A treatise of the Loricariidae Bonaparte, 1831, a family of South American mailed catfishes, with emphasis on the subfamily Loricariinae (Pisces, Siluriformes) and a provisional key to the genera of Loricariidae.

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Foreword

The work now published for the first time was completed early October 1981. It was produced as a thesis, consisting of three parts, see the references on this page. Part 1 was published in 1980, Parts 2 and 3 were 15 times photocopied and bound, eleven copies of each were deposited in the library of the Laboratoire de Zoologie approfondie, Université de Nancy. Parts 2 and 3 were hitherto unpublished and are herein issued without changes.

Disclaimer

All new scientific names and nomenclatural acts in this work are to be excluded for the purposes of zoological nomenclature.

References

Isbrücker, I. J. H. (1980): Classification and catalogue of the mailed Loricariidae (Pisces, Siluriformes). PhD thesis, Part 1., Université de Nancy. Verslagen en technische Gegevens, Instituut voor taxonomische Zoölogie (Zoölogisch Museum), Universiteit van Amsterdam 22: 1-181 available at: http://www.repository.naturalis.nl/document/550152.

Isbrücker, I. J. H. (1981, unpublished): A treatise of the Loricariidae Bonaparte, 1831, a family of South American mailed catfishes, with emphasis on the subfamily Loricariinae (Pisces, Siluriformes). PhD thesis, Part 2., Université de Nancy. 281 pp. (herein published on pages 2-283)

Isbrücker, I. J. H. (1981, unpublished): Provisional key to the genera of Loricariidae. PhD thesis, Part 3., Université de Nancy. 15 pp. (herein published on pages 284-299)

<u>recommended form for reference:</u>
Isbruecker, I.J.H. (2017):
A treatise of the Loricariidae Bonaparte, 1831, a family of South American mailed catfishes, with emphasis on the subfamily Loricariinae (Pisces, Siluriformes) and a provisional key to the genera of Loricariidae.
Ichthyological Contributions of PecesCriollos 48: 1-299
available as pdf-file at www.pecescriollos.de since 14.January.2017

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Cover illustration:

Male of Ancistrus triradiatus Eigenmann, 1917, showing the singular secondary sexual dimorphism characteristic for the genus Ancistrus. This specimen is the holotype, 113 mm, from an altitude of about 456 metres, Quebrada Cramalote, a brook at Villavicencio east of Bogotá, Andes of Colombia.

Reproduction from illustrations in Eigenmann, 1922, pl. 13 figs. 3 and 4.

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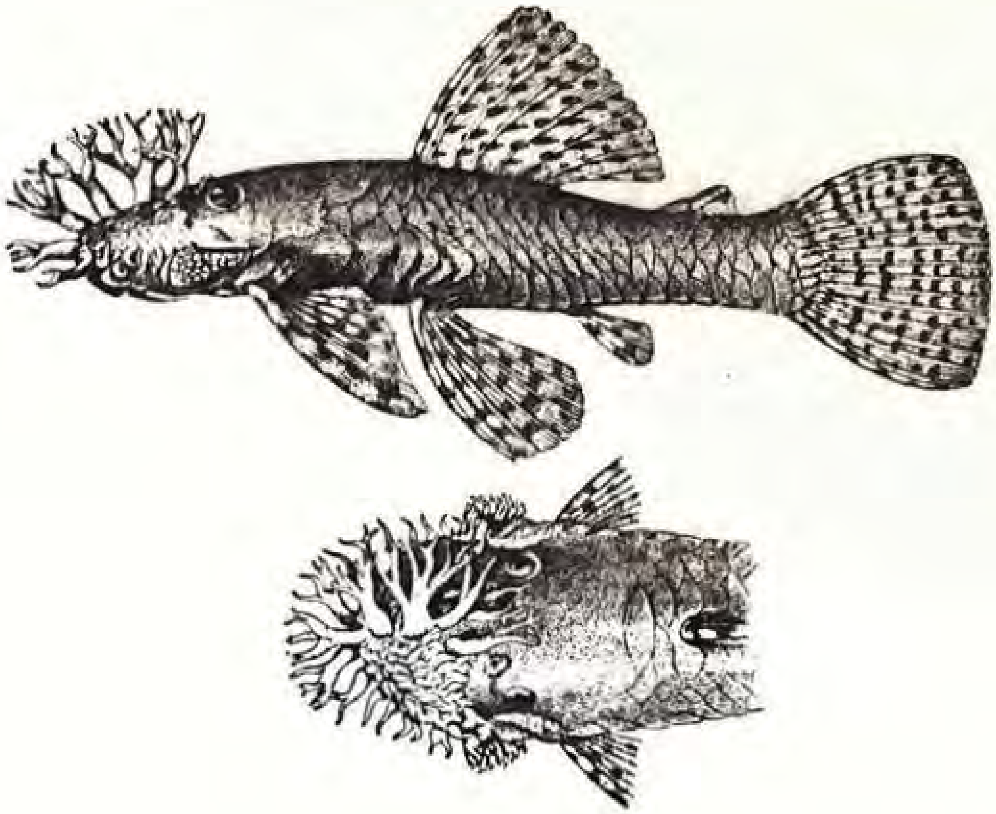

1981

CONTENTS

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52 plates outside the text

I ABSTRACT

Together with the author's publication: Classification and catalogue of the mailed Loricariidae (1980), this paper forms a survey of a large South American family of highly specialized catfishes, the Loricariidae, or mailed catfishes. The subfamily Loricariinae is almost wholly revised after examination of representatives of practically all recognized (about 200) species. In addition, representatives of all other subfamilies except for the Hypoptopomatinae (which are being revised by Dr Britski in São Paulo) have been taken into account, partly on examination of specimens and supplemented by information from literature. A (necessarily preliminary) revision of the family Loricariidae – which exclude Astroblepidae and Scoloplacidae – has resulted in the following classification, purporting to reflect the supposed phylogenetic relationships (more primitive categories are listed first); the number of species of each genus is added in parentheses:

family Loricariidae Bonaparte, 1831
subfamily Lithogeneinae Gosline, 1947
  Lithogenes Eigenmann, 1909 (1)
subfamily Neoplecostominae Regan, 1904
  Neoplecostomus Eigenmann & Eigenmann, 1888 (2)
subfamily Hypostominae Kner, 1853
  Rhinelepis von Spix, 1829 (3)
  Pseudorinelepis Bleeker, 1862 (3)
  Delturus Eigenmann & Eigenmann, 1889 (3)
  Pogonopoma Regan, 1904 (1)
  Pseudancistrus Bleeker, 1862 (6)
  Hemipsilichthys Eigenmann & Eigenmann, 1889 (6)
  Pareiorhaphis A. de Miranda Ribeiro, 1918 (2)
  Kronichthys A. de Miranda Ribeiro, 1908 (2)
  Corymbophanes Eigenmann, 1909 (2)
  Upsilodus A. de Miranda Ribeiro, 1924 (1)

Pareiorhina Gosline, 1947 (1)
Pogonopomoides Gosline, 1947 (1)
Isorineloricaria Isbrücker, 1980 (2)
Hypostomus Lacepède, 1803 (116)
Cochliodon Heckel, 1854 (6)
Pterygoplichthys Gill, 1858 (20)
subfamily Ancistrinae Kner, 1853
tribe Ancistrini Kner, 1853
Lasiancistrus Regan, 1904 (21)
Dolichancistrus Isbrücker, 1980 (3)
Cordylancistrus Isbrücker, 1980 (1)
Hemiancistrus Bleeker, 1862 (14)
Megalancistrus Isbrücker, 1980 (3)
Peckoltia A. de Miranda Ribeiro, 1912 (19)
Monistiancistrus Fowler, 1940 (1)
Parancistrus Bleeker, 1862 (6)
Hypocolpterus Fowler, 1943 (1)
Chaetostoma von Tschudi, 1845 (40)
Leptoancistrus Meek & Hildebrand, 1916 (2)
Lipopterichthys Norman, 1935 (1)
Ancistrus Kner, 1854 (50)
Panaque Eigenmann & Eigenmann, 1889 (6)
tribe Acanthicini Bleeker, 1862
Acanthicus von Spix, 1829 (1)
tribe Pseudacanthicini Isbrücker, 1980
subtribe Pseudacanthicina Isbrücker, 1980
Pseudacanthicus Bleeker, 1862 (5)
subtribe Lithoxina Isbrücker, 1980
Lithoxus Eigenmann, 1910 (2)
Exastilithoxus Isbrücker & Nijssen, 1979 (1)
subfamily Hypoptopomatinae Eigenmann & Eigenmann, 1890
tribe Otocinclini Isbrücker, 1979
Parotocinclus Eigenmann & Eigenmann, 1889 (13)
Otocinclus Cope, 1871 (26, probably less)
Microlepidogaster Eigenmann & Eigenmann, 1889 (1, probably more)

Othothyris Myers, 1927 (1)
2 unnamed genera, Britski MS (1 in each)
Pseudotocinclus Nichols, 1919 (2)
tribe Hypoptopomatini Eigenmann & Eigenmann, 1890
Hypoptopoma Günther, 1868 (11, possibly less)
Oxyropsis Eigenmann & Eigenmann, 1889 (1, possibly more)
subfamily Loricariinae Bonaparte, 1831
tribe Harttiini Boeseman, 1971
subtribe Harttiina Boeseman, 1971
Harttiella Boeseman, 1971 (1)
Harttia Steindachner, 1876 (5)
Cteniloricaria Isbrücker & Nijssen, 1979 (3)
Lamontichthys P. de Miranda Ribeiro, 1939 (2)
Pterosturisoma Isbrücker & Nijssen, 1978 (1)
Sturisomatichthys Isbrücker & Nijssen, 1979 (4)
Sturisoma Swainson, 1838 (15)
subtribe Metaloricariina Isbrücker, 1979
Metaloricaria Isbrücker, 1975 (2)
tribe Farlowellini Fowler, 1958
unnamed genus, Isbrücker, Britski, Nijssen & Ortega MS (1)
Farlowella Eigenmann & Eigenmann, 1889 (37)
tribe Acestridiini Isbrücker & Nijssen, 1974
Acestridium Haseman, 1911 (1)
tribe Loricariini Bonaparte, 1831
subtribe Rineloricariina Isbrücker, 1979
Ixinandria Isbrücker & Nijssen, 1979 (2)
Rineloricaria Bleeker, 1862 (41)
Dasyloricaria Isbrücker & Nijssen, 1979 (5)
Spatuloricaria Schultz, 1944 (11)
subtribe Ricolina, new
Ricola Isbrücker & Nijssen, 1978 (1)
subtribe Loricariina Bonaparte, 1831
Paraloricaria Isbrücker, 1979 (3)
Loricaria Linnaeus, 1758 (11)
Brochiloricaria Isbrücker & Nijssen, 1979 (2)
Crossoloricaria Isbrücker, 1979 (3)

Pseudohemiodon Bleeker, 1862 (7 + 1, undescribed)
Rhadinoloricaria Isbrücker & Nijssen, 1974 (1)
subtribe Planiloricariina Isbrücker, 1979
Planiloricaria Isbrücker, 1971 (1)
subtribe Reganellina Isbrücker, 1979
Reganella Eigenmann, 1905 (1)
subtribe Pseudoloricariina, new
Limatulichthys Isbrücker & Nijssen, 1979 (1)
Pseudoloricaria Bleeker, 1862 (1)
subtribe Loricariichthyina Isbrücker, 1979
Loricariichthys Bleeker, 1862 (16)
subtribe Hemiodontichthyina Isbrücker, 1979
Hemiodontichthys Bleeker, 1862 (1)

Chapters are included on previous classifications within the Loricariidae (from Linnaeus, 1758 to the present), on the systematic position of this family within the order of catfishes (Siluriformes), followed by the main treatment of the family, as a Guide to the genera, then a discussion of some of the taxonomic problems; a comparison of the osteology of the jaws of several Loricariid representatives; and the zoogeography of the family. A chapter "Miscellaneous notes" consists of a review of the various aspects of structure and life of the Loricariidae hardly or not discussed in the previous chapters, including a section on the structure, one on the ecology, behaviour and aquarium experiences, and a section on convergent adaptations. The final chapter includes the references, which are additional to those given in the author's 1980 paper.

II INTRODUCTION

The present paper deals with the results of a continuing study on the fishes of the family Loricariidae. This study started about 11 years ago, resulting in the publication of 17 papers (1971-1980), 7 of which with Dr H. Nijssen as joint author. An additional publication (revision of the genus Loricaria) is now in press and will be issued this year.

The knowledge about the Loricariids is still immature. It is a family of remarkably specialized catfishes confined to freshwater biotopes in South and Central America. Since 1758, when Linnaeus described and named the first two species (Loricaria cataphracta and Hypostomus plecostomus), more than 600 species and subspecies have been described. In the first part of this thesis (Isbrücker, 1980), these were assigned to 70 genera and to 6 subfamilies. A slight proportion of this abundant number of taxa has received intensive consideration. Many species, however, are still known only from a single specimen, and the range of variation in morphometric and meristic characters of the majority of described Loricariid species is insufficiently documented. This means that we have no certainty about the actual number of valid species. In addition, there is little general agreement about their classification in the literature. About 95% of the publications dealing with all aspects of Loricariid knowledge has been consulted by me.

While visiting European museums, I was able to examine abundant material, covering representatives of most of the recognized genera.

The subfamily Loricariinae was initially selected for a detailed study, after experience of often great difficulties to identify specimens even at the generic level with available literature. Almost all (primary) type-material stored in various European, North- and South American museums has been re-examined, forming the basis for a revision of the species, genera, and finally the entire subfamily.

Representatives of four of the five other subfamilies have been much more superficially examined than was possible with the Loricariinae. However, it was sufficient for subsequent attempts to preliminary interprete the correct generic position of non-Loricariinae members of the family. An additional source for impressions about Loricariid characters has been gained from observing living aquarium specimens.

