthini by having one unbranched and five branched anal-fin rays (vs. one unbranched and four branched rays) and by lacking the dorsal flap of the iris, and from the Ancistrini and the Pterygoplichthini by lacking highly evertible cheek plates.

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APPENDIX 1

SPECIMENS EXAMINED

The list of specimens examined includes only those specimens that were cleared and stained. Numbers of cleared and stained specimens are in parentheses.

OUTGROUP
Callichthyidae
Corydoras aeneus – INHS 29214 (2), INHS 31704 (3); *Corydoras bondi* – INHS 31681 (1); *Corydoras osteocarus* – INHS 30100 (2); *Corydoras septentrionalis* – INHS 30029 (2); *Dianema longibarbis* – INHS 37625 (1); *Hoplosternum littorale* – INHS 69360 (2).

INGROUP
Astroblepidae
Astroblepus chotae – USNM 121129 (1); *Astroblepus longifilis* – FMNH 70017 (1); *Astroblepus whymperi* – MCZ 31512 (1); *Astroblepus* sp. – MCNG 6468 (1), MCNG 16251 (1), USNM 302674 (1).

Hypoptopomatinae
Hypoptopoma sp. – INHS 28696 (2), INHS 28997 (3), INHS 29973 (2); *Nannoptopoma spectabilis* – INHS 28298 (2); *Microlepidogaster* sp. – INHS 37356 (3); *Otocinclus vestitus* – INHS 30093 (3), INHS 60418 (1); *O. vittatus* – USNM 305584 (1), USNM 318593 (1); *Parotocinclus britskii* – INHS 27631 (2), INHS 31733 (5); *Schizolecis guentheri* – FMNH 71338 (2), INHS 37362 (3).

Hypostominae
ANCISTRINI
Acanthicus hystrix – INHS 36803 (1), INHS 39840 (1); *Ancistrus pirareta* – UMMZ 206085 (5); *Ancistrus* sp. 1 – INHS 31835 (1), INHS 31858 (1); *Baryancistrus niveatus* – INHS 40912 (1), AUM 27733 (1); *Chaetostoma anomala* – INHS 59863 (1); *C. pearsei* – INHS 34589 (2); *C. platyrhyncha* – ANSP 84570 (7), FMNH 96945 (2), FMNH 97569 (2); *C. sovichthys* – INHS34957 (1); *C. stannii* – INHS 28838 (1), INHS 60478 (1); *Cordylancistrus torbesensis* – MCNG 8066 (1), USNM 121002 (2 paratypes); *Dekeyseria pulcher* – INHS 37471 (1), FMNH 103494 (2); *D. scaphirhyncha* – FMNH 85832 (1), USNM 269958 (1); *Dolichancistrus cobrensis* – MCNG 6470 (1); *D. pediculatus* – CAS 58789 (1), CAS 58820 (1), FMNH 58566 (2); *Exastilithoxus fimbriatus* – AMNH 91400 (1); *Exastilithoxus* sp. – MBUCV V-18551 (1); *Hemiancistrus landoni* – FMNH 93099 (1); *Hemiancistrus megacephalus* – CAS 56703 (1); *Hemiancistrus* sp. – UF 77850 (2), ANSP 162173 (2), ANSP 162174 (4); *Hemiancistrus* sp. Brazil – USNM 279751 (3); *Hypancistrus inspector* – FMNH 106009 (1), FMNH 106012 (1); *Hypancistrus zebra* – INHS 37472 (1); *Lasiancistrus maracaiboensis* – INHS 59866 (4), INHS 60465 (2); *Lasiancistrus* sp. – INHS 28263 (4), INHS 29866 (6); *Leporacanthicus galaxias* – INHS 40910 (1); *Leptoancistrus canensis* – INHS 36108 (1), USNM 273716 (1); *Lithoxancistrus orinoco* – AMNH 31023 (1), ANSP 160600 (5); *Lithoxus bovalii* – AMNH 54961SW (1); *L. lithoides* – BMNH 1972.7.17 : 66–115 (2), USNM 225917 (1); *Megalancistrus gigas* – MZUSP 21143 (1), MZUSP 24435 (1); *Neblinichthys pilosus* – AMNH 56138SW (2, paratypes); *N. roraima* – MBUCV V-21304 (1); *Panaque albomaculatus* – FMNH 96951 (1); *P. maccus* – INHS 28933 (1), INHS 29862 (2), INHS 29906 (1); *P. nigrolineatus* – INHS 29902 (1), INHS 37470 (1); *P. pariolispos* – ZMA uncatalogued aquarium specimen (1); *Parancistrus aurantiacus* – INHS 40911 (1); *Peckoltia oligospila* – MNRJ 13304 (2); *P. ucayalensis* – INHS 40916 (1), LACM 36318–2 (1), LACM 36325–1 (1); *Peckoltia* sp. 1 – CAS 6476 (1); *Peckoltia* sp. 2 – FMNH 70863 (1), INHS PERU97-20 (1), USNM 305824 (3); *Peckoltia* sp. big spot – MCNG 37043 (1); *Pseudacanthicus leopardus* – FMNH 95554 (1), *Pseudancistrus barbatus* – AMNH 54950 (3), CAS 56702 (1); *Pseudancistrus brevispinnis* – NRM 32374 (3), *Pseudancistrus* sp. – USNM 226181 (1); *Pseudancistrus* sp. Gold Spot – MCNG 26125 (1); *Pseudolithoxus anthrax* – ANSP 162175 (1); *Spectracanthicus punctatissimus* – FMNH 95556 (1), INHS 40914 (1), MZUSP 34265 (1); *S. murinus* – MZUSP 34279 (1).

CORYMBOPHANINI
Corymbophanes andersoni – AUM 28149 (1); *C. kaiei* AUM 28163 (1).

HYPOSTOMINI
Hypostomus ammophilus – INHS 34785 (6), MCNG 13504 (3), MCNG 13773 (1), UF 80360 (1); *H. albopunctatus* – MZUSP 24458 (2); *H. bolivianus* – UMMZ 204994 (2); *H. boulengeri* – USNM 326313 (1); *H. cochliodon* – AMNH 97880 (1), UMMZ 206338 (3), UMMZ 207988 (2), USNM 326319 (1), USNM 326357 (1); *H. commersoni* – FMNH 95548 (1); *H. cordovae* – UF 82322 (2), USNM 314314 (1), USNM 314334 (1); *H. emarginatus* 1 – AMNH 12607 (1), UMMZ 187225 (1); *H. emarginatus* 2 – INHS 29085 (1); *H. francisci* – ANSP 172107 (2), MNRJ 13559 (2); *H. hondae* – CAS 149472 (1), INHS 60463 (1); *H. micromaculatus* – ANSP 160774 (3); *H. plecostomoides* – ANSP 133235 (1), INHS 28744 (2), INHS 30000 (1), INHS 31263 (2), INHS 31365 (2), INHS 31448 (1); *H. plecostomus* – YPM 4194 (1), ZMA 105.306 (2); *H. plecostomus* 2 – INHS 33435 (1), INHS 30039 (2), UF 77909 (2); *H. punctatus* – INHS 37350 (2), MNRJ 13557(1); *H. robinii* – MCNG 8215 (1); *H. spinosissimus* – CAS 32461 (1), FMNH 58546 (1); *H. squalinus* – ANSP 134182 (2), MCNG 7389 (1), USNM 258283 (4); *H. unicolor* – AMNH 77429 (1), AMNH 77434 (2), FMNH 84145 (6), FMNH 101120 (2), FMNH 103282 (4), UMMZ 205129 (2), USNM 301642 (3) USNM 319355 (2), USNM 319357 (2), USNM 329281 (1); *Hypostomus hemicochliodon* – FMNH 92633 (1), INHS 36878 (1), INHS 40385 (1); *Hypostomus* sp. round snout 1 – USNM 302485 (2); *Hypostomus* sp. round snout 2 – USNM 300099 (1), USNM 318199 (3).