A comparative study of Loricariid anatomy (principally osteology) was rather recently started under the guidance of Mr G. J. Howes of the British Museum (Natural History); this study is still largely in an initial stage.

After consideration, I have refrained from inclusion herein of most of the 'technical' detail at hand, such as complete references to each species mentioned, a catalogue of every examined specimen, extensive tabulation of morphometric and meristic data, and so on. Just to give an impression, 893 specimens of Loricariinae were thoroughly studied and all their characters measured and counted. Several species of Hypostominae, Ancistrinae, and Hypoptopomatinae in particular still require more study, before they can be delimited and identified. Inclusion herein of all the data at hand (indispensable when preparing accounts for actual publication) would result in a heavy account, which would be tiring to read. When the present work is required for publication in parts, such data will be extensively presented. I hope to be able to prepare this work for publication soonly.

III ACKNOWLEDGEMENTS

Many people have contributed importantly to this and to previous studies on Loricariidae in various ways. I am very much obliged to all of them. Mere listing of their name, town and/or institution and a brief specification of their particular contribution to me seems insufficient here, because it is hardly possible to list them all without the risk of forgetting just another, who as well participated in this subject. A long list of names etc. is at hand. At this point it is more meaningful, or so I believe, to restrict myself to those much fewer persons who have given me more than half the support one could ever anticipate.

On the 1st of November 1958 Mr J. J. Hoedeman, in charge of the department of Ichthyology of the Zoological Museum, University of Amsterdam, allowed me to set the first steps in the impressive collection of preserved fish specimens and the rich ichthyological library. Although initially an appointment was made to visit and interview him for about 45 minutes, to gather information to be published in an article for the monthly school bulletin, he further allowed me to frequently visit his premisses, until his withdrawal from ichthyological work in 1962. I am very much indebted for his early encouragement in excercising the count of fin rays, and instructing me how tell a cycloid from a ctenoid fish scale, among many other things. Due to his inspiration my interest in biology became more than previously deepened and widened.

Mr Hoedeman's successor (since 1963), Dr H. Nijssen, very kindly allowed me to continue my activities under his guidance. Since, we joined work on several smaller and larger subjects (we authored 22 publications together) and both we are looking forward very much to seeing many more projects to be done together. Without Nijssen's support, this and all other papers would never have been realized. Mrs C. Lindenaar-Sparrius,

secretary to the department during more than 11 years, Mr L. van Tuyl, zoological technical assistant, Dr P. J. H. van Bree, curator of Mammalia, Dr W. L. van Utrecht, curator, Dr C. A. W. Jeekel, director, Prof. Dr J. H. Stock, Mr L. A. van der Laan, photographer, and Mr J. Zaagman, artist, as well as many other persons of the Institute, and Mrs Drs F. F. J. M. Pieters of the Artis Library, Amsterdam are also friendly acknowledged for their generous help in my work.

I am much indebted to Prof. Dr J. Géry (GEESA, les Eyzies) for his proposal and support to complete the present work as a Thése d'Université.

Prof. Dr B. Condé (Université de Nancy I) kindly adopted me as his student. I am deeply grateful for his faith and for his encouragement.

Mr G. Howes of the British Museum (Natural History), London, throughout many years voluntarily, untiringly and most friendly offered constructive criticism on various drafts of Loricariid studies, fully sharing his profound knowledge of ichthyology whenever necessary, in spite of his amazing bulk of additional activities to further the study of so many groups of fishes.

I would like to dedicate the present work to these persons, and to my parents, who patiently heared me talk fish so long a period.

I am grateful for the financial support received by a grant from the K. F. Hein Foundation (Utrecht) to complete this study.

IV PREVIOUS CLASSIFICATIONS OF LORICARIIDAE

Linnaeus

Prior to 1758 (in addition to the 2 species named and diagnosed by Linnaeus in 1758), a small number of Loricariidae were described by some authors; there is little point in a detailed treatment of these species here, although they are mentioned shortly below.

Linnaeus (1758) established the genus Loricaria, which included Loricaria cataphracta only. Loricaria was considered as a member of the Linnaean order called "Pisces abdominales", together with the genera Cobitis, Silurus, Salmo, Fistularia, Esox, Argentina, Atherina, Mugil, Exocoetus, Polynemus, Clupea, and Cyprinus.

Another species now assigned to the Loricariidae was named by Linnaeus (1758) Acipenser plecostomus (= Hypostomus plecostomus). The genus Acipenser was initially classed among the Amphibia, in the order "Amphibia nantes". This order contained also the genera Petromyzon, Raja, Squalus, Chimaera, and Lophius.

Linnaeus transferred Acipenser plecostomus to the genus Loricaria in 1766.

Gronovius

Plecostomus was originally proposed by Gronovius (1754) as an uninominal generic name. Gronovius described in 1754 three species which instead of specific names were given serial numbers. The first of these Plecostomus spp., no. 67, is known now as Hypostomus plecostomus; no. 68 is Loricariichthys maculatus, and no. 69 is Loricaria cataphracta. In 1756, Gronovius described a fourth Loricariid, Plecostomus no. 167, which is presently known as Ancistrus temminckii. The four Gronovian species were again diagnosed in 1763, as Plecostomus number 391 through 394, representing the same species as no. 68, 69, 167, and 67, respectively, of 1754 & 1756.

Meuschen (1781) assigned these four species to the genus "*Plecostomus* seu *Loricaria*", naming no. 391 "*Cataphracta*" (= *Loricariichthys maculatus*), no. 392 "*Loricaria*" (= *Loricaria cataphracta*), no. 393 "*Plecostomoides*" (= *Ancistrus temminckii*), and no. 394 "*Plecostomus*" (= *Hypostomus plecostomus*). These publications by Gronovius and by Meuschen were in 1954 rejected for nomenclatorial purposes (Hemming, ed., 1954a & b).

Gray (1854) edited and published a manuscript left by Gronovius (who died in 1777), introducing available binominals within the genus *Plecostomus* (as with many other Gronovian taxa) for its 4 species, which by that time, however, were already provided with valid names. The type-species of *Plecostomus* Gronovius (ed. Gray), 1854 was only most recently (Isbrücker, 1980: 17-18) designated: *Plecostomus bicirrosus* Gronovius (ed. Gray), 1854. *Plecostomus cataphractus* sensu Gronovius (ed. Gray), 1854 = *Loricariichthys maculatus*, *P. flagellaris* = *Loricaria cataphracta*, *P. aculeatus* = *Ancistrus temminckii*, and *P. bicirrosus* = *Hypostomus plecostomus*. Nomenclatural stability seems best served by the designation of *P. bicirrosus* as the type-species of *Plecostomus* Gronow (= Gronovius), 1854, since the genus thus remains a junior synonym of *Hypostomus*, a generic name with which *Plecostomus* was historically confused. Both *Hypostomus* and *Plecostomus* are now based upon the same type-species (by synonymy): *Hypostomus plecostomus* (Linnaeus, 1758) (cf. Boeseman, 1968).

There is a sinister problem, however. Whilst reading the literature, I tried to find the first use of *Plecostomus* as an available generic name. Prior to 1854 (viz., Gronovius, ed. Gray), only a single author appears to have (at least quite potentially) validated *Plecostomus* –subsequent to 1758, including one named species. Swainson (1838: 336) stated: "The *Plecostomus* of Gronovius is another, and a most interesting form, at once distinguished by the great length of its tail; while the caudal fin has one of its external rays prolonged into a filament, ...etc." He added a reference to "Zooph. pl. 2, fig. 1, 2." Swainson (1839: 303-304) listed 3 subgenera within the genus *Loricaria*: *Acanthicus*, *Rhinelepes* (sic), and *Plecostomus*. Only a single species resides among the latter subgenus, namely *P. maculatus* "Gronovius, pl. 2. Bloch, 375. fig. 2." This species is known now as *Loricariichthys maculatus* (Bloch, 1794). If Swainson's interpretation had been observed in time, Bleeker would not have established the genus *Loricariichthys*, which also has Bloch's *Loricaria maculata* as its type-species. It is strongly preferable to preserve *Plecostomus* as a junior synonym of *Hypostomus*, rather than accepting *Plecostomus* as the oldest generic name for the taxon presently well-known as *Loricariichthys*.

La Cepède

Marcgrave –whoms name is known with different spellings– (1648: 166-167, ill.), described and figured a Brazilian fish, the "Gvacari", which is the vernacular name of some Loricariid. Marcgrave's description and figure concern some otherwise unidentifiable representative of either *Hypostomus* or *Pterygoplichthys*.

La Cepède (1803) proposed the genus *Hypostomus*, which contained a single nominal species, *Hypostomus guacari* La Cepède, 1803.

Boeseman (1968, 165 years after its original description) settled the always somewhat problematical identity of *Hypostomus guacari* by designating the neotype for this species. At the same time, this neotype was also designated the neotype for *Acipencer plecostomus* Linnaeus, 1758.

Spix & Agassiz

Agassiz, in Spix & Agassiz (1829) was the first who classified the Loricariids at full familial rank, proposing for them the family name "Gonyodontes".

In the same work, Spix & Agassiz described and illustrated 4 previously unknown species, each being referred to a different genus.

Bonaparte

Bonaparte (1831) was apparently the first who used the family-group name: "Loricarini", as a subfamily of the Siluridae, including Aspredo and Loricaria; Hypostomus was accepted as a subgenus of the latter genus.

Valenciennes

Valenciennes, in Cuvier & Valenciennes (1840) recognized already 32 species of Loricariidae, including 25 previously undescribed species. He assigned them to 3 genera: Loricaria, Rinelepis (= Rhinelepis), and Hypostomus.

Kner

Kner (1853a & b, 1854a & b) published important contributions to the knowledge of the mailed catfishes. He stated (1854a: 73-74): "Die durch Agassiz bewirkte Aufstellung der Panzerwelse als eigene Familie ist (daher) meiner Ansicht nach unbedingt zu billigen, und nur gegen der Namen "Goniodontes" Verwahrung einzulegen, ..." "Ich ziehe demnach vor, den Namen Loricata für die ganze Familie zu gebrauchen, und die (beiden) Gruppen derselben mit den Benennungen Loricarinae und Hypostomidae zu belegen." In a footnote to this statement, Kner even suggested that both groups might eventually be regarded as two separate families.

The Loricariinae are (1854a) represented by 14 species, 9 of which were new to science, and placed in 3 genera (2 new): Loricaria, Hemiodon, and Acestra. Unfortunately, both generic names proposed by Kner were preoccupied. Aside from subsequent generic splitting, Hemiodon is now Reganella, and Acestra became Farlowella.

Kner's (1854b) "Hypostomiden" contained 22 species, 14 of which were in original descriptions. They were subdivided as follows: the "Inermes vel Clypeati", with the genera *Sisor* and *Hypostomus*, and the "Lictores vel Ancistri", containing the genera *Chaetostomus* (= *Chaetostoma*) and *Ancistrus*. The latter genus was further subdivided into two groups, the "Brachypteri" and the "Macropteri". Kner's inclusion of *Sisor* Hamilton, formerly Buchanan, 1822 proved to be unacceptable: it is the type-genus of the family Sisoridae.

Von Tschudi (1845: 25) originally published the new genus *Chaetostoma*, described and illustrated (1845: 26-29, pl. 4 figs. 1-6) its type-species, *C. loborhynchos*, and indicated himself as the author of both the generic and the specific name.

Kner (1853b: 281-282) remarked: "Eine aus Tschudi's Sammlung gerettete schöne Art wurde bereits vom Hrn. Akademiker Heckel als neue Gattung aufgestelt und in der *Fauna Peruviana* unter dem Namen *Chaetostomus loborhynchus* beschrieben." Kner (1854b: 271) again emphasized Heckel as the author of "*Chaetostomus loborhynchus*", whereas Bleeker (1862: 2) cited Heckel as the author of *Chaetostomus* and Kner as the author of *loborhynchus*.

Günther (1864: 240, in a footnote) added to the rumour: "Although Tschudi claims the authorship of this genus and the typical species (*Ch. loborhynchus*), it is evident, from the scientific character of the description, that it is from another pen. Kner, indeed, informs us that it is Heckel who named, described, and figured that genus and the species in the 'Fauna Peruana.' This fact reminds us of a similar claim laid by Bibron to some of the genera of Batrachians published by the same author."

There is no reason to doubt the integrity of Kner's indication of the actual author of the description of this genus and its type-species. Still, it is impossible to deny that Von Tschudi did not state that another person assisted him in any way. Therefore, I prefer to refer to Von Tschudi as the author of Chaetostoma loborhynchos. How many people freely assisted and positively influenced authors with descriptions, discussions, in the formation of names, or in other ways is not always clear. Perhaps, Heckel did a lot for Von Tschudi's book. Then, Von Tschudi must have contacted and encouraged Heckel, showing him his material (which must have been the same delightful experience to Heckel as it is to us, when facing 'something odd'). In my opinion, citation of author(s), date, and publication reference has no other function than allowing one access to the source of information. In this case, Heckel may anecdotically be acknowledged for his contribution through Von Tschudi.

Bleeker

Bleeker (1858: 330-332) summarized the 55 known species of Loricariidae, generally following Kner's classification. The "Loricarioidei" were split into the "Loricarini" (20 species), and the "Hypostomini" (35 species).

Bleeker subsequently (1862, 1863, and 1864, in part) altered this classification drastically, establishing 13 new genera. For each of the genera he recognized, he cited only their type-species (1862, 1863). His classification was as follows:

Loricarioidei

Plecostomiformes

Plecostomini: Plecostomus (syn.: Hypostomus), Pseudancistrus, Ancistrus, Hemiancistrus, Chaetostomus, Pterygophlichthys, Parancistrus, and Pseudacanthicus.

Acanthicini: Acanthicus, Rinelepis, Pseudorinelepis.

Loricariaeformes

Loricariini: Loricariichthys, Loricaria, Pseudoloricaria, Parahemiodon, Hemiloricaria, Pseudohemiodon, Rineloricaria, Oxyloricaria, Sturisoma, Hemiodon, and Hemiodontichthys.