APPENDIX 1 *Continued*

PTERYGOPLICHTHINI
Hemiancistrus holostictus – CAS 56707 (1); *Hemiancistrus panamensis* – ANSP 126440 (2), USNM 78315 (2), USNM 78323 (1), USNM 293166 (1), USNM 316530 (2); *Hemiancistrus maracaiboensis* – EBRG 2855 (1), MCNG 33522 (1); *Pterygoplichthys etentaculatus* – ANSP 172096 (2), ANSP 172097 (1), FMNH 59730 (1); *P. gibbiceps* – FMNH 95576 (1), MZUSP 24340 (3); *P. lituratus* – AMNH 39945 (1); *P. multiradiatus* – INHS 28133 (2), INHS 28260 (1), INHS 29787 (1); *P. pardalis* – CAS 77274 (1), FMNH 95546 (1), FMNH 101384 (1); *P. punctatus* – FMNH 96959 (1), FMNH 96960 (1); *P. zuliaensis* – INHS 35384 (1), MCNG 32219 (1).

RHINELEPINI
Pogonopoma wertheimeri – USNM 302292 (1), USNM 318202 (1); *Pogonopomoides parahybae* – MNRJ 13562 (1); *Pseudorinelepis genibarbis* – FMNH 95570 (1), INHS 36938 (1), INHS 39730 (1), MZUSP 6339 (1); *Rhinelepis aspera* – MNRJ 13561 (1), MZUSP 23067 (2).

LITHOGENINAE
Lithogenes villosus – AUM 28152 (1).

LORICARIINAE
Crossoloricaria venezuelae – INHS 60378 (1); *Crossoloricaria* sp. – USNM 314302 (1); *Harttia* sp. – AMNH 14408SW (1); *Ixinandria montelbelloi* – USNM 314300 (3); *Lamontichthys llanero* – INHS 29957 (2); *Loricaria* sp. – INHS 31689 (1); *Loricariichthys brunneus* – INHS 35413 (3); *Rineloricaria rupestris* – INHS 35602 (3), INHS 60381 (1); *Sturisoma festivum* – INHS 35575 (1), INHS 59948 (1); *Sturisomatichthys citruensis* – USNM 293667 (1).

NEOPLECOSTOMINAE
Hemipsilichthys bahianus – USNM 318203 (3); *H. cameroni* – USNM 279585 (3); *H. nudulus* – MCP 10436 (4 paratypes); *H. splendens* – MCP 20334 (2); *Hemipsilichthys* sp. – USNM 320377 (3); *Hemipsilichthys*? – MZUSP 42205 (3); *Isbrueckerichthys alipionis* – MCP 20122 (1); *I. duseni* – UMMZ 215262 (2); *Kronichthys* sp. 1 – FMNH 71334 (1), FMNH 92364 (3), MZUSP 35286 (1); *Kronichthys* sp. 2 – MZUSP 27545 (2); *Pareiorhina rudolphi* – MNRJ 13560 (3); *Pareiorhina* sp. – AMNH 174125 (3); *Neoplecostomus microps* – MNRJ 12802 (1), MNRJ 13555 (1), MNRJ 13556 (2); *N. paranensis* – USNM 320071 (3).

NEW SUBFAMILY
Delturus anguilicauda – USNM 315901 (1), USNM 318180 (1), USNM 318209 (1); *Upsilodus victori* – MCP 19780 (1).

APPENDIX 2

Character state matrix

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

OUTGROUPS

Corydoras 4 spp.

```
0000000000000000000000000110000000000000000100000000000000030001010000000000000000???00?000000
000000?000000030000000000010000000001000000010000000000A00110000000000000000010000000000000000
000000011000000000000000000
```

Dianema longibarbis

```
1000000000000000000000000110000000010000000001000000000000000001020000000000000000???00?000000
000000?0000100300000000010100000000000000000100000000000A000100000010000000?0000000000000000000
000000011000000000000000000
```

Hoplosternum littorale

```
1000000000000000100000000110000000000000000100000000000000000001020000000000000000???00?000010
000000?0000100300000000010100000000000000000100000000000A000100000010000000?0000000000000000000
000000011000000000000000000
```

Scoloplax dicra (not included in most analyses or character descriptions)

```
0021000000000000000000000020000000?00?00???000000000000000000000??00000000010?001000???000???000
000000?000?100000000000?00?01000000010010011?0120100020000101000000?01011100????010?00000001000000
000000010000000000200100010
```

INGROUP

Astroblepidae

Astroblepus 4 spp.

```
1020000000000000000110110000000000000000000000?000000000000000000010010000001000011000???000021000
0200010000000000000000000001000000200000000012100002 1?1?000100012010111101100010141000001000000
000010100000000000000000000
```

Loricariidae–Lithogeninae:

Lithogenes villosus

```
00??0000000000000000000000110000010100000000210001010000000000001000000001000001000???000021100
0011010000000000100000100000100010020010000001210000 21?1?000100012010101100110010021000001000000
001010120000000000000000000
```

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Loricariidae–new subfamily:
Delturus anguilicauda
1010001100100100010100100001110000010000000100000011000000000000201000000100000110???001012000
0011020000100000000010000120000001200001100020011010100A00000102010110102101010020000001100001
00111013200010000000000000

Upsilodus victori
1010001100000100010110100001110000010000000100000011000000000000201000000100000110???001011000
0021020000100000000010000100000101200101100020000010110A01000012010110102101000020000001100001
00111013200010000000000000

Loricariidae–Hypoptopomatinae
Hisonotus sp.
00200011000000111100000000020110000010000001100000012101020000011000000000100000101000011011010
11110200101010210000000000?110011000010011011200000000101000200000010010000?0000020000001000000
00101002100011100000000000

Hypoptopoma sp.
0020001101000011110000000002011000001000000010?0000012110000000011000000000100000101000010011010
1110020010200000000000000011100110010000010012010000001?1000200000010010001000000200000010000000
00101002200011100000000000

Nannoptopoma spectabila
00200011000000111100001000200000001100000010?0000012110000000011000000000100000101000010011010
1110020010200020000000000011100110000000110112010001001?1000200000010010000?0000120000001000000
00101002200011100000000000

Otocinclus vestitus
002000110110011111000000000201100001100000010?0000000000000000212000000000100000001000011011010
1100020010201020000000000?110011010010001011200000100001000201001010010001000100200000010000000
00101002200011100000101000

Otocinclus vittatus
002000210110011111000000000201100001100000010?0000000000000000212000000000100000001000011011010
1100020010201020000000000?1100110100100A1011200000100001000201001010010001000100200000010000000
00101002200011100000101000

Parotocinclus britskii
00200011000000111100000000020110000010000000100000012101020001011000000000100000001001001011010
111102001010002100000000001110011010010011001200000100001000200010010010000?0000020000001000000
00101002200010100000000000

Schizolecis guentheri
00200011000000011100000000020000000010000000100000012100020000011000000000100000001000001011010
0121020010100021100000000?1100100000100110112010001001?1010101020110010000?00100200000010000000
00101002200010100000000000

Loricariidae–Neoplecostominae:
Hemipsilichthys bahianus
1020002100000101110100100010110000110000000100000012200010000011000000000000000111001101011010
01210200001000010000000001110011000000011001201000100101000000020111010001000100200000001100011
00101012200010000000000000

Hemipsilichthys cameroni
10100021000001011101000000010110000110000000100000012200020000011000000000100000101101101011010
01210200001000000000000000111001101000001100120000010010101000002010110000100010020100011100011
00101012200010000000000000

Hemipsilichthys nudulus
10200011000001011101001100101100000100000001100000121000200002110010000000100000001001100011010
01210201001000000000000000?2000100020000010100??00021?1?C00000102010111001100001020100001100011
00101013000010000000000000

Hemipsilichthys splendens
102000210000010111010000000101100001100000001000000121000200000110010000000100000011101101011010
01210201001000000000000000110001100000001100020000010010101000102010111000100000020100011100011
00101012200010000000000000