Acestrini: Acestra.

In his very numerous ichthyological publications, Bleeker used to give credit to the authors of actually applied name combinations, contrary to the system which is now in general use, in which only the author(s) of specific names become(s) placed in parentheses when a species is found to belong to another genus than in which it was originally described. Plecostomus "Art., Gron." in Bleeker (1862a: 2), according to him equals Hypostomus "auct." The type-species of Plecostomus sensu Bleeker is Plecostomus brasiliensis "Blkr." = Hypostomus plecostomus sensu Valenciennes (Boeseman, 1968: 35-36, however, rightly disagrees with Bleeker's opinion about this part of the synonymy).

Among the numerous synonyms which Bleeker listed in his detailed treatment of Plecostomus brasiliensis (1864: 7-9) are Cataphractus brasiliensis of Willughby (1685, pre-Linnaean), and, among others, Acipenser indicus of Linnaeus (1754, pre-Linnaean), Acipenser plecostomus Linnaeus, 1758, Hypostomus guacari La Cepède, 1803, and Plecostomus bicirrosus Gronovius (ed. Gray), 1854. Bleeker (1864: 9) stated: "Il n'y a presque pas de doute que c'est cette espèce, que Willoughby a déjà décrite et figurée. Aprés lui Seba, Linné et Gronovius en ont donnée presque simultanément des figures et des descriptions nouvelles."

In the case of Plecostomus brasiliensis, Bleeker (1862) introduced a new specific name, being the first post-Linnaean author who used Willughby's "Cataphractus brasiliensis". Boeseman (1968: 38) designated one of the syntypes of P. brasiliensis as the lectotype of this nominal species. The lectotype is conspecific with Hypostomus plecostomus. As a result, the synonymy of Plecostomus sensu Bleeker with Hypostomus, and of their respective type-species (P. brasiliensis and H. guacari remaining junior synonyms of H. plecostomus) became thus firmly established.

Günther

Günther (1864) assigned the Loricariids to his group "Hypostomatina" of the subfamily "Siluridae proteropodes." 71 Species were recognized as valid, whereas another 10 species were indicated as doubtfully identifiable.

Günther (1864: 221-222) offered an interesting discussion which I would like to quote in full here:

"The union of apparently such different genera as Arges, Callichthys, Loricaria, &c., is so opposed to the views of former ichthyologists, that it will be necessary to add a few words in explanation. The mailed body of the Loricariidae and Hypostomes, reflected in some way internally by the skeleton, is a very striking character: so much so, that Kner is inclined to separate them from the Siluroids altogether, and Bleeker forms of them his first Siluroid family. However, that the development of dermal scutes is not a character of so much value, is not only proved by Doras, where similar dermal productions cover a part of the lateral line, and by the numerous modifications of the dermal carapace on and behind the occiput, but especially by the Indian genus Sisor, which has a series of dorsal plates, the sides being almost naked. With regard to the skeleton, the compression of the caudal vertebrae and the dilation of their neural portion are not only found in Loricaria and Hypostomus, but also in other slender-tailed Siluroids, as Sisor, Bunocephalus, and Aspredo, genera which we associate with the former, but which are excluded from the Loricaroids of Kner and Bleeker.

Every doubt that Loricaria and the genera allied to it are true Siluroids, and nothing but Siluroids, must disappear when they are compared with those with which they have been associated by myself. There we find the gill-opening reduced to a foramen or short slit, in consequence of the gill-membranes being confluent with the skin of the broad isthmus; the nasal openings placed close together in a small groove; the ventrals inserted far forwards, below, or even in front of, the short dorsal; the pectorals and ventrals horizontal; a short anal; the remarkable development of the lower lip; and, finally, the anterior vertebrae never coalescent into one large one, the first being somewhat larger than the others, and provided with large transverse processes. A combination of such characters indicates a natural affinity even when we consider other points as being of minor importance, such as the spiny covering of the first ray of the fins of *Arges*, *Stygogenes*, &c., which is identical with the spiny armature of the Hypostomes and of some Loricariae; the spinous adipose fin of *Stygogenes*; the size of the mature eggs, which is equal in *Arges* and *Loricaria*, &c. Thus, I consider *Arges* as naked *Loricaria*, or, *vice versâ*, *Loricaria* as mailed *Arges*; and although these forms are sufficiently diversified to admit of further subdivision, it is a most artificial method, by which their natural union is destroyed."

Günther thus united representatives of groups which are now classified into 4 families: Loricariidae, Astroblepidae (*Arges* and *Stygogenes* are currently junior synonyms of *Astroblepus*), Callichthyidae, and Sisoridae. He assigned 8 genera of Loricariids, some of which included subgenera: *Plecostomus*, *Liposarcus*, *Chaetostomus*, *Pterygoplichthys*, *Rhinelepis*, *Acanthicus*, *Loricaria*, and *Acestra*.

Eigenmann & Eigenmann

Eigenmann & Eigenmann (1890) concluded two preliminary papers (1888, 1889) in a revision of the neotropical catfishes. Their classification of the then 150-odd known species of Loricariids is the following:

Loricariidae

Loricariinae (39 species): *Farlowella*, *Hemiodontichthys*, *Loricaria* (with 8 subgenera: *Hemiodon*, *Sturisoma*, *Rineloricaria*, *Pseudohemiodon*, *Parahemiodon*, *Loricariichthys*, *Pseudoloricaria*, and *Loricaria*), *Harttia*, *Oxyropsis*.

Hypoptopominae (7 species): *Hypoptopoma*, *Hisonotus*, *Paroto-*

cinclus, Otocinclus.

Plecostominae (105 species, including 'varieties'): Microlepidogaster, Neoplecostomus, Plecostomus, Rhinelepis, Hemiancistrus, Parancistrus, Cochliodon, Panaque, Pterygoplichthys, Pseudancistrus, Delturus, Hemipsilichthys, Acanthicus, Chaetostomus, and Ancistrus.

It is remarkable that Eigenmann & Eigenmann's genera Oxyropsis and Microlepidogaster soon after their establishment were referred to the Hypoptopomatinae, a subfamily which these authors proposed themselves.

Regan

The most renown worker on the study of mailed catfishes is Regan. In 1904 he published a monograph of the Loricariidae. The genera Arges and Astroblepus (which are now considered as a single genus, Astroblepus) were included as the subfamily "Argiinae" (= Astroblepidae). Regan recognized almost 190 valid species (20 of which are Astroblepidae), which he classified as follows:

Loricariidae

Plecostominae (95 species, including 1 'variety'): Plecostomus (with the subgenera Plecostomus, Pogonopoma, and Rhinelepis), Hemipsilichthys, Ancistrus (with the subgenera Ancistrus, Parancistrus, Lasiancistrus, and Pseudancistrus), Panaque, Chaetostomus, Xenocara, Pseudacanthicus, and Acanthicus.

Hypoptopomatinae (15 species): Hypoptopoma and Otocinclus.

Loricariinae (59 species): Loricaria (with the subgenera Rhineloricaria, Pseudoloricaria, Loricariichthys, and Loricaria), Hemiodontichthys, Oxyloricaria, and Farlowella.

Neoplecostominae (1 species): Neoplecostomus.

Argiinae (20 species): Arges and Astroblepus.

The meritorious work by Regan (supplemented by him in several subsequent contributions) contains some unfortunate misconceptions of genera. Apart from this, he accepted far less genera than later workers (and also less than various previous authors).

The genus *Xenocara* was established in the monograph. Originally, it included the type-species of *Ancistrus* Kner, 1854, as validly designated by Bleeker (1862: 2), viz., *A. cirrhosus*. In 1906, Regan established a new subgenus of *Xenocara*, *Thysanocara*, also with *Ancistrus cirrhosus* as its type-species. *Thysanocara* is an objective synonym of *Ancistrus*. I believe that we have to consider *Xenocara* (of which *Chaetostomus latifrons* was subsequently —by Eigenmann, 1910— designated as the type-species) as a subjective synonym of *Ancistrus*.

Regan's concept of *Ancistrus* was influenced by Gill (1858: 407-408) (cf. Regan, 1906: 95-96), who emended and restricted Kner's *Ancistrus*. However, Gill neither designated the type-species of *Ancistrus*, nor did he exclude *Ancistrus cirrhosus* explicitly from that genus, although Regan was not at all ignorant of Gill's definition of the interoperculum of *Ancistrus*: "...movable, and armed with a tuft of rather long and slender spines, ...". In *Ancistrus cirrhosus*, these spines are actually rather short and comparatively thick, not slender as in several other genera.

Regan's nominal subgenus *Ancistrus* comprises 4 genera: *Pterygoplichthys* Gill, 1858, *Hemiancistrus* Bleeker, 1862, *Peckoltia* A. de Miranda Ribeiro, 1912, and *Megalancistrus* Isbrücker, 1980. Regan's subgenus *Pseudancistrus* Bleeker, 1862 likewise contains species now assigned to 3 genera: *Pseudancistrus*, *Lasiancistrus* Regan, 1904, and *Delturus* Eigenmann & Eigenmann, 1889. Regan's subgenus *Parancistrus* Bleeker, 1862 is well-defined, although it is currently considered as of full generic rank.

Regan (1904: 297) considered *Sturisoma* Swainson, 1838 inadmissible, as a "nomen hybridum", and used *Oxyloricaria* Bleeker, 1862 instead. Although he was followed in this idea during some years, Oxyloricaria is now currently correctly accepted as a junior synonym of Sturisoma.

Regan (1905: 534), in a publication replying to critical remarks expressed by Evermann & Kendall (1905), remarked: "The statement that I object to the family name Argiidae of Gill is hardly correct. On the contrary, I should consider it a most excellent name for the group if it is to be regarded as a distinct family. Provided that they be correctly defined and their relationships made clear, it appears to me to be a point of comparatively small importance whether the Argiinae or Argiidae be regarded as a specialized group of Loricariidae or as a distinct family. I am inclined to believe, however, that the practice of making every somewhat abnormal or peculiar genus the type of a family tends to obscure its relationships."

Eigenmann

Eigenmann (1910) published a systematic arrangement of the Loricariids in a catalogue of South American freshwater fishes. It differs in several respects from the classification proposed by Regan. A total of 209 species is considered as valid. Eigenmann accepted all but one of Regan's subfamilies, ranking the Astroblepidae as the family Cyclopidae.

In the Plecostominae, Eigenmann included 21 genera (118 species): Plecostomus, Lithogenes, Pogonopoma, Canthopomus, Rhinelepis, Corymbophanes, Hemipsilichthys, Hemiancistrus, Pterygoplichthys, Parancistrus, Lasiancistrus, Pseudancistrus, Delturus, Cochliodon, Panaque, Chaetostomus, Xenocara, Ancistrus, Pseudacanthicus, Lithoxus, and Acanthicus.

In the Hypoptopomatinae, 5 genera are included (20 species): Hypoptopoma, Oxyropsis, Parotocinclus, Otocinclus, and Microlepidogaster.

70 Species of Loricariinae are assigned to Loricaria, Hemiodontichthys, Reganella, Harttia, Sturisoma, and Farlowella.

The Neoplecostominae consisted of a single species of Neoplecostomus.

Gosline

The next enumeration, Gosline's catalogue of South and Central American catfishes, appeared in 1945. The Loricariids are richly represented with 428 species and subspecies. The Astroblepidae are listed, containing a single genus with 39 species and subspecies. Gosline's arrangement was:

Loricariidae

Plecostominae (252 species and subspecies): Plecostomus, Carinotus, Lithogenes, Cheiridodus, Pogonopoma, Canthopomus, Rhinelepis, Corymbophanes, Hemipsilichthys, Kronichthys, Pareiorhaphis, Upsilodus, Peckoltia, Hemiancistrus, Pterygoplichthys, Parancistrus, Cochliodon, Monistiancistrus, Panaque, Delturus, Lasiancistrus, Pseudancistrus, Chaetostoma, Hypocolpterus, Lipopterichthys, Xenocara, Ancistrus, Pseudacanthicus, Lithoxus, Stoneiella, Leptoancistrus, and Acanthicus.

Hypoptopomatinae (36 species): Hypoptopoma, Pseudotocinclus, Parotocinclus, Otocinclus, Otothyris, and Microlepidogaster.

Loricariinae (139 species): Loricaria (5 subgenera), Spatuloricaria, Hemiodontichthys, Reganella, Harttia, Lamontichthys, Sturisoma, Parasturisoma, Farlowella, and Acestridium.

Neoplecostominae (1 species): Neoplecostomus.

Two years later, Gosline (1947) published the most extensive account on the classification of the mailed catfishes since those of Regan and Eigenmann. Within the Loricariidae he recognized the subfamilies Astroblepinae, Lithogeninae, Neoplecostominae, Plecostominae, Hypoptopomatinae, and the Loricariinae.

Particularly, the definition of the Neoplecostominae is widely expanded to include 12 genera (2 of which were new), most of which were previously assigned to the Plecostominae: Neoplecostomus, Upsilodus, Hemipsilichthys, Pareiorhaphis, Pareiorhina, Kronichthys, Corymbophanes, Delturus, Rhinelepis, *Canthopomus*, *Pogonopoma*, and *Pogonopomoides*.

Fowler

Fowler (1954) provided a compilation of the freshwater fishes of Brazil and of some river drainages in adjacent countries. 324 Species and subspecies of Loricariidae are listed and provided with numerous references. A number of these references were rather hastily compiled, but are nevertheless still useful.

Boeseman

Boeseman (1968, 1969) published a revision of the Surinam species and subspecies of *Hypostomus*. Next to 2 known species (*H*. *plecostomus* and *H*. *watwata*; a neotype was designated for each of these species), he described 12 new species and 3 new subspecies from the relatively small area.

Partly on Gosline's information (1947), Boeseman (1971) presented a tentative phylogenetic diagram of the 'higher' Loricariidae. He accepted the subfamilies Loricariinae, Harttiinae, Neoplecostominae, Hypostominae, Ancistrinae, and Hypoptopomatinae. The problems he found to be still existing concerning the correct phylogenetic situation of the Astroblepinae and the "Lithogenidae" were not considered.