Hemipsilichthys sp.
10200021000001011101100000010110000110000000100000012200020000011000000000100000111101100011010
01200200001000000000000000111001100000001100120000010010101000002010111000110010020000011100011
00101012200010000000000000

Hemipsilichthys?
10210021000000001110100100020110000110000001101000012101010000011000000000100000001000002011010
0121020000100001000000000111001000000001100120100010010100000012011101000110010020100001?000?0
00101013200010000000000000

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Isbrueckerichthys alipionis
0021001100000101110000000001011000001000000021000001210001000001100000000100000011120011101 1010
01210200001000000000000000111001100000000110012010001001?1010000120101100001100100201000111000 11
0010111320001010000000000000

Isbrueckerichthys duseni
00210021000001011100000000010110000010000000210000012100010000011000000000100000011120011101 1010
012102000010000000000000000010011000000001100120100010 01?1010000120101100001000100201000111000 11
0010111320001010000000000000

Kronichthys sp. 1
1020001100000101110100000020110000010000000100000012100020000011000000000100010001000001011010
01210200001000010000000A00111001100000000110012010 00A001010000010201011100 00?001002010000 1000000
0010101220001000000000000000

Kronichthys sp. 2
1020002100000101110100100020110000010000000100000012100020001011000000000100010001000001011010
0121020000100001000000100111001100000000110012010001001010000010201011100 00?0010020100001000000
0010101220001000000000000000

Neoplecostomus microps
00200011000000011100001000100000000100000002000000100000100000110000000010000101110001010 11010
002102000010000000000010001A1001001000001100120100010010111000012010110000110011010100011000000
0010101220001010000000000000

Neoplecostomus paranensis
0020001100000001110000100010000000A01000000002000000122000200000110000000010000101110001110 11010
002102000010000000000010001A1001001000001100120100010010111000012010110000110011010100011000000
0010111220001010000000000000

Pareiorhina rudolphi
1020001100000001110100100010110000010000000110000001220002000001100000000010001000120101101 1010
0121020000100000000000000?11001100000000110112010001001010000010201011100010001002010000 1000000
0010111220001000000000000000

Pareiorhina sp.
10200011000001011101001000201100000000000000002A0000012200020001011000000000100010011000101011010
0121020000100000000000000?1100110000000011011201000100101011000120101101000?0010020100011000000
0010111220001000000000000000

Loricariidae–Loricariinae
Crossoloricaria venezuelae
000100001111120000000100010100000101000000000?000011240102001000100001001000000001011000020111 10
00210100101101010000000000?01011010200000101120100100 01?100101002000110 0000?000000000 1001000000
1000100210001010010000000000

Crossoloricaria sp.
000100001111120000000000001010000010100000000?000011240102001000100001001010000010110000201 1110
00210200101101010000001000?010110102000001011201001000 1?1001010120101100000?0000000001001000000
1000100210001010010000000000

Harttia sp.
100000110110000001101000000101110000001000000001000000122000200000001000000000100000011100000101 1110
0010020010100000110000000 0?01011010000000100112000000000101000000102111101002100100020000001000000
0000100210001010000000000000

Ixinandria montelbelloi
0000000000000000001000010010100000000100000001000001100000000101010000100101000000101000000 1011110
00210200001001000000000000?010110100000000011200001000101000011020101010011001000300000011000 01
1000100220001010000000000000

Lamontichthys llanero
010000110110000001100000000101010010010000000010000001221002000000010000000000100000111000002011110
001002001010000010000000000?0101101000000100112000010001010000000200100100210000002000000100 0000
0000100210001010000000000000

Loricaria cataphracta
000000001111120000000100010100000000100000000?00001124010200110010000100100000000101100002011110
002102000011010100000000000?01011010000000101120100110 01?100101002011100 0000?01000300010010 00000
1000100210001010010000000000

Loricariichthys brunneus
00000000110002000100010011010000010100000000100000112401100011101000010010000000010110000101211 0
0021020000110101000001000?0101101000010000112010010001?1001010020111010011000010000000010000 00
1000100220001010000000000000

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Rineloricaria rupestris
00000000100002000100001001010000000010000000100000110000000011100000010010100000101000001011110
002102000010010000000000?01011010000000001120000100010100001102010101001100100030000001100001
1000100220001010000000000000

Sturisoma festivum
0000001101100100110000000201010000010000001100000012200020000001000000000100000101001001011110
002002000110000100000000?01011010000100001120100100010100000102001000001100001030000001100001
0000100220001010000000000000

Sturisomatichthys citrensis
0000001101100100110000000201010000010000001100000012200020000001000000000100000101001001011110
002002000110000100000000?01011010000100001120100100010100000102001001002100101020000001100001
0000100220001010000000000000

Loricariidae–Hypostominae–Corymbophanini
Corymbophanes andersoni
10100021000001111100000000110100001010000000201000012200021000111010000000100000101101001011010
00110101001000010000000001111000000000001010200000100001000000020101110011101010200000001000000
0011101220001000000000000000

Corymbophanes kaiei
1010002100000111110000000011000000101000000001010000122000210001110100000000100000101101001011010
001101000010000100000000011110000100000000102000001000020000000010101110001101010200000001000000
0011101220001000000000000000

Loricariidae–Hypostominae–Rhinelepini
Pogonopoma parahybae
002000220100010011010000101001100010000000001000000122100101011010000000001000000111000002011011
001012000021000100000000?11100000101000101120000010000100000101001001002110111120000001000000
0110111310001010000000130000

Pogonopoma wertheimeri
102000220100010011110000101001100011000000001000000122100101011010000000001000000101000002011011
00101200002100010000000001111000000101000000120000010000100000101000011002110111120000001200001
0010111310001010000000130000

Pseudorinelepis genibarbis
002000220110010011010000000200110A011000000001000100122000201000020000000000100000101100002011011
001002000021000100000000?201000001000000001120000010000100000000001001001110111020000001200001
0010101310001010000000110000

Rhinelepis aspera
1020002201000100111100101010011000010000000010000001220002010110100000000000100000101200002011011
00101200002100000000000001201000001000001011200000100001001010010000110011101010200000001000000
0010111310001010000000120000

Loricariidae–Hypostominae–Hypostomini
Hypostomus albopunctatus
1010002201000100110100000210010011010000000020000001220002000000010100000000100010111100002012011
0011020000100001110000000111010000000001100001200000100002000001010001110011101010200000001010000
0110101320001010000000000000

Hypostomus ammophilus
00210021010001011100001100200100110100000000100000012200010000000101000000001000101B1100002022111
001012000010000101000000010001000000000110000120000010000200000101000111001100101020011001010000
0110101310101011000000000000

Hypostomus bolivianus
1010002201100100110100000210010011010000000020000001220002000000010100000000100010111100002011011
0010020000100001110000000111010000000001100001200000100002000001010001110011001010200000001010000
0110101310001010000000000000

Hypostomus boulengeri
101000220100010011010000121001001101000000001000000122000200000001010001000100010111100002011011
0010020000100001110000000111010000000000000001200000100002000001000001110011001010200000001010000
0110101310001010000000000000

Hypostomus cochliodon
1010002201000110110100000A21001001100000000002010000122000200000001010011000100010111100002011011
0020020000100001110000000111010000000001100101200000100002000001000001110011001010200000001010000
0110101310001010100000000000

Hypostomus commersoni
0020002201000100110000000121001001101000000001000000122000100000001010001000100010111100002011011
002002000010000111000000011101000000000000000120000010000200000101000111001100101020010001010000
0110101310101010000000?????0

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Hypostomus cordovae
101000220100010011010000121001001101000000002000000122000200000010100000000000010111100002011011
002002000010000111000000111010000000000111000120000010000200000101000111001100101020000001010000
0110101310001010000000000000

Hypostomus emarginatus 1
001000220100011111000010021001001101000000001000000122000100000010100000000000010111100002012111
000012000010000111000000111010000000000110000120000010000200000100000111001100101020010001010000
0110101310101010000000000000

Hypostomus emarginatus 2
001000220100011111000010021001001101000000001000000122000100000010100000000100010111100002022111
001012000010000111000000100010000000000110000120000010000200000101000111001100101020010001010000
0110101310101010000000000000

Hypostomus francisci
1010002201000100110100000A2100100110101000000201000012200020000001010000000001000101111000020120011
001002000010000101000000111010000000000110000120000010000200000101000111001100101020000001010000
0110101310001010000000000000

Hypostomus hemicochliodon
101000220110010011010000121001001101000000002010000122000200000010101100000000010121100002011011
002002000010000111000000111010000000000110000120000010000200000100000111001100101020000001010000
0110101310001010000000000000

Hypostomus hondae
100000220100010011010000121001001100000000002010000122000200000010101110000000010121100002011011
001002000010000111000000111010000000000110010120000010000200000100000111001100101020000001010000
0110101310001010100000000000

Hypostomus micromaculatus
101000220110010011010000121001001101000000001000000122000200000010100000000000010111100002011011
001002000010000101000000112010000000000110000120000010000200000100000111001100101020000001010000
0110101310001010000000000000

Hypostomus plecostomoides
101000220100010011010000121001001100000000002010000122000200000010101110000000010121100002011011
0020020000100001110000001A1010000000000110000120000010000200000100000111001100101020000001010000
0110101310001010100000000000

Hypostomus plecostomus
101000220100010011010000121001001101000000002000000122000200000010101000000000010111100002011011
001002000010000101000000111010000000000110000120000010000200000100000111001100101020000001010000
0110101310001010000000000000

Hypostomus plecostomus 2
101000220100010011010000121001001101000000002000000122000200000010100000000000010111100002011011
002002000010000101000000111010000000000110000120000010000200000100000011001100101020000001010000
0110101310001010000000000000

Hypostomus punctatus
101000220110010011010000021001001101000000002000000122000200000010101000000100010111100002011011
0010020000100001010000001A101000000000011000012000001000020000010A000111001100101020000001010000
0110101310001010000000000000

Hypostomus robinii
100000220110010011010000121001001101000000001000000122000200000010100010000000010111100002011011
001002000010000101000000111010000000000110000120000010000200000100000111001100101020000001010000
0110101310001010000000000000

Hypostomus sp. round snout 1
101000220110010011010000021001001101000000002010000122000200000010100000000100010111101002011011
001002000010000111000000112010000000000111000120000010000200000101000111001100101020000001010000
0110101310001010000000000000

Hypostomus sp. round snout 2
101000220100010011010000121001001101000000001000000122000200000010100000000000010111100002011011
001002000010000111000000111010000000000A10000120000010000200000101000111001100101020000001010000
0110101310001010000000000000

Hypostomus spinosissimus
100000220100010011010010011001001101000000011000000122000200000010101000000000010111100002012011
0010120000100001110000001A0010000000000000000120000010000200000101000111001100101020010001110001
0110101310101010000000000000

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Hypostomus squalinus
0010002201000111110000100120010011010000001100000012200010000001010000000100010111100002012111
0010120000100001110000001000100000000110000120000010000200000100000111001100101020010001010000
0110101310101010000000000000

Hypostomus unicolor
0021002101000101110000110020010011010000000100000012200010000001010000000100010111100002022111
0010120000100001010000001000100000000110000120000010000200000101000111001100101020011001010000
0110101310101011000000000000

Loricariidae–Hypostominae–Pterygoplichthini
Hemiancistrus holostictus
1010002201100100110100000210010011010000001100000012200020000001010001000000010121100003011011
0010020000100001110000001110100000000010000120000010000200000000000111001100101020000001220000
0110101310001010000000000100

Hemiancistrus maracaiboensis
1010002201100100110100000210010011010000001100000012200020000001010000000000000121100003011011
0010020000100001110000001110100000000010000120000010000200000000000111001100101020000001220000
0110101310001010000000000100

Hemiancistrus panamensis
1010002201100100110100000210010011010000000100000012200010000001010100000000000121100003011011
001002000010000111000000111010A000000000000120000010000200000000000111001100101020000001220000
0110101310001010000000000100

Pterygoplichthys etentaculatus
1010002201000110110100000020010011010000001100000012200010000001010000000100000121100003011011
00100200002000011000000011201000000000110000120010 0A000020000000000001110011001010200000012200000
0110101310001010000000000100

Pterygoplichthys gibbiceps
1010002101A00100110000000020010011010000001100000012200120000001010000000000000121100003012011
001002000010000110000000111201000000000000000120010 0A000020000000000000110011001010200000001220000
0110101310001010000000000100

Pterygoplichthys lituratus
1010002101000100110000000020010011010000001100000012200110000001010000000000000121100003012011
0010020000100001100000001112010000000000000001200100000000200000000000011100110011102000000 1220000
0110101310001010000000000100

Pterygoplichthys multiradiatus
002000210100010011010000A020010011010000001100000012200110000001010000000100000121100003012011
0010120000200001000000001120100000000000000012001000000002000000000000111001100101020000001020000
0110101310001010000000000100

Pterygoplichthys pardalis
0020002101000100110100000020010011010000001100000012200110000001010000000100000121100003012011
0010020000200001100000000112010000000010000012001001000020000000000000110011001010200000001020000
0110101310001010000000000100

Pterygoplichthys punctatus
0010002201000100110100000020010011010000000100000012200010000001010001000100001121100003012011
0010020000100001100001001120100000200000000120010000000200000000000000110011001010200000001220000
0110101311001010000000000100

Pterygoplichthys zuliaensis
0020002201100100110000000020010011010000001100000012200110000001010000000100000121100003011011
0010020000200001100000000112010000000000000001200100000002000000000000001100110010102000000 01220000
0110100310001010000000000100

Loricariidae–Hypostominae–Ancistrini
A*canthicus hystrix*
1000002201100101110100100010010011000000000020000001220002000110100010000000100001211010030111 10
001002000000101121000000 0?bA100001211001101120010010000100000102100111001110101020000000 1220001
0110101311001010000000000001

A*ncistrus pirareta*
0010002201000101110110000210110111010011010200010012200020001100010000000121200121101002011010
0011021000200001200001001110100000200001000120000010000200000102000111000100101020000000 1220000
0110101220000000000032000000

Ancistrus sp.
0010002201000101110110000210110111010011010200010012200020001100010000000121200121101002011010
0021021000200001200000001120100000200001000120000010100200000102000111000100101020000000 1220000
0110101220000000000032000000

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Baryancistrus niveatus
1010002201000101110100000210010011010000000200000012200020001101010000000110000111101003012010
00210200001000012000000011201000002000000001200010100002000000010101110011001010200000001220000
0110101310001000000000000000

Chaetostoma anomala
0100012201000111110110000200010010010110000200000012101020001102111000000121100111111002011010
0021020100000001000000000120100000200001000120010010101100000012010110001110101020100101220000
0110101320000000000000000000

Chaetostoma pearsei
0100012201000111110110000200010010010110000200000012101020001101111100000121200111111002011010
0021020100000001000000000120100000200001000120010010101100000002010110001110101020100101220000
0110101320000000000000000000

Chaetostoma platyrhynchus
0100012201100111110110000200010010010110000200000012101020001102111000000121100111111002011010
0021020100000001000000000120100000200001000120010010101300000002010110001110101020100001220000
0110101320001000000001000000

Chaetostoma sovichthys
0100012201000111110110000200010010010110000200000012101020001101111000000121000111111002011010
0021020100000001000000000110100000200001100120010010101200000002010110001110101020100101220000
0110101320000000000000000000

Chaetostoma stannii
0100012201000111110110000200010010010110000200000012101020001102111000000121000111111002011010
0021020100000001000000000110100000200001000120010010101200000002010110000110101020100101220000
0110101320000000000000000000

Cordylancistrus torbesensis
00000122000000101110000000200110011010110010200000012100020001101111000000121100111111100201b010
0021020100000001100001000120100000200101100120010010101100000002010110002110101020100001220000
0110101320001000000000000000