Boeseman's (1971) new subfamily Harttiinae contained 5 genera, viz., *Harttiella*, *Harttia*, *Parasturisoma*, *Sturisoma*, and *Farlowella*. With the exception of a complete enumeration of the speciose genus *Farlowella* (3 new species), he listed the 30 other species of Harttiinae, while all species occurring in Surinam —all but one, *Harttiella* *crassicauda* (Boeseman, 1953), new to science— were described and figured. Two further studies on Surinam Loricariidae were published by Boeseman: one on a new *Hypoptopoma* sp., and a new *Parotocinclus* sp. (1974), and one on the Surinam Loricariinae, with additional information on Surinam Harttiinae (1976). In this last publication, my genus *Metaloricaria* (1975) is synonymized with *Harttia*, and a new species, *Harttia* *nijsseni* was published. Boeseman (1976) expressed some very encouraging criticism on some opinions I had published, especially in papers on Loricaria cataphracta (1972), and on Loricariichthys maculatus (1971).

Chardon

In 1968, Chardon published an extensive study on the comparative anatomy of the Weberian apparatus and connected structures within the Siluriformes. He redefined 7 suborders within this order, the most specialized of which was the Loricarioidei. The suborder Loricarioidei contained 3 superfamilies, the Aspredinoidea, Trichomycteroidea, and the Loricarioidea, arranged from the most archaic to the most specialized.

Baskin

Baskin (1978) thoroughly and excellently studied the comparative anatomy –mostly osteology– and relationships of the Trichomycteridae. He concluded that the suborder Loricarioidei consists of 2 superfamilies, viz., the Nematogenyoidea (with only the family Nematogenyidae) and the Loricarioidea, including the Trichomycteridae, Callichthyidae, Loricariidae, Astroblepidae, and an at the time of writing (1972) unnamed catfish, referred to as "loricarioid sp.", now Scoloplax dicra Bailey & Baskin, 1976. In the meantime, this species was described and assigned by Bailey & Baskin (1976) as the unique member of the remarkable Scoloplacinae, a subfamily of the Loricariidae. The Aspredinidae were excluded from the suborder Loricarioidei by Baskin (1978).

Isbrücker & Nijssen

On the basis of preliminary studies, we (1978) proposed a new classification of the subfamily Loricariinae. It was subdivided into 4 tribes: the Loricariini, Harttiini, Farlowellini, and the Acestridiini.

In 1979 I published a catalogue of the Loricariinae, in which 179 species were accepted as valid. 27 Genera were classified, and the tribes Loricariini and Harttiini were further subdivided into subtribes. In 1980 (as the first part of this thesis) a catalogue of the entire family Loricariidae (excluding the Astroblepids and *Scoloplax* as representatives of two separate families) was given together with an updated classification, resulting in:

Loricariidae (592 species)

- Lithogeneinae (1 species): *Lithogenes*.
- Neoplecostominae (2 species): *Neoplecostomus*.
- Hypostominae (175 species): *Rhinelepis*, *Pseudorinelepis*, *Delturus*, *Pogonopoma*, *Pseudancistrus*, *Hemipsilichthys*, *Pareiorhaphis*, *Kronichthys*, *Corymbophanes*, *Upsilodus*, *Pareiorhina*, *Pogonopomoides*, *Isorineloricaria*, *Hypostomus*, *Cochliodon*, and *Pterygoplichthys*.
- Ancistrinae (178 species)
  - Ancistrini: *Lasiancistrus*, *Dolichancistrus*, *Cordylancistrus*, *Hemiancistrus*, *Megalancistrus*, *Peckoltia*, *Monistiancistrus*, *Parancistrus*, *Hypocolpterus*, *Chaetostoma*, *Leptoancistrus*, *Lipopterichthys*, *Ancistrus*, *Panaque*.
  - Acanthicini: *Acanthicus*.
  - Pseudacanthicini: Pseudacanthicina: *Pseudacanthicus*; Lithoxina: *Lithoxus*, *Exastilithoxus*.
- Hypoptopomatinae (57 species)
  - Otocinclini: *Parotocinclus*, *Otocinclus*, *Otothyris*, 2 unnamed genera, *Pseudotocinclus*.
  - Hypoptopomatini: *Hypoptopoma*.
- Loricariinae (179 species):
  - Harttiini: Harttiina: *Harttiella*, *Harttia*, *Cteniloricaria*, *Lamontichthys*, *Pterosturisoma*, *Sturisomatichthys*, *Sturisoma*; Metaloricariina: *Metaloricaria*.
  - Farlowellini: *Farlowella*.
  - Acestridiini: *Acestridium*.
  - Loricariini: Rineloricariina: *Ixinandria*, *Rineloricaria*, *Dasyloricaria*, *Spatuloricaria*; Loricariina: *Ricola*, *Paraloricaria*, *Loricaria*, *Brochiloricaria*, *Crossoloricaria*,

Pseudohemiodon, *Rhadinoloricaria*; Planiloricariina: *Planiloricaria*; Reganellina: *Reganella*; Loricariichthyina: *Limatulichthys*, *Pseudoloricaria*, *Loricariichthys*; Hemiodontichthyina: *Hemiodontichthys*.

The following generic names were accepted as invalid: *Canthopomus* Eigenmann, 1910, and *Canthopomus* Eigenmann & Allen, 1942 = *Pseudorinelepis*; *Carinotus* = *Delturus*; *Xenomystus* Lütken, 1874 (preoccupied) = *Hemipsilichthys*; *Plecostomus* Gronovius (ed. Gray), 1854, and *Plecostomus* sensu Bleeker, 1862 = *Hypostomus*; *Cheiridodus* = *Cochliodon*; *Liposarcus* = *Pterygoplichthys*; *Peckoltichthys* = *Peckoltia*; *Acanthodemus* = *Parancistrus*; *Xenocara*, *Thysanocara*, and *Pristiancistrus* = *Ancistrus*; *Stoneiella* = *Pseudacanthicus*; *Hisonotus* and *Microlepidogaster* = *Otocinclus*; *Oxyropsis*, *Aristommata*, and *Diapeltoplites* = *Hypoptopoma*; *Oxyloricaria* and *Parasturisoma* = *Sturisoma*; *Acestra* Kner, 1853 (preoccupied) = *Farlowella*; *Hemiloricaria* with some reservation = *Rineloricaria*; *Euacanthagenys* = *Spatuloricaria*; *Fusiloricaria* = *Loricaria*; *Hemiodon* Kner, 1853 (preoccupied) = *Reganella*; *Plecostomus* Gronovius (in Swainson), 1839 (nomen 'oblitum'??), and, finally, *Parahemiodon* = *Loricariichthys*.

Golvan

Golvan (1965: 65-66), in a catalogue of genera of Recent fishes, included an enumeration of the genera of Loricariidae. Apart from some omissions, some incorrect dates of publication and incorrect spelling of some names, three genera (*Hassar*, *Pseudosynodontis*, and *Rhinoglanis*) are included which are not Loricariidae.

V SYSTEMATIC POSITION OF LORICARIIDAE

Siluriformes

The Loricariidae forms one of the families of the order Siluriformes. Greenwood (in Norman, 1975: 383) summarized 31 families. Thirteen of these (exclusive of a family discovered in 1976) are confined to South America: Diplomystidae, Doradidae, Auchenipteridae, Aspredinidae, Pimelodidae, Ageneiosidae, Hypophthalmidae, Helogeneidae, Cetopsidae, Trichomycteridae, Callichthyidae, Loricariidae, and Astroblepidae. The 14th family is the Scoloplacidae, which was originally established as a subfamily of the Loricariidae (Bailey & Baskin, 1976).

The only catfish family occurring in South America and other continents is largely marine, the Ariidae.

Except for some Aspredinidae, all catfish families confined to South America are primary freshwater fishes. Like catfishes in general, the very numerous members of South American families mainly consist of species with nocturnal and carnivorous habits, contrary to the Loricariidae.

The Loricariidae are almost always ranked as either the most, or as among the most, specialized of all catfishes. Some members of the Asian family Sisoridae (e. g., Bagarius) and the African Amphiliidae (e.g., Phractura) have several features (general body·shape, dermal ossifications) which strikingly suggest those also present in Loricariinae. These resemblances are clearly due to convergent evolution, Bagarius, Phractura, and Loricariinae being adapted to, or just well able to dwell in similar biotopes, in this case torrential streams. There is no evidence of a close relationship between Sisoridae and Amphiliidae versus Loricariidae.

There are no families of freshwater catfishes which South America shares with other continents. Many catfish genera are osteologically so poorly known that it seems practical to unite them into families continentwise, except where there exists evidence of the contrary, as is the case with some Afroasian families. Other Siluriform families than those listed above (a few of them largely or exclusively marine) occur in Africa, Asia, North America, Europe, and Australia.

According to the classification proposed by Chardon (1968), only 5 out of the 14 South American catfish families belong to superfamilies or suborders occurring elsewhere.

The most primitive of these 5 families appears to be the Helogeneidae, which is ranked as a distinct superfamily of the suborder Siluroidei, also occurring in Europe and Asia.

The Pimelodidae are considered as a family of the superfamily Bagroidea.

The Auchenipteridae, Doradidae, and Ageneiosidae are united with the (exclusively African) Mochokidae in the superfamily Doradoidea of the suborder Bagroidei (widespread in Asia, Africa, North America, and Australia).

Four suborders appear to be endemic to South America. One of these is the suborder Diplomystoidei, which is recognized as the most primitive of all Siluroids, unique by the possession of maxillary teeth. There are one or two species known.

The Cetopsoidei and Hypophthalmoidei are likewise suborders with a small number of species, and confined to South America.

Loricarioidei

The fourth suborder endemic to South America is the Loricarioidei, which was subdivided by Chardon (1968) into 3 superfamilies, viz., the Aspredinoidea, the Trichomycteroidea, and the Loricarioidea.

The first superfamily has a moderate number of genera, none of which with many species, forming together the family Aspredinidae.

Contrary to Chardon's (1968) conclusion, according to Baskin (1978), the Aspredinoidea (consisting only of the family Aspredinidae) should be excluded from the Loricarioidei on account of the different structure of the Weberian apparatus and the complete lack of odontodes (called integumentary teeth, or dermal denticles, by Baskin), both characters in contrast with the condition found in the Loricariodei sensu Baskin.

The Aspredinidae are usually divided into two subfamilies, the Aspredininae and the Bunocephalinae. Some or perhaps all Aspredininae are the only known South American catfishes except Ariidae with a high salt-tolerance.

Two ill-known genera of the Bunocephalinae, Hoplomyzon Myers, 1942, and Dupouyichthys Schultz, 1944, bear a very strong superficial resemblance to Scoloplax Bailey & Baskin, 1976, a singular, monotypic genus forming a very distinct Loricarioid family. Hoplomyzon and Dupouyichthys are osteologically unknown, rendering a comparison with Scoloplax impossible at this time. It is quite probable that their resemblance to Scoloplax is due only to a remarkably close convergent evolution.

Baskin (1978: 57-76), in his work on the structure and relationships of the Trichomycteridae, found that all (except for a few highly specialized Trichomycteridae) members of the suborder Loricarioidei share the possession of odontodes plus certain advanced modifications of the Weberian apparatus. Baskin included the Trichomycteridae, Callichthyidae, Loricariidae, Astroblepidae, an at the time of his writing (1972) undescribed "Loricarioid sp." (= Scoloplax dicra), and the Nematogenyidae.

Baskin (1978) proposed to divide the Loricarioidei into two superfamilies, the Nematogenyoidea (containing only the family Nematogenyidae) and the Loricarioidea, including the Trichomycteridae, Callichthyidae, Astroblepidae, the Loricariidae, and "Loricarioid sp." (read: Scoloplacidae).

The Nematogenyidae consists of a single species, occurring in the fresh waters of central Chile (Eigenmann, 1918: 280). Nematogenys inermis was proposed by Baskin (1978: xix) as "...the closest relative of the monophyletic group formed by trichomycterids, loricariids and their relatives." It represents the most generalized member of the suborder Loricarioidei, reminding rather of a Pimelodid (Eigenmann, 1918: 280); the presence of odontodes on the pectoral spine, and the structure of its Weberian apparatus, however, indicate that its relationships are with Loricarioids.

The Trichomycteridae is a rather large family in terms of subfamilies and genera. It was raised to the rank of superfamily by Chardon (1968), but Baskin (1978) considered it a family of the Loricarioidea. It consists of the subfamilies Trichomycterinae (4 genera), Vandelliinae (5 genera), Stegophilinae (11 genera), Tridentinae (4 genera), Sarcoglanidinae (2 genera), and the Glanapteryginae (3 genera). Of these subfamilies, the Trichomycterinae (and particularly the genus Trichomycterus) is the most speciose and the most widespread. Several members of the Trichomycteridae have odontodes well developed on the posterodorsal corner of the opercle and on the posterior and ventral edge of the interopercle (Baskin, 1978: 61).

The members of the Callichthyidae are divided into two subfamilies, the Callichthyinae with the genera Callichthys, Hoplosternum, Cascadura, and Dianema (of which Cataphractops may be a synonym or a very closely related genus). Callichthys and Hoplosternum are widely distributed, but like the other two or three genera of the subfamily, contain a few species only (Gosline, 1940; Hoedeman, 1952).

The second subfamily, the Corydoradinae, consists of three genera, Corydoras, Brochis, and Aspidoras. Brochis is known from 2 quite distinct species (Nijssen & Isbrücker, 1970; S. Wheeler, 1978: 16-17). There are 14 described species of Aspidoras (Nijssen & Isbrücker, 1976; 1980a); these are usually more closely related to each other than are the species of Brochis. The genus Corydoras is the most speciose of all Callichthyidae, containing about 100 valid species (Nijssen & Isbrücker, 1980b) and several more awaiting formal naming and description, be it that several of the species show a more or less obsolete interrelationship, apparently due to their rather recent and rapid evolution. In number of forms, Corydoras provides an interesting parallel with the Loricariid genus Hypostomus.