Dekeyseria pulcher
0010002201000101110100000001001000101001001010000001220012000110101000000001211001211010030110 10
0011020000100001200000001110101000000000100012000001000010000110201011100211011102000000122000 1
0110101211001000000011000000

Dekeyseria scaphirhyncha
0010002201A00101110000000001001000101001001010000001220002000110001000000001210001111010030 1b010
00110201001000012000000001201010000000001A0012000001000010000011020A01110021101010200000001220001
0110101211001000000011000000

Dolichancistrus cobrensis
0000012101000101110100000200110011010110010200000012101020001101111000000121100111111002011010
0021020100000001100001000121101000200001100120010010101100000012010110011110101020000001221001
0110101320001000000000000000

Dolichancistrus pediculatus
0100012201000101110110000200A10011010110010200000012101020001101111000000121100111111002011010
002102010000000110000100012110100020000110012001001010 1b00000012010110011110101020000001221001
0110101320001000000000000000

Exastilithoxus fimbriatus
0110?0110000000001000010001000010101001110021001001100001000110100011010012 1?0010110100?012010
002100?00010000120000100012110100020000110012000001000010000000120101100000100000200000001220000
0010101220001000201000000000

Exastilithoxus sp.
0?100011000000000101101000100001010100111002?00100110000100011010?01101001210001011010020110 10
002100?0001000012000010001111010002000011001200000101001000000012010110000010000020000000122000 0
011010122000100020100?000?0

Hemiancistrus landoni
1010002201100100110100000210110011010000010200000012200020001101010101000110000111101003011010
0010020000100001200000001110100000000000000120000010000200000000000111001100101020000000122000 0
0110101310?0101000000000000

Hemiancistrus punctulatus
1010002201100100110000000210110011010000000200000012200020001001010000000100000111100003011010
0020020000000001100000001310100000000000000112000001000020000010100011100100010102000000012200 00
0110100320?01000000??000000

Hemiancistrus sp.
0000002201000101110100000210010011010000010 20A00001220102100110111000000001101011111010030110 10
0010020000100001210000000112010000020000000012000001000020000010200011100010010102000000012200 00
0110101310001010000000000000

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Hypancistrus inspector
0010002201100100110100000110110001010000010200000000000001000000101011000011000111110100301101O
0010020000100001200000001121100000200000000120000010000200000100000111000000101020000001220000
0110101310?0101000000000000

Hypancistrus zebra
1010002201100101110100000210110011010000010200001002401020000101010110000110001121 10?003011010
0000021000100001210000001?2010000000000000012000001000020000010100011100010010102000000 1220000
01101013100010102000000000

Lasiancistrus maracaiboensis
0010102201100101110110000210110111010011010100010012200020001100110000000121200121101003111 01A
0010020000100001201100101120100001200001000120000010000100000102000111000100101020000001220101
01101012200010000002200000O

Lasiancistrus sp.
0010102201100101110110000210110111010011010100010012200020001100110000000121200121101003111011
0010020000100001201100101120100001200001000120000010000100000102000111000100101020000001220101
011010122000100000022000000

Leporacanthicus galaxias
10000011000001010101001000100000110000000002010010122000100000010011101000100001110010030221 10
0020021000100001110000010120100000200001000120010010000100000102000111000100101020000001220001
011010132100100020000000000

Leptoancistrus canensis
1100012200000111110110000200010011010110010210010012101020001101111000000121100111111002011010
002102010000000110000100 0?2010000020000110102001001010140000001201011000010010102010000 1221001
011110132000100000000000000

Lithoxancistrus orinoco
0100102201A0010111011000020001001011000000010100001220002100000101000000001100001011010030110 10
00110200000000012000001011201 00A0020000110012000001000010000000201011000111011102000010122000 1
011010132000100000011000000

Lithoxus bovallii
0020001100000000010000100010000101010011110100110011000012001101111110100121100111101002011000
0011011000110001200001000111101001200001100120000010000100101012010110000100100020000001220000
011010122000100020000100010

Lithoxus lithoides
002000110000000001000010001000010101 0A111101001100110000120011011111101001212001111010020110 00
0021011000100001200001000 1B1101001200001100120000010000100101012010110000100100020000001220000
011010122000100020000100010

Megalancistrus gigas
1000002101100100110100000110010001010000000201001012401020001101000110000110000121101003012010
0011021000101011210000100120100001211000100120010010000100000002000111001100101020000001220001
011010131100101020000000001

Neblinichthys pilosus
1010002201000111110100000210110111011010010101000012200020001101110000000121100111101003011010
0021020000100001200000001120100001200001000120000010000100000002000111000110101020000001220001
011010122011100000011000000

Neblinichthys roraima
1010002201000 1?1110100000???1101010110100101010000122000200011011100000001210001111010030110 10
0011020000100001200000001110100001200001100120000010000100000002010111000100101020000001220001
011010122011100000011000000

Panaque albomaculatus
0010002201100111110100000200110011000000010201000012100020000101011111000110001111101003012011
0020121000100001210000101120100000200000010120000010000200000000000111000100101020000001220000
011010131010101010000000000

Panaque maccus
0010002201100111110100000210110011000000010201000012100020000101011111000110001111101003 01B011
0020121000100001210000101 1B010A00020010001012000001000020000010000011100010010102000000 1220000
011010131010101010000000000

Panaque nigrolineatus
0000002201000111110000000210010011000000010201000012200020001101011110000110001111101003121011
002012100010100121000010 11B0100000010100000120000010000200000100000111001100101020000001220000
011010131000101010000000001

Panaque pariolispos
1000002201100110110100000210010011000000010201000011000020000101011111000110001121101003011011
0020121000100001210000001110100100200110000120000010000200000101000111000110101020000001220000
011010131000101020000000000

APPENDIX 2 *Continued*

A = states 0 and 1, B = 1 and 2, C = 2 and 3.

Parancistrus auarantiacus
1000002201100100110101000110110001010001010100010012201010000101010110000110001121101003011010
0010021000100011201001001120100000200000000120001010000200000000000111000100101020000001220000
011010131010101000001000000

Peckoltia oligospila
1020002201100101110100000210110011010000010200000012200020001101110000000110001111101003012011
0010020000100001210000000112010000020001000012000001000020000010100011100010010102000000122000 0
011010131010101000000000000

Peckoltia sp. big spot
0010102201000111100110000110010011010000001200000012200020000101010100000110001111001003011011
0010020000100001200000000111010000000000000012000001000020000010100011100010010102000000122000 0
0110101310?0101000000000000

Peckoltia sp. 1
1000002201100111110100000210110011010000010200000012200020000001010111000110001111100003012011
0010021000100001210000000112010000000001000012000001000020000010000011100010010102000000122000 0
011010131010101000000000000

Peckoltia sp. 2
1000002201100111110100000210110011010000010100000012200020000001010111000110001111100003012011
0010021000100001210000101110100000200000000120000010000200000100000111000100101020000001220000
011010131010101000000000000

Peckoltia ucayalensis
0010002201100110110000000210110011010100010101000012200020000001010110000110001111101003012111
0010121000100001210000000111010000020010000012000001000020000010000001100010010102010000122000 0
011010131010101000000000000

Pseudacanthicus leopardus
1000002101000110110100000110010001000000000200001012200020000001000111000010000111101002012010
0020021000100011100000001120100000000000110012001001000010000010201011100110010102000000122000 1
011010131100101020000000000

Pseudancistrus barbatus
1010002201100101110110000210010010110000000101000012200121000001010000000110000111100003012010
0021020000000001110000101120100001200001000120000010000100000002010111001110111020000001210001
011010131000100000010000000

Pseudancistrus brevispinnis
0010002201000000110110000110010000110000000101000012200021001101010000000110000111101003011010
0021020000000001100000101120100000000000100112000001000010000000201011000211011102000000122000 0
011010131000100000000000000

Pseudancistrus megacephalus
0010002201100001110110000210010010110000000100000012200121001101010000000110000111101003011010
0011021000000001200000101120100000000000100012000001000020000000200011100111011102000000122000 0
0110101310?0100000000?????0

Pseudancistrus sp.
1010002201100101110110000210010010110000000101000012200121000001010000000110000111101003011010
0011020000000001110000101120100101200001000120000010000100000002010111002110111020000001210001
011010131000100000010000000

Pseudancistrus sp. gold spot
0000002201100100110100000200010010110000000100000012200121001100000000000110000111101002022010
0011020100000001210000101110100000000000100012000001000010000000201011100211011102000000122000 0
011010131000100000000000000

Pseudolithoxus anthrax
0010002201000101110100000200010101010011010100010012200020001101010000000121200 1B1101003011010
0011020000100001201000001120100000200001000120000010000100000102000111000100101020000001220001
011010121000100000011000000

Spectracanthicus murinus
1010002200000101110100000210010001000000010201000012301021000001011110100100010111100002011010
0011021000100001010000101120100000200001000120001010000300000101000111000100101020000001010000
011010132000100020000000000

Spectracanthicus punctatissimus
1010A022000001011101000002100100110000000102010000122010210000010101110001100001111010030 1B010
0011021000100001110000000112010000120 0A01A0012000101000020000010200011100010010102000000122000 0
011010131000101020000000000

APPENDIX 3

CHARACTER STATE CHANGES BY CLADE AS PLOTTED ON ONE OF THE MOST PARSIMONIOUS TREES

Clades with a taxonomic rank have the name indicated after the clade number. Genera of the Astroblepidae, *Lithogenes*, the new subfamily, the Neoplecostominae, and the Hypostominae for which there is only one species in this analysis have their character state changes indicated after the last numbered clade, genera arranged in alphabetical order. The character number is on the left and the change in states is on the right (→ is an arrow indicating change from one state to another). NUC = no unambiguous changes.

Clade 1
79: 0→1
121: 1→0
140: 0→1
145: 1→2
146: 0→1
157: 0→1
176: 0→1

Clade 2: Loricariidae
7: 0→1
8: 0→1
14: 0→1
18: 0→1
30: 0→1
52: 0→1
97: 0→2
100: 1→2
105: 0→1
120: 0→1
201: 0→1

Clade 3
27: 1→0
28: 0→1
64: 1→2
66: 0→1
73: 0→1
81: 0→1
115: 0→1
128: 0→1
147: 0→1
167: 0→2
170: 0→1
183: 0→1
188: 0→1
192: 0→1
196: 2→3

Clade 4
17: 0→1
52: 1→2
53: 0→2
57: 0→2
74: 0→1
82: 0→1
93: 0→1

Clade 5
16: 0→1
63: 0→1
96: 0→1
126: 0→1

Clade 6
80: 1→0
177: 0→1

Clade 7
194: 0→1

Clade 8
44: 1→2
81: 0→1
86: 0→1
152: 0→1
157: 0→1
164: 1→0
181: 0→1

Clade 9
1: 1→0
20: 1→0
80: 0→1
203: 0→1

Clade 10: *Neoplecostomus*
14: 1→0
29: 1→0
30: 1→0
96: 1→0
116: 0→1
126: 1→0
128: 0→1
151: 0→1
173: 0→1
175: 2→1

Clade 11: *Isbrueckerichthys*
4: 0→1
23: 1→0
45: 0→1
53: 2→1
78: 1→0
83: 0→2
183: 0→1
187: 0→1
188: 0→1
196: 2→3

Clade 12
27: 1→2
53: 2→1

Clade 13: *Kronichthys*
156: 0→1

Clade 14
14: 1→0
161: 0→1
163: 1→0

Clade 15: Hypoptopomatinae
1: 1→0
20: 1→0
103: 0→1
109: 0→2
131: 0→1
154: 0→1
162: 1→0
177: 1→0
195: 1→0
203: 0→1

Clade 16
15: 0→1
95: 0→1
97: 2→1
141: 1→0
154: 1→2
160: 1→0
172: 1→0

Clade 17
43: 0→1
87: 0→1
202: 0→1

Clade 18
44: 1→0
57: 2→0
98: 1→0
105: 1→2
110: 1→0

Clade 19
54: 0→1
88: 1→0
131: 1→0
141: 0→1

Clade 20: *Otocinclus*
11: 0→1
14: 0→1
51: 1→0
52: 2→0
53: 1→0
62: 0→2
64: 1→2
97: 1→0
128: 0→1
148: 1→0
156: 0→1
159: 0→1
172: 0→1
210: 0→1
212: 0→1

Clade 21: *Hemipsilichthys*
7: 1→2
35: 0→1
85: 0→1
86: 0→1
183: 0→1
187: 0→1
188: 0→1

Clade 22
83: 0→1
152: 0→1
181: 0→1

Clade 23
177: 0→1

Clade 24
53: 2→1
67: 0→1
80: 1→0
102: 0→1
122: 1→0
138: 1→0
156: 0→1
172: 1→0

Clade 25
137: 0→1
167: 0→1
172: 1→0

Clade 26: Loricariinae
1: 1→0
27: 1→0
28: 0→1
92: 0→1
121: 1→0
124: 0→1
127: 0→1
144: 0→1

APPENDIX 3 *Continued*

145: 1→0
163: 1→0
191: 1→0
195: 1→0
Clade 27
7: 1→0
8: 1→0
14: 1→2
17: 1→0
30: 1→0
50: 0→1
60: 0→1
69: 0→1
72: 0→1
108: 0→1
155: 0→1
189: 0→1
Clade 28
22: 0→1
55: 0→1
74: 1→0
83: 0→1
106: 0→1
141: 0→1
153: 0→1
Clade 29
11: 0→1
12: 0→1
13: 0→1
18: 1→0
44: 1→0
88: 1→2
135: 0→1
164: 1→0
167: 1→0
168: 1→0
179: 0→1
197: 2→1
206: 0→1
Clade 30: *Crossoloricaria*
4: 0→1
103: 0→1
129: 0→2
163: 0→1
Clade 31
23: 0→1
52: 2→0
110: 1→0
183: 0→1
188: 0→1
Clade 32
11: 0→1
98: 1→0
Clade 33
14: 1→0
81: 0→1
97: 2→1
103: 0→1
134: 0→1
197: 2→1
Clade 34
26: 1→2
43: 0→1
85: 0→1
104: 0→1
132: 0→1
141: 0→1
173: 0→1
183: 0→1
188: 0→1
Clade 35: Hypostominae
7: 1→2
83: 0→1
97: 2→1
123: 0→1
148: 1→0
173: 0→1
Clade 36
8: 1→2
88: 1→2
94: 0→1
98: 1→0
122: 1→0
160: 1→0
196: 2→3
197: 2→1
Clade 37
33: 0→1
81: 0→1
111: 0→1
119: 0→1
137: 1→0
150: 1→2
184: 0→1
190: 0→1
Clade 38
88: 2→3
183: 0→2
184: 1→2
Clade 39: *Corymbophanes*
15: 0→1
16: 0→1
30: 1→0
46: 0→1
58: 0→1
62: 0→1
63: 0→1
85: 0→1
100: 2→1
138: 1→0
192: 0→1
Clade 40: Rhinelepini
31: 0→1
59: 0→1
105: 1→2
106: 0→1
129: 0→1
162: 1→0
210: 0→1
211: 0→1
Clade 41
25: 0→1
61: 0→1
62: 0→1
99: 0→1
194: 0→1
211: 1→2
Clade 42: *Pogonopoma*
54: 0→1
57: 2→1
73: 0→1
74: 1→0
122: 0→1
131: 0→1
156: 0→1
167: 1→2
174: 0→1
211: 2→3
Clade 43: *Hypostomus*
78: 0→1
112: 0→1
156: 0→1
Clade 44
132: 0→1
133: 0→1
Clade 45
74: 1→0
Clade 46
23: 0→1
91: 1→2
99: 0→1
178: 0→1
199: 0→1
Clade 47
1: 1→0
15: 0→1
16: 0→1
20: 1→0
57: 2→1
92: 0→1
Clade 48
74: 0→1
120: 1→0
Clade 49
3: 1→2
4: 0→1
8: 2→1
15: 1→0
24: 0→1
26: 2→0
111: 1→0
179: 0→1
204: 0→1
Clade 50
25: 0→1
Clade 51
158: 1→0
Clade 52
46: 0→1
68: 0→1
69: 0→1
81: 1→2
Clade 53
36: 1→0
70: 0→1
205: 0→1
Clade 54
136: 0→1
Clade 55
11: 0→1
44: 2→1
Clade 56
44: 1→2
Clade 57
91: 1→2
Clade 58
NUC
Clade 59
25: 0→1
70: 0→1
Clade 60: Pterygoplichthini
81: 1→2
158: 1→0
213: 0→1
Clade 61: *H. annectens* group
11: 0→1
74: 1→0
112: 0→1
Clade 62
133: 0→1
Clade 63: *Pterygoplichthys*
26: 2→0
27: 1→2
121: 1→2
142: 0→1