All Callichthyidae possess odontodes, present all over the dermal ossifications (which are well developed), and on the fin spine and rays.

Bailey & Baskin (1976) described Scoloplax dicra, which they stated to be: "...a tiny catfish displaying a spectrum of features that not only mark it as novel but pose a problem as to its proper systematic position." It is the Loricarioid sp. discussed previously by Baskin (1978, mimeographed from a manuscript completed in 1972). Bailey & Baskin (1976) established the subfamily Scoloplacinae of the family Loricariidae, to accommodate Scoloplax dicra. Among the characters tabulated in their table I (presenting a comparison of Callichthyidae, Scoloplax, Astroblepus, and "other Loricariidae") there are seven which, in my opinion, indicate that ranking Scoloplax at family level is warranted: (1) absence of a mouth disc, (2) absence of a lateropterygium, (3) presence of 5 simple and 2 bifid preanal haemal spines, (4) presence of a large, toothed (= provided with odontodes) rostral pla-

Plate XLIII (for pls. I-XLII, see chapter VI).

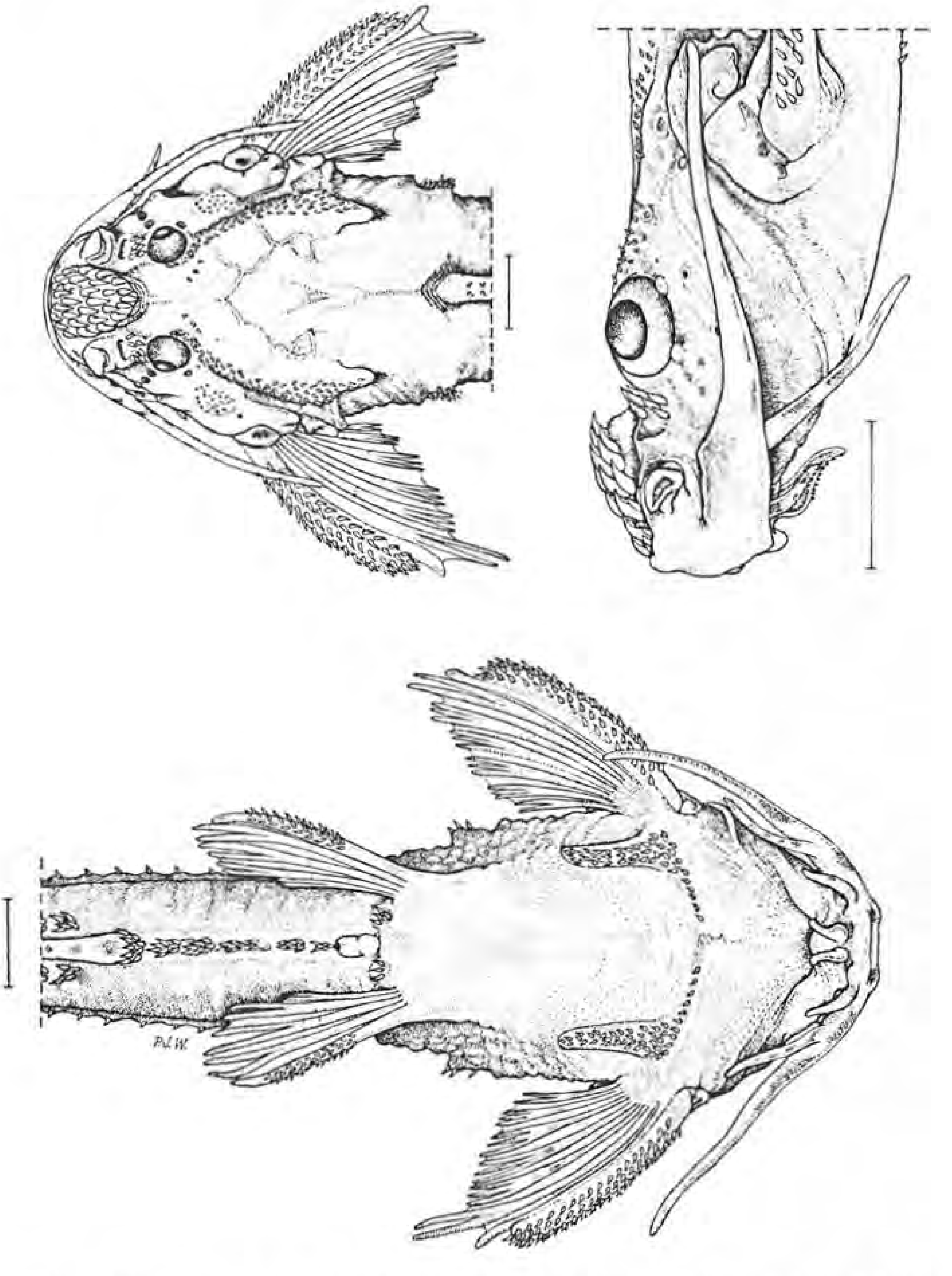


Fig. V,1. - Scoloplax dicra Bailey & Baskin, 1976, holotype (after Bailey & Baskin, 1976, figs. 1-2; scale lines are 1 mm).

te, (5) quadrangular caudal peduncle with four series of scutes, (6) a forked maxillary barbel, and (7) presence of a midventral series of preanal plates.

The Astroblepidae is currently understood to contain a single genus, Astroblepus, with about 45 described species. Astroblepus is much in need of revision; I doubt whether is is monophyletic. To quote from Gosline (1947: 92), who included Astroblepus as a subfamily within the Loricariidae, it is: "...limited to the Andean region, where it is one of the genera found highest in the mountain torrents." He also stated: "In the sucker-like mouth, in the asperous [because of the presence of odontodes] fin spines, and in most internal structures [...], Astroblepus is a Loricariid, ..." and: "The present author [Gosline] feels that many peculiarities of the subfamily, including the absence of scutes, may have been adaptations to its [torrential] environment," and: "...whatever adaptation may have taken place in correlation with a torrential environment, the Astroblepine stock separated from that of other Loricariids before the rest of the family evolved to its present status. The basis of this belief lies chiefly in the high pectoral count of Astroblepus; ..."

It is sufficiently clear and known since long that Astroblepus (sensu lato) of all Siluroids stands closest to the Loricariidae. More so than with any other family, it is a matter of mere preference to exclude Astroblepus at family level from the closely related Loricariidae, or to include it as a highly distinct subfamily. Aside from the external peculiarities of Astroblepus, its jaws and dentition are unique in structure. There are prominent teeth in several rows, and the jaws are distinctly more like a generalized catfish rather than like the jaws of Loricariidae. Some species of Astroblepus possess teeth of two different shapes on the dentary and the premaxilla: the anterior rows are roundish spade-shaped, whereas the posterior rows are strong-

Plate XLIV.

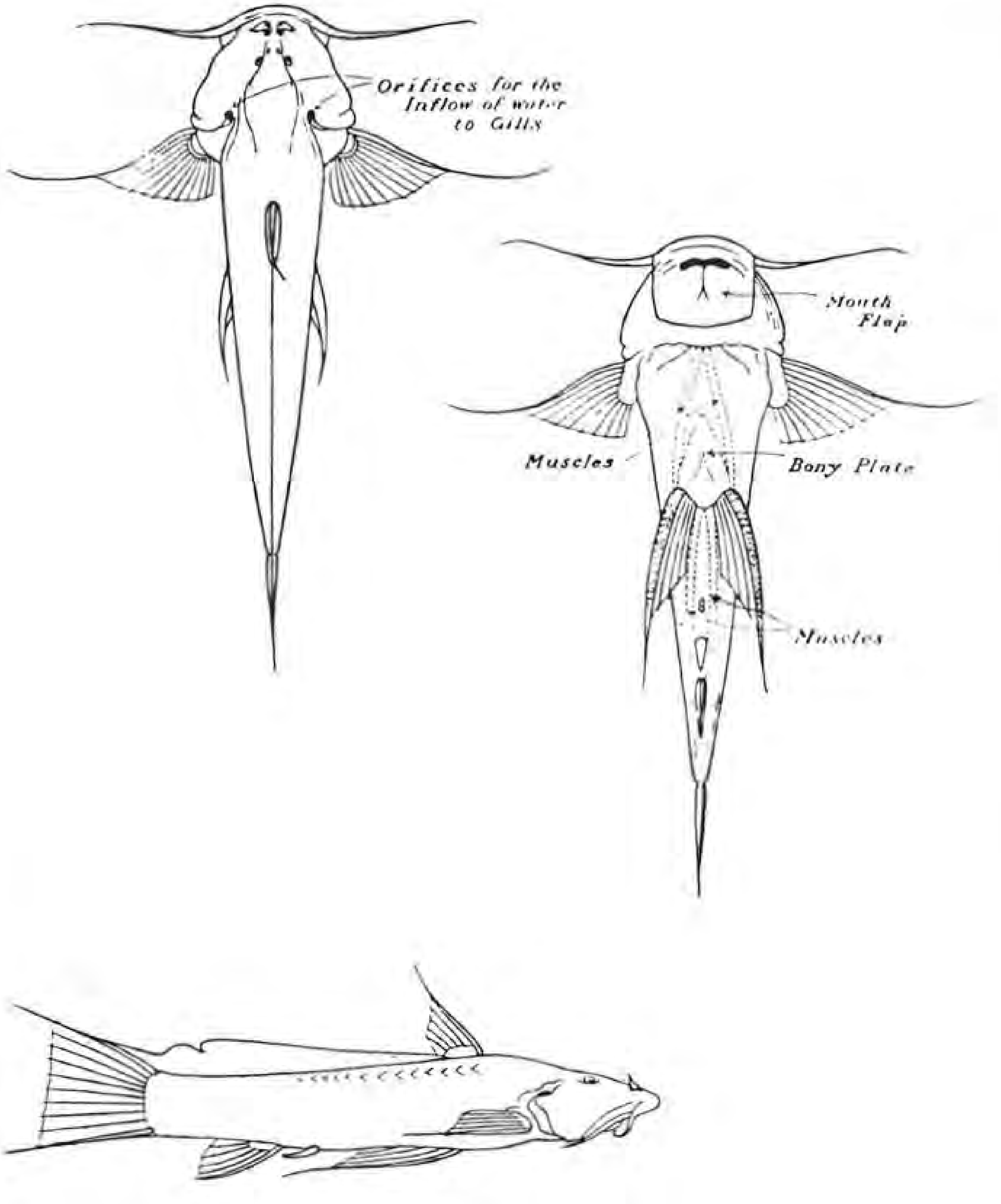


Fig. V,2. - Astroblepus marmoratus (Regan, 1904); details of a specimen from Colombia, in dorsal, ventral, and lateral view (after Johnson, 1912, figs. 1-3), see also fig. V,3.

Plate XLV.

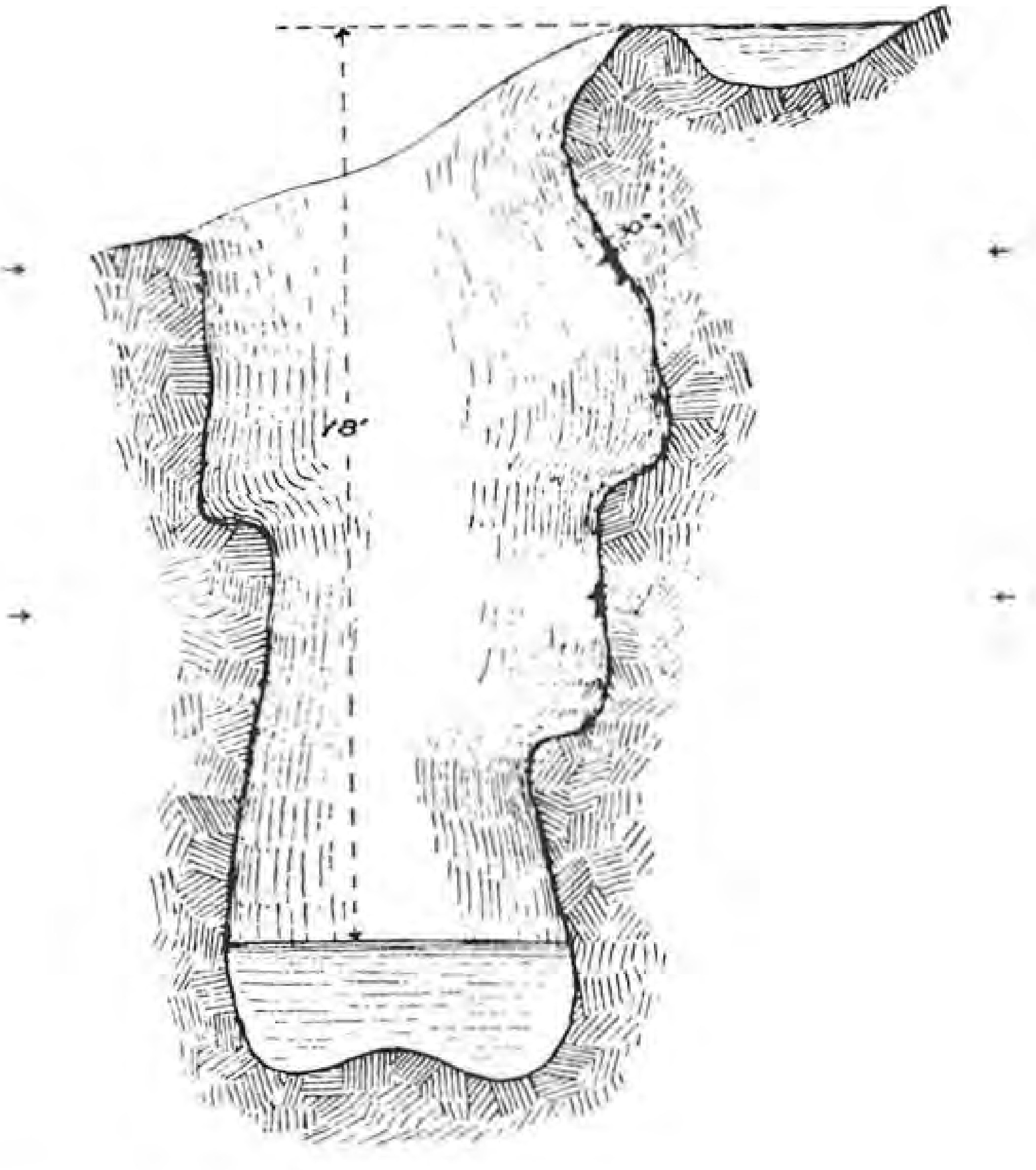


Fig. V,3. - Habitat of <u>Astroblepus</u> <u>marmoratus</u> (Regan, 1904). "Section of a pot-hole, twenty-two feet deep, in Santa Rita Creek, Colombia, showing "capitanes" ascending its rocky walls." (after Johnson, 1912, fig. 4; 4 arrows in margin added).

ly bifid (see p. VIII,3 fig. 1). In addition, the lateropterygium of Astroblepus expands dorsally into a roundish plate, a character unique for the Astroblepidae.

The Loricariidae, the main subject of this paper, are extensively discussed in the following chapters. Alexander, in an excellent work on structure and function in the catfish concluded (1966: 143): "The Callichthyidae and Loricariidae are very peculiar and specialized, but probably evolved from small-mouthed ancestors which resembled Pseudodoras [Doradidae] in many features."

As already mentioned above, Baskin (1978) convincingly has indicated that the relationships of the Loricariidae lie with the Trichomycteridae, both probably with a shared ancestor which possessed odontodes and dermal ossifications. Baskin (1978: xx) stated: "The common ancestor of all loricarioids had a full set of Weberian ossicles and partially encapsulated swimbladder vesicles. Loricarioids other than Nematogenys lost the claustrum and intercalarium, and developed the fully encapsulated Weberian apparatus. The Weberian capsule was independently reduced in size and modified into a vase shape in the Astroblepidae and Trichomycteridae. The common ancestor of all trichomycterids is hypothesized to be a nonparasitic species, although several of the advanced characters of the family can be considered advantageous to a parasitic fish."

The more primitive Loricariidae (such as the Hypostominae and the Ancistrinae) are apparently mainly algea feeders. The common ancestor of the present Loricarioidei likely was a carnivore which produced on the one hand a lineage developing parasitic habits (Trichomycteridae) and on the other hand a lineage adopting herbivorous habits (Loricariidae). Some highly specialized Loricariidae (Loricaria and Hemiodontichthys) appear to be omnivorous, considering their relatively short intestine and the possession of a pharyngeal dentition much like that found for instance in snail-eating Cichlids and in Labrids (see chapter X).

VI GUIDE TO IDENTIFICATION OF GENERA OF LORICARIIDAE

In my 1980 publication "Classification and catalogue of the mailed Loricariidae" –forming the first part of this work– literature references are given for each taxon, with quotation of type-localities, type-material, and maximum sizes.

In the present chapter, distinguishing characters of the numerous genera and higher taxa are briefly recorded as an aim towards identification. Detailed literature references are omitted to avoid a mere repetition of those already included in the Catalogue. At this point it may be said again that much work on Loricariid systematics remains to be done.

LORICARIIDAE

A family of the Siluriformes, suborder Loricarioidei, superfamily Loricarioidea. Inferior lips form a sucking disk. Body covered by 5 longitudinal rows of scutes (except for the subfamily Lithogeneinae, which has a reduced number of poorly developed scutes). Odontodes always richly present, covering dermal ossifications, fin spines and rays.

LITHOGENEINAE

Lithogenes Eigenmann, 1909

In 1908 the (still) unique specimen of Lithogenes villosus Eigenmann, 1909 (the only representative of the subfamily) was collected at Aruataima Falls, Upper Potaro River, formerly British Guiana. Aruataima is situated about 65 km from the eastern edge of the plateau of Guiana, the most distant point at which Eigenmann and collaborators made collections of fish. Eigenmann (1912: 52) stated in his itinerary of 20th October 1908: "William later collected in the cataract and sent me two new genera and three new species, ...", including Lithogenes villosus (and Corymbophanes andersoni Eigenmann, 1909).

Plate I.

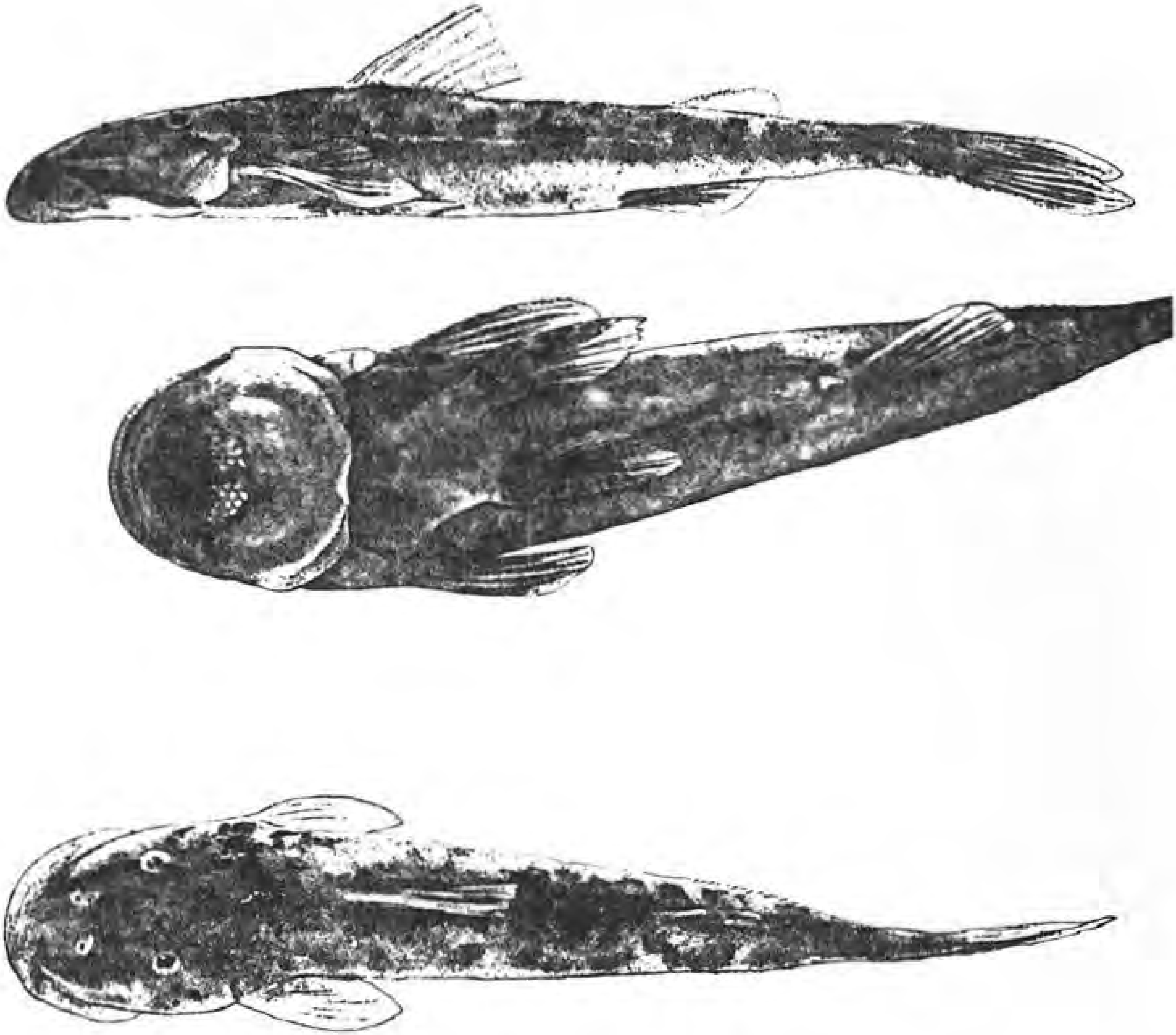


Fig. VI,1. - Lithogenes villosus Eigenmann, 1909, holotype (after Eigenmann, 1912, pl. 26 figs. 2-4).

The following is quoted from Eigenmann's (1909 & 1912) descriptions: "P. I,8...oral disk large...about twenty-five blunt villi in immediate association with the dentary... dentary with two teeth, each with two nearly parallel cusps, of which the inner is much the longer...outer ventral ray very thick and fleshy, covered with spines, its base much wider than that of the rest of the fin...naked except for a double series of plates along the ventral surface of the caudal peduncle from near the tip of the anal and curved up on either side of the caudal to the base of the middle rays; about fourteen platelets along the middle of the sides from above the origin of the anal to the base of the middle caudal rays...a double series of plates on the back, beginning on either side of the spine of the adipose to the caudal..."

Lithogenes villosus is unusually slender for a Loricariid and appears to have little characters in common with Hypostomus, contrary to Eigenmann's suggestion. The number of caudal fin rays was not stated. Adipose fin spine well-developed. Eigenmann (1912: 104) wrote that Lithogenes is the only genus of the Loricariidae with the armature reduced to a few prickles. He further wrote: "Whether we regard this nakedness as primitive or as secondarily acquired it points to a long separation from the other Loricariidae and Lithogenes may (...) be a left-over."

Gosline erected the subfamily Lithogeneinae, believing that Lithogenes villosus is about intermediate between Astroblepids (which he included as a subfamily within the Loricariinae) and the Neoplecostominae (see below for comments upon Gosline's concept of this latter subfamily). The subfamily Lithogeneinae can only be tentatively accepted. The holotype of L. villosus may be a juvenile; if the species retains a comparatively much reduced scutation when adult, it forms an interesting parallel with the Astroblepidae. Like the members of this family, Lithogenes shows strong adaptation towards living in swift mountain streams.

The relationships of Lithogenes are obsolete. Its reduced number of teeth clearly distinguishes the genus from all other Loricariids. Astroblepidae have several rows of numerous teeth on the premaxillary and dentary (see fig. 1 in chapter VIII, p. 3). Loricariidae usually have the teeth in a single, rarely in an irregular 'double' row.

NEOPLECOSTOMINAE

Neoplecostomus Eigenmann & Eigenmann, 1888

For convenience, the subfamily Neoplecostominae is retained in Regan's original (1904) sense, with only the genus Neoplecostomus included. Neoplecostomus was originally established as a subgenus of Plecostomus (= Hypostomus). It was diagnosed originally in a key to the species of Hypostomus, distinguished from Cochliodon and the nominate subgenus in having 6-8 instead of 5 anal fin rays. Eigenmann & Eigenmann (1890: 395) raised Neoplecostomus to generic rank, stating: "This genus is very closely related to Plecostomus from which it differs in the general form, the number of fin rays, the granulation of the ventral surface and the position of the adipose fin." In their key to the genera (1890: 354) the entry to Neoplecostomus reads: "A. 6; tail comparatively long, terete; adipose fin far removed from the dorsal fin; ventral surface with a median, subcircular patch of granules; (species of small size)." Two species were included: Neoplecostomus granosus and N. microps, the latter is the type-species. Often both have been synonymized. Although Regan studied the syntypes of N. granosus and assigns N. microps to the synonymy, a revision of Neoplecostomus is again necessary. N. granosus was originally described after syntypes from Cayenne and at the same time recorded to occur also in or around Rio de Janeiro; N. microps was also described from the surroundings of Rio de Janeiro "(Rio Parahyba?)" – it seems unlikely that both represent the same species, if indeed it would occur around Rio de Janeiro and in Cayenne; this latter locality needs verification.

Plate II.

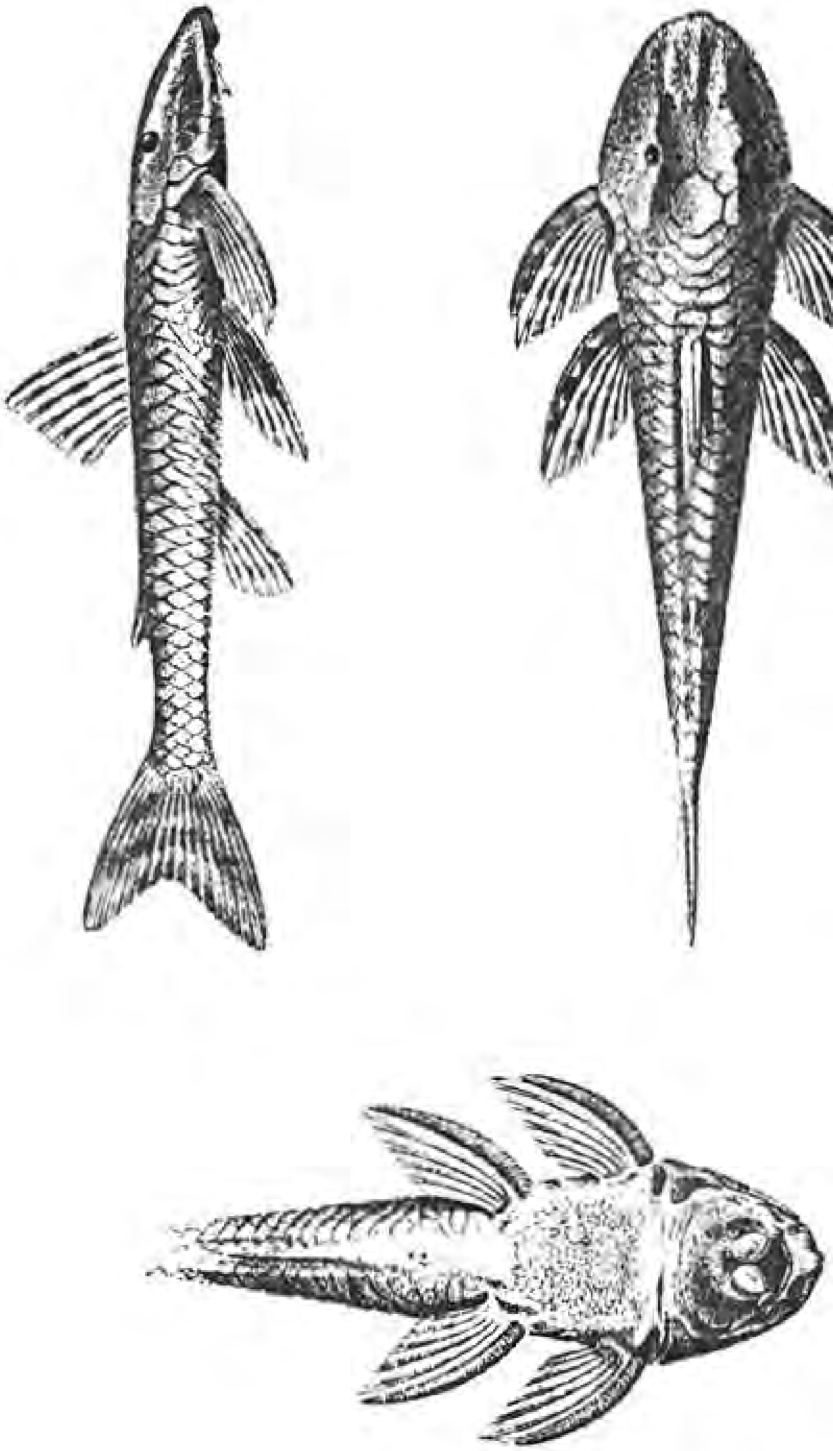


Fig. VI.2. - *Neoplecostomus microps* (Steindachner, 1876), largest syntype (after Steindachner, 1876c, pl. 13).