APPENDIX 3 *Continued*

Clade 64
91: 1→2
Clade 65
3: 1→2
105: 1→2
Clade 66
8: 2→1
183: 2→0
Clade 67
8: 2→1
20: 1→0
74: 1→0
118: 0→1
Clade 68: Ancistrini
44: 1→2
61: 0→1
94: 1→0
Clade 69
62: 0→1
75: 0→1
85: 0→1
111: 1→2
Clade 70
79: 0→1
156: 0→1
167: 1→0
Clade 81
69: 0→1
101: 0→1
Clade 72
36: 1→0
79: 1→0
111: 2→1
134: 0→1
Clade 73
3: 1→0
8: 2→1
42: 1→0
49: 0→1
66: 1→0
74: 1→0
91: 1→2
142: 0→1
150: 2→1
188: 0→1
198: 0→1
Clade 74
109: 0→1
135: 0→1
167: 0→1
Clade 75
11: 0→1
61: 0→1
62: 0→1
81: 1→2
107: 0→1
111: 1→2
128: 0→1
130: 0→1
131: 0→1
215: 0→1
Clade 76: *Spectracanthicus*
55: 0→1
58: 0→1
98: 0→1
143: 0→1
Clade 77
158: 1→0
199: 0→1
Clade 78
16: 1→0
26: 2→1
33: 1→0
57: 2→1
112: 1→0
Clade 79
15: 0→1
91: 1→2
94: 0→1
Clade 80
1: 1→0
46: 0→1
99: 0→1
132: 0→1
Clade 81: *Panaque*
36: 1→0
67: 0→1
97: 1→2
205: 0→1
Clade 82
53: 2→1
136: 0→1
Clade 83
3: 1→0
29: 1→0
91: 2→1
199: 1→0
Clade 84
3: 1→0
85: 1→0
Clade 85
98: 0→1
121: 1→2
160: 0→1
Clade 86
1: 1→0
134: 0→1
150: 2→1
158: 1→2
167: 1→2
169: 0→1
Clade 87
39: 0→1
42: 0→1
75: 1→2
76: 0→1
77: 0→1
Clade 88
40: 0→1
48: 0→1
77: 1→2
Clade 89
21: 0→1
64: 1→0
208: 1→2
209: 1→2
Clade 90: *Ancistrus*
44: 1→2
88: 3→2
101: 0→1
105: 1→2
150: 1→2
188: 1→0
201: 1→0
208: 2→3
Clade 91: *Lasiancistrus*
5: 0→1
11: 0→1
65: 0→1
89: 0→1
98: 1→0
114: 0→1
117: 0→1
128: 0→1
186: 0→1
Clade 92
88: 3→2
116: 0→1
119: 1→0
135: 0→1
164: 1→0
Clade 93
3: 1→0
6: 0→1
27: 1→0
38: 0→1
84: 0→1
102: 0→1
105: 1→0
111: 2→1
142: 0→1
147: 0→1
149: 0→1
177: 0→1
Clade 94
2: 0→1
21: 0→1
55: 0→1
167: 2→1
Clade 95: *Chaetostoma*
34: 1→0
42: 1→0
111: 1→0
116: 1→0
135: 1→0
Clade 96
77: 1→0
121: 2→1
Clade 97
157: 0→1
185: 0→1
188: 0→1
Clade 98: *Dolichancistrus*
122: 0→1
125: 0→1
166: 0→1
177: 1→0
Clade 99
7: 2→1
8: 2→1
14: 1→0
17: 1→0
23: 0→1
26: 2→0
30: 1→0
32: 0→1
40: 0→1
41: 0→1
48: 0→1
52: 2→1
57: 2→1
68: 0→1
69: 0→1
71: 0→1
100: 2→1
122: 0→1
125: 0→1
157: 0→1
167: 2→0
173: 1→0
205: 0→2
Clade 100: *Exastilithoxus*
42: 1→0
81: 1→0
100: 1→0
168: 1→0
171: 1→0
207: 0→1
Clade 101: *Lithoxus*
3: 1→2

APPENDIX 3 *Continued*

47: 0→1
58: 0→2
93: 1→0
128: 0→1
153: 0→1
155: 0→1
169: 1→0
210: 0→1
214: 0→1

Clade 102: *Dekeyseria*
26: 2→0
125: 0→1
155: 0→1
198: 0→1

Clade 103: *Neblinichthys*
1: 0→1
37: 0→1
46: 0→1
65: 0→1
128: 0→1
199: 0→1
200: 0→1

Clade 104: *Pseudancistrus*
34: 1→0
35: 0→1
58: 0→1
105: 1→0
117: 0→1
172: 0→1

Clade 105
46: 0→1
61: 1→0
62: 1→0
129: 0→2
188: 0→1
208: 0→1

Clade 106
1: 0→1
111: 2→1
112: 0→1
128: 0→1
184: 2→1

Astroblepus
21: 0→1
24: 0→1
27: 1→0
44: 1→0
67: 0→1
74: 0→1
96: 0→2
167: 0→1
174: 0→1
175: 2→ 4
196: 2→0

Acanthicus
8: 1→2
23: 0→1
49: 1→0
69: 1→0
91: 2→1
92: 0→1
101: 1→0
105: 1→0
137: 0→1
159: 0→1
169: 0→1
205: 2→0

Baryancistrus
91: 1→2
143: 0→1

Cordylancistrus
29: 0→1
132: 0→1

Delturus
11: 0→1
91: 1→2
97: 2→1
121: 1→2
142: 0→1
143: 0→1
148: 1→0
156: 0→1

H. landoni
11: 0→1
29: 0→1
70: 0→1
158: 1→0

***Hemiancistrus* sp. Brazil**
11: 0→1
20: 1→0
29: 0→1
105: 1→0
120: 1→3
137: 0→1
156: 0→1
168: 1→0
195: 1→0
197: 1→2

***Hemipsilichthys*?**
4: 0→1
7: 1→2
35: 0→1
43: 0→1
46: 0→1
57: 2→1
88: 1→2
157: 0→1
169: 0→1
196: 2→3

Leporacanthicus
7: 2→1
17: 1→0
23: 0→1
30: 1→0
57: 2→1
67: 0→1
71: 0→1
83: 1→0
90: 1→2
92: 0→1
118: 0→1
197: 1→2
203: 1→0

Leptoancistrus
1: 0→1
45: 0→1
48: 0→1
137: 0→1
138: 1→0
150: 1/2→ 4
167: 1→0
169: 1→0
192: 0→1

Lithogenes
1: 1→0
28: 0→1
34: 0→1
44: 1→2
49: 0→1
73: 0→1
92: 0→1
97: 0→1
110: 0→1
116: 0→1
126: 0→1
132: 0→1
169: 0→1

Megalancistrus
36: 0→1
53: 2→ 4
55: 0→1
74: 0→1
98: 0→1
117: 0→1
134: 1→0
156: 1→0

Parancistrus
3: 1→0
22: 0→1
40: 0→1
44: 2→1
48: 0→1
55: 0→1
81: 1→2
109: 0→1
113: 0→1
116: 0→1
143: 0→1
156: 1→0
209: 0→1