Neoplecostomus appears to be a well-defined genus. Eigenmann & Eigenmann (1890: 395) recorded 12 teeth on each premaxillary and 16 on each dentary, whereas Gosline (1947: 98) counted 20. Regan (1904: 201, 306) erected the subfamily Neoplecostominae for this single genus, which, "...although it has been referred to *Plecostomus*, proves to be far more allied to *Loricaria* than to that genus. It is also of considerable interest as being the nearest representative among the forms with the body enclosed in bony scutes to the naked Argiinae (= Astroblepidae)." This statement is remarkable, because *Loricaria* (or for that matter, the Loricariinae) is regarded to represent the most specialized of all Loricariidae, whereas Astroblepidae (even if included within the Loricariidae as a subfamily) is not at all closely related to the Loricariinae. At present, a close comparison of *Hypostomus* with *Neoplecostomus* is required to discover the affinities between these two genera as a start – with hesitation I have accepted subfamily rank for *Neoplecostomus*, frankly without being able to support this rank on the basis of the characters said to distinguish it from the other subfamilies. However, Regan was a most competent comparative osteologist and he may rightly have seen distinctions which I fail to see.

Gosline (1947) expanded the limits of the Neoplecostominae greatly, including 12 genera. He stated (1947: 81): "The genera of these two subfamilies (viz., Neoplecostominae and Gosline's Plecostominae – actually consisting of Hypostominae plus Ancistrinae: cf. Boeseman, 1971) practically merge into one another, and the subfamily dividing line might have been made with almost equal justification at at least two other places." and (loc. cit.: 93): "... the Plecostominae is believed to be a more or less direct continuation of the Neoplecostomine stock." Finally, Gosline (1947: 93) remarks: "But for the two subfamilies to be combined because there is no clear separation between them would seem to clarify no concept of Loricariid classification."

Gosline's concept of Neoplecostominae is too vague to work with, and calls for integration within the Hypostominae. Pending further consideration of the relationships of Neoplecostomus, the Neoplecostominae are tentatively reduced to a subfamily with a single genus; the 11 genera ascribed to this subfamily by Gosline are now referred to the Hypostominae.

HYPOSTOMINAE

The Hypostominae includes those genera with inevertible bristle-like odontodes in the interopercular are (genera with evertible bristles all belong to the Ancistrinae), with the pectoral girdle not exposed (Hypoptopomatinae have the lower transverse portion of the pectoral girdle exposed, just like the Acestridiini of the Loricariinae), and with a relatively short, compressed or cylindrical caudal peduncle, not with a single longitudinal dorso- and ventromedian row of flat scutes (as in Loricariinae).

Gosline (1947) reviewed 11 out of the 16 genera which are here assembled in the Hypostominae. These 11 genera were together with Neoplecostomus referred to an expanded subfamily Neoplecostominae. In his key to subfamilies, Gosline (1947: 96) distinguished the Neoplecostominae from a section of his Plecostominae (= Hypostominae) as follows:

> "Anal rays usually I 5 (said to be I 4 in Corymbophanes andersoni, sometimes I 6 in Neoplecostomus); supracleithral (supratemporal) plate bordered posteroventrally at least in part by a naked area or by a few to several small platelets." against "Anal rays I 4; supracleithral plate bordered posteroventrally by the exposed cleithrum; cheeks never with bristles; ..."

Together with Neoplecostomus, Gosline's Neoplecostominae comprised only 27 species. The identity and interrelationships of most of these are still rather obscure and the characters described to distinguish the genera and species as a rule await confirmation. Several genera obviously possess secondary sexual dimorphism – each of the species of such genera thus should preferably be redescribed from good samples including mature females and males.

Rhinelepis Von Spix, 1829

Externally, *Rhinelepis* resembles *Hypostomus* very much. Of the 3 species included, *R. paraguensis* is a species inquirenda, being described originally (poorly, and without illustration) from very small specimens (size as of some Otocinclini).

Rhinelepis aspera (from the Rio São Francisco; the unique holotype is lost and should be replaced by a neotype) and *R. strigosa* (from the Rio Paraná and other rivers in Corrientes) at least seem to be closely related to each other (occassionally they have been synonymized). Adipose fin absent (an adipose fin is present, with few exceptions, in *Hypostomus*). A group of small granular plates behind the lower half of the temporal plate and the upper part of the clavicle, and the anal fin with 5 instead of 4 rays distinguish *Rhinelepis* and some other genera from *Hypostomus*. *Rhinelepis* includes large species, up to 335 mm in total length. Secondary sexual dimorphism unknown, but very probably present (see next genus).

Pseudorinelepis Bleeker, 1862

It is uncertain whether this genus (known better as its synonym, *Canthopomus* Eigenmann, 1910) is distinct from *Rhinelepis* (cf. Boeseman, 1971: 18). Three species have been described from the middle and upper Amazon; they possess bristle-like odontodes along the cheek and reach about the same size as species of *Rhinelepis*.

Plate III.

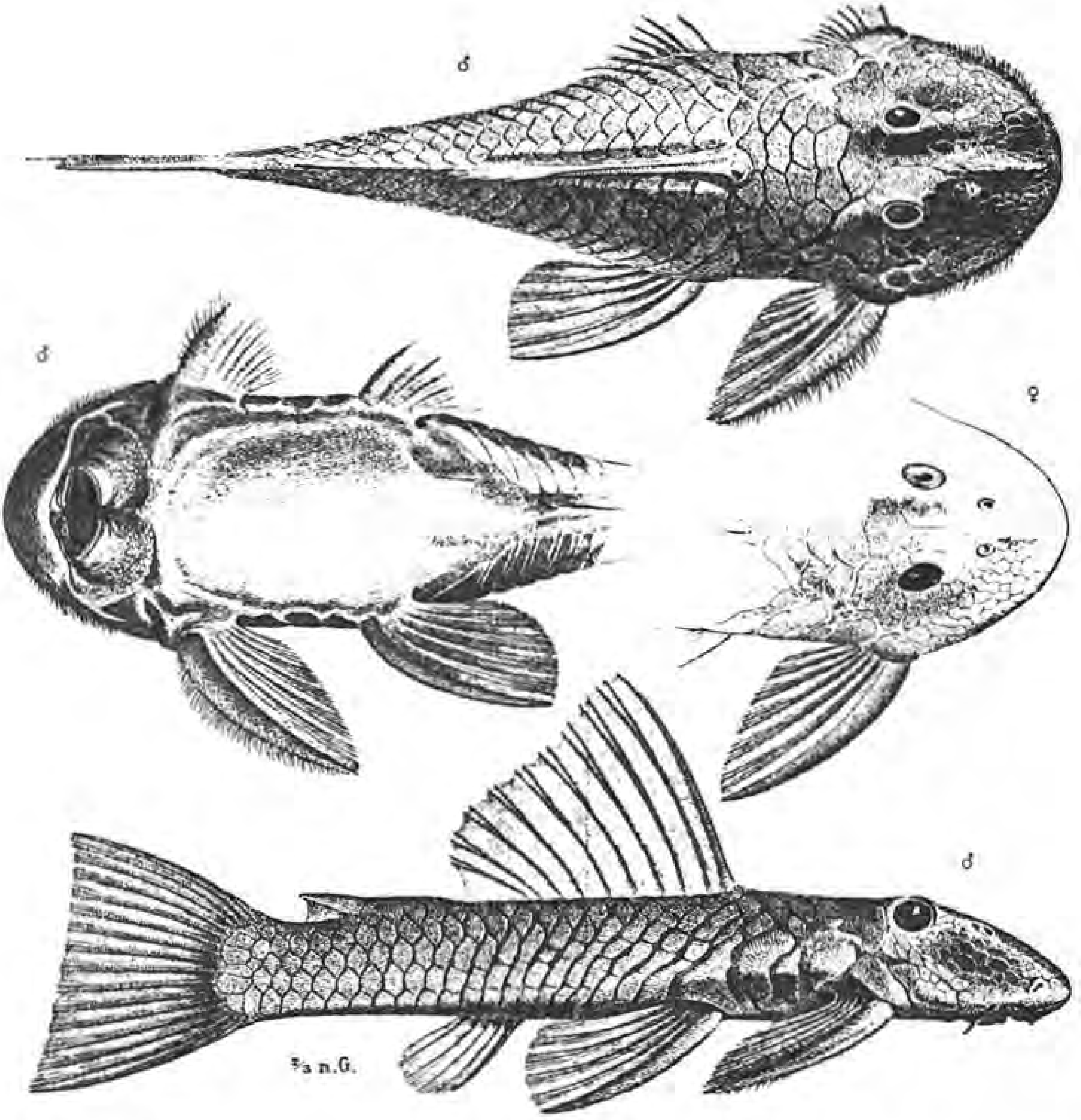


Fig. VI,3. - *Delturus angulicauda* (Steindachner, 1876), syntypes (after Steindachner, 1876c, pl. 12 figs. 1-2).

Plate IV.

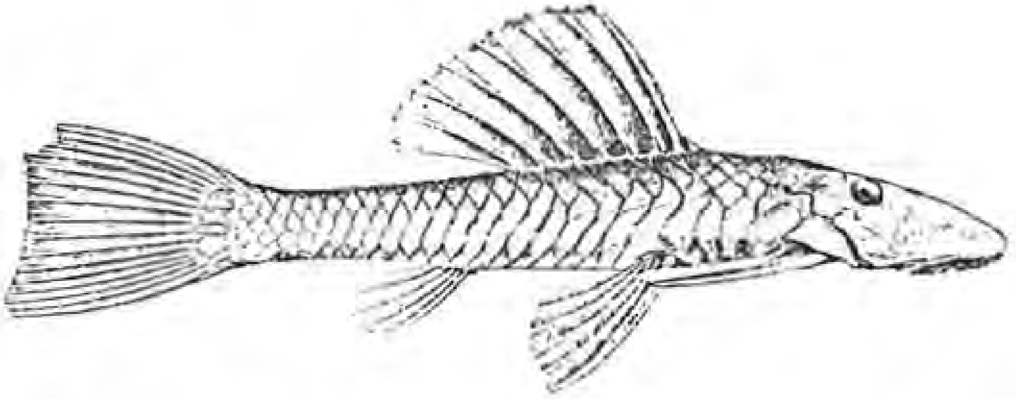


Fig. VI,4. - Pogonopomoides parahybae (Steindachner, 1877), syntype? (after Steindachner, 1877, pl. 2).