Pareiorhina rudolphi
14: 1→0
43: 0→1
83: 0→2
85: 0→1
156: 0→1

***Pareiorhina* sp.**
27: 1→2
36: 1→0
61: 0→1
153: 0→1
165: 0→1
168: 1→0

Pseudacanthicus
15: 0→1
70: 0→1
88: 3→2
112: 1→0
129: 2→0
160: 0→1

Pseudolithoxus
27: 1→0

Pseudorinelepis
1: 1→0
11: 0→1
27: 1→2
48: 0→1
64: 1→2
158: 1→0
161: 0→1
163: 1→0
183: 0→2
188: 0→1

Rhinelepis
23: 0→1
110: 1→0
153: 0→1
155: 0→1

Upsilodus
21: 0→1
121: 1→0
126: 0→1
132: 0→1
152: 0→1
157: 0→1
172: 1→0

APPENDIX 4

THE SPECIES OF *HYPOSTOMUS*

[1]Placed in the synonymy of *H. plecostomus* (see Isbrücker, 1980); [2]Placed in the synonymy of *H. unicolor* by Armbruster (1998a); [3]Probably a synonym of *H.* sp*inosissimus*, possibly representing a juvenile (Isbrücker, 1980); [4]Placed in the synonymy of *H. hondae* by Lilyestrom (1984).

H. affinis (Steindachner, 1876)
H. agna (Ribeiro, 1907)
H. alatus Castelnau, 1855
H. albopunctatus (Regan, 1908)
H. ammophilus (Armbruster & Page, 1996)
H. annae (Steindachner, 1882)
H. ancistroides (Ihering, 1911)
H. angipinnatus (Leege, 1922)
H. argus (Fowler, 1943)
H. asperatus Castelnau, 1855
H. aspilogaster (Cope, 1894)
H. atropinnis (Eigenmann & Eigenmann, 1890)
H. auroguttatus Natterer & Heckel, 1854
H. bicirrosus (Gronow, 1854)[1]
H. biseriatus (Cope, 1872)
H. bolivianus (Pearson, 1924)
H. borellii (Boulenger, 1897)
H. boulengeri (Eigenmann & Kennedy, 1903)
H. brasiliensis (Bleeker, 1863)[1]
H. brevicauda (Günther, 1864)
H. brevis (Nichols, 1919)
H. butantanis (Ihering, 1911)
H. carinatus (Steindachner, 1882)
H. carvalhoi (Ribeiro, 1937)
H. chaparae (Fowler, 1940)[2]
H. cochliodon Kner, 1854
H. comersonii Valenciennes, 1840
H. comersonoides (Marini *et al.*, 1933)
H. coppenamensis Boeseman, 1969
H. corantijni Boeseman, 1968
H. cordovae (Günther, 1880)
H. crassicauda Boeseman, 1968
H. derbyi (Haseman, 1911)
H. dlouhy Weber, 1985
H. emarginatus Valenciennes, 1840
H. eptingi (Fowler, 1941)
H. ericius Armbruster, 2003
H. festae (Boulenger, 1898)[3]
H. fluviatilis (Schubart, 1964)
H. fonchii Weber & Montoya-Burgos, 2002
H. francisci (Lütken, 1874)
H. frankei (Isbrücker & Nijssen, 1982)[2]
H. garmani (Regan, 1904)
H. gomesi (Fowler, 1942)
H. goyazensis (Regan, 1908)
H. guacari Lacépède, 1803[1]
H. gymnorhynchus (Norman, 1926)
H. hemicochliodon Armbruster, 2003
H. hemiurus (Eigenmann, 1912)
H. hermanni (Ihering, 1905)
H. hondae (Regan, 1912)
H. hoplonites Rapp Py-Daniel, 1988
H. horridus Heckel, 1854
H. iheringii (Regan, 1908)
H. indicus (Linnaeus, 1754)[1]
H. interruptus (Ribeiro, 1918)
H. isbrueckeri Reis *et al.*, 1990
H. itacua Valenciennes, 1840
H. jaguribensis (Fowler, 1915)
H. johnii (Steindachner, 1876)
H. laplatae (Eigenmann, 1907)
H. latifrons Weber, 1986
H. latirostris (Regan, 1904)
H. levis (Pearson, 1924)
H. lexi (Ihering, 1911)
H. lima (Reinhardt, 1874)
H. limosus (Eigenmann & Eigenmann, 1888)
H. longiradiatus (Holly, 1929)
H. luetkeni (Steindachner, 1877)
H. luteomaculatus (Devicenzi & Teague, 1942)
H. madeirae (Fowler, 1913)[2]
H. macropthalmus Boeseman, 1968
H. macrops (Eigenmann & Eigenmann, 1888)
H. margaritifer (Regan, 1908)
H. meleagris (Marini *et al.*, 1933)
H. micromaculatus Boeseman, 1968
H. micropunctatus (La Monte, 1935)[2]
H. microstomus Weber, 1987
H. myersi (Gosline, 1947)
H. nematopterus Isbrücker & Nijssen, 1984
H. niceforoi (Fowler, 1943)
H. nickeriensis Boeseman, 1969
H. niger (Marini *et al.*, 1933)
H. nigromaculatus (Schubart, 1964)
H. nudiventris (Fowler, 1941)
H. obtusirostris (Steindachner, 1907)
H. occidentalis Boeseman, 1968
H. oculeus (Fowler, 1943)
H. pagei Armbruster, 2003
H. pantherinus Kner, 1854
H. papariae (Fowler, 1941)
H. paranensis Weyenberg, 1877
H. paucimaculatus Boeseman, 1968
H. paulinus (Ihering, 1905)
H. phrixosoma (Fowler, 1940)
H. piratatu Weber, 1986
H. plecostomus (Linnaeus, 1758)
H. plecostomoides (Eigenmann, 1922)
H. popoi (Pearson, 1924)[2]
H. pospisili (Schultz, 1944)[4]
H. pseudohemiurus Boeseman, 1968
H. punctatus Valenciennes, 1840

APPENDIX 4 *Continued*

H. pusarum (Starks, 1913)
H. pyrineusi (Ribeiro, 1920)
H. rachovii (Regan, 1913)
H. regani (Ihering, 1905)
H. robinii Valenciennes, 1840
H. rondoni (Ribeiro, 1912)
H. roseopunctatus Reis *et al.*, 1990
H. saramaccensis Boeseman, 1868
H. scabriceps (Eigenmann & Eigenmann, 1888)
H. scaphyceps (Nichols, 1919)
H. scopularis (Cope, 1871)
H. sculpodon Armbruster, 2003
H. seminudus (Eigenmann & Eigenmann, 1888)
H. sipaliwinii Boeseman, 1968
H. spiniger (Hensel, 1870)
H. spinosissimus (Steindachner, 1880)
H. squalinus Schomburgk, 1841
H. strigaticeps (Regan, 1908)
H. subcarinatus Catelnau, 1855
H. surinamensis Boeseman, 1968
H. taeniatus (Regan, 1908)
H. tapanahoniensis Boeseman, 1969
H. taphorni (Lilyestrom, 1984)
H. tenuicauda (Steindachner, 1878)
H. tenuis Boeseman, 1968
H. ternetzi (Boulenger, 1895)
H. tietensis (Ihering, 1905)
H. topavae (Godoy, 1969)
H. unae (Steindachner, 1878)
H. unicolor (Steindachner, 1908)
H. uruguayensis Reis *et al.*, 1990
H. vaillanti (Steindachner, 1877)
H. variipictus (Ihering, 1911)
H. varimaculosus (Fowler, 1945)
H. variostictus (Ribeiro, 1912)
H. ventromaculatus Boeseman, 1968
H. vermicularis (Eigenmann & Eigenmann, 1888)
H. verres Valenciennes, 1840
H. villarsi (Lütken, 1874)
H. virescens (Cope, 1874)
H. watwata Hancock, 1828
H. winzi (Fowler, 1945)
H. wuchereri (Günther, 1864)