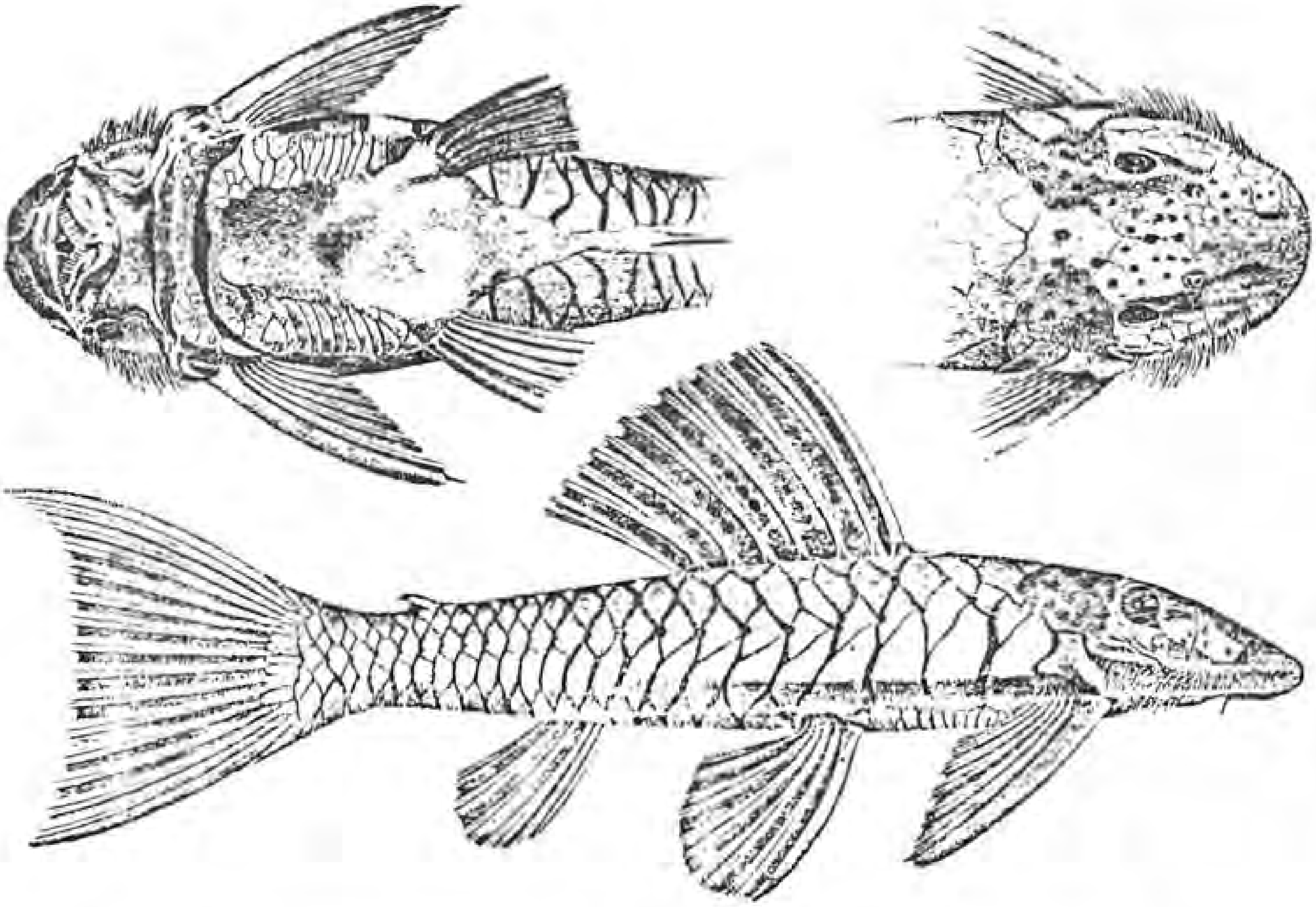


Fig. VI,5. - Pogonopoma wertheimeri (Steindachner, 1867), holotype (after Steindachner, 1867, pl. 1).

Delturus Eigenmann & Eigenmann, 1889

Delturus seems easily identifiable by its relatively high number of dorsal fin rays, 9 to 10. Eigenmann & Eigenmann (1890: 437) noted that *Delturus*: "...is most closely allied to *Hemipsilichthys*...", "The tail is flat below, trenchant above; a cross-section being Δ-shaped. The sides of the head with short fine bristles which do not encroach on the preopercle." Three species, up to 280 mm.

Pogonopoma Regan, 1904

Pogonopoma was originally erected as a subgenus of *Plecostomus*, with 3 species included: *Plecostomus wertheimeri*, *Pl. pellegrini*, and *Pl. genibarbis*. Eigenmann (1910: 404 & 407) designated *wertheimeri* as the type-species of *Pogonopoma*, referring *pellegrini* and *genibarbis* to his new genus *Canthopomus* (type-species, *C. genibarbis*, already the type-species of *Pseudorinelepis*).

Pogonopoma wertheimeri is the single species that so far remained in this genus (raised to generic rank by Eigenmann, 1910). It is still known only from the holotype, described and illustrated by Steindachner in 1867. Like *Pseudorinelepis*, *Pogonopoma* has bristle-like odontodes along the sides of the head. *Pogonopoma* has an adipose fin, which is absent in *Rhinelepis* and *Pseudorinelepis*.

Pseudancistrus Bleeker, 1862

Several species with long, evertible odontodes in the interopercular area have in the past been incorrectly referred to *Pseudancistrus*; these species actually are members of the subfamily Ancistrinae (e.g., *Lasiancistrus*). However, true *Pseudancistrus* species superficially very much resemble the representatives of *Lasiancistrus*. Except for *Pseudancistrus luderwaldti* (a species inquirenda, described from a small holotype from Hansa, S.E. Brazil and still the only known specimen), *Pseudancistrus* is confined to the Guiana plateau.

The absence of evertible odontodes, their relatively de-

Plate V.

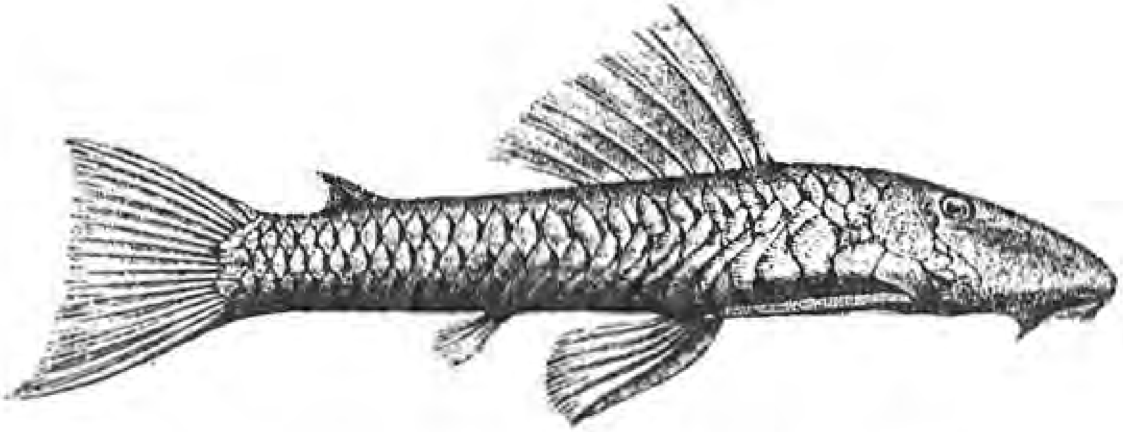


Fig. VI,6. - Pseudancistrus guentheri (Regan, 1904), holotype (after Regan, 1904, pl. 12 fig. 3).

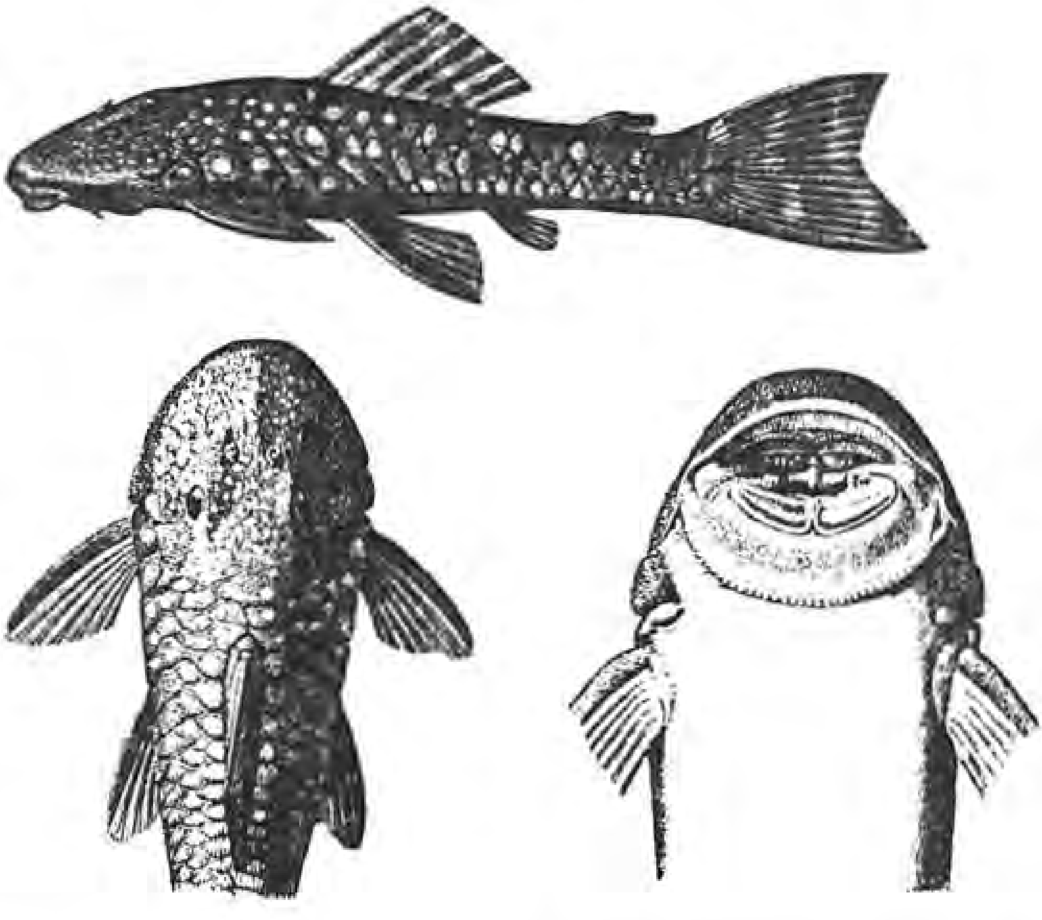


Fig. VI,7. - Pseudancistrus coquenani (Steindachner, 1915), syntype (after Steindachner, 1915c, pl. 11 figs. 3-5).

pressed and broad head and body, and the numerous conspicuous odontodes along the margin of the head in both sexes (although much longer in some males) easily distinguish Pseudancistrus from other Loricariids.

Hemipsilichthys Eigenmann & Eigenmann, 1889

Hemipsilichthys is the substitute name for Lütken's (1874b) Xenomystus, a preoccupied generic name. Hemipsilichthys gobio is the type-species, based upon the unique holotype, a male without locality information. Nielsen (1974: 52) listed the holotype as originating from Northern South America with a question mark, but this is not in agreement with the S.E. Brazilian localities from which specimens were subsequently identified as H. gobio. Hemipsilichthys gobio was described originally in Danish, diagnosed in Latin and accurately illustrated. The body scutes are peculiar, appearing as series of isolated from one another (each being surrounded by a narrow naked margin), rugose platelets, the keeled azygous scutes in front of the adipose spine, the short and thick pectoral fin spine and the swollen, partly naked cheeks irregularly bearing elongate and comparatively thick odontodes. Five species were discovered in addition to H. gobio; one (H. cerosus) without locality data, H. cameroni, H. garbei, and H. steindachneri from S.E. Brazil. H. regani was described originally from the Rio Curi Curiay (= Rio Curicuriari), a tributary of the Amazonian Rio Negro. Giltay (1936), the author of H. regani, also identified H. cameroni from the Rio Jahu (= Rio Jaú), likewise a tributary of the Rio Negro. These Amazonian records of Hemipsilichthys, as already suggested by Gosline (1947), require confirmation.

Pareiorhaphis A. de Miranda Ribeiro, 1918

Pareiorhaphis was originally established for 3 species which were previously considered as representatives of Hemipsilichthys: calmoni (an invalid substitute name for H. cameroni),

Plate VI.

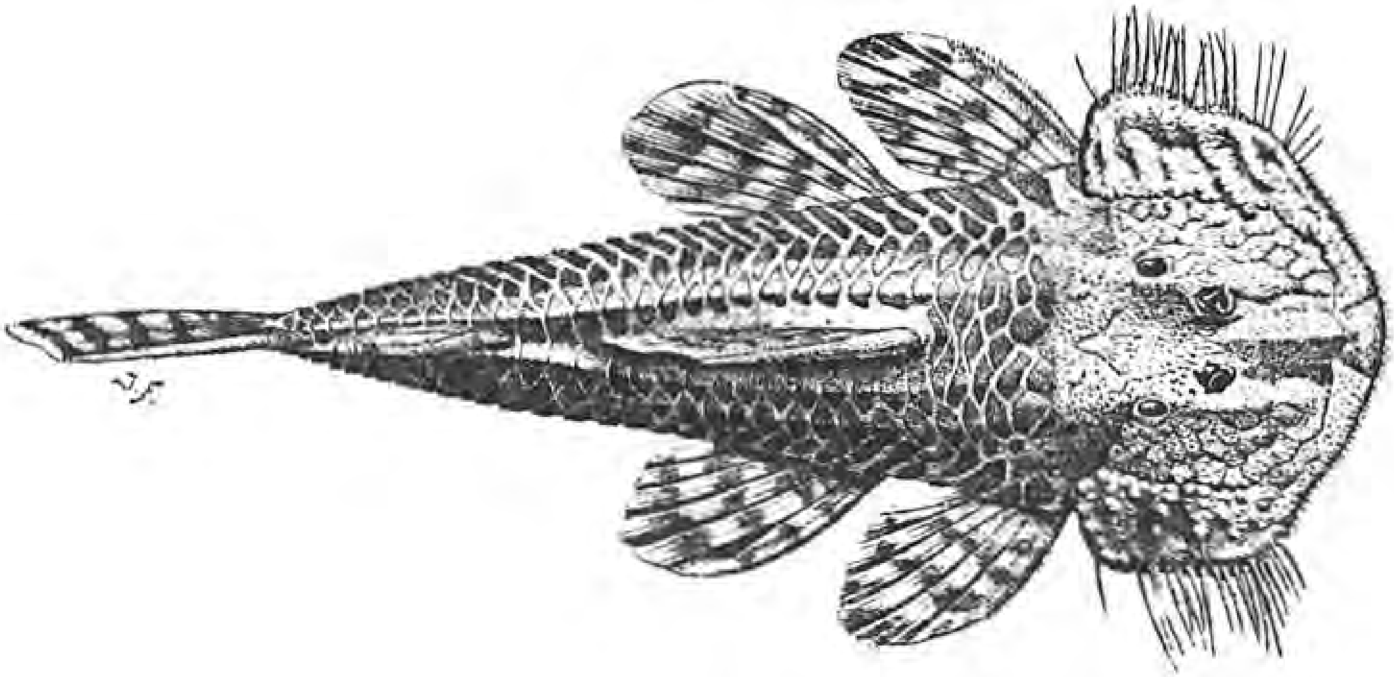


Fig. VI,8. - Hemipsilichthys steindachneri A. de Miranda Ribeiro, 1918, syntype (after Steindachner, 1911a, fig. on : 431).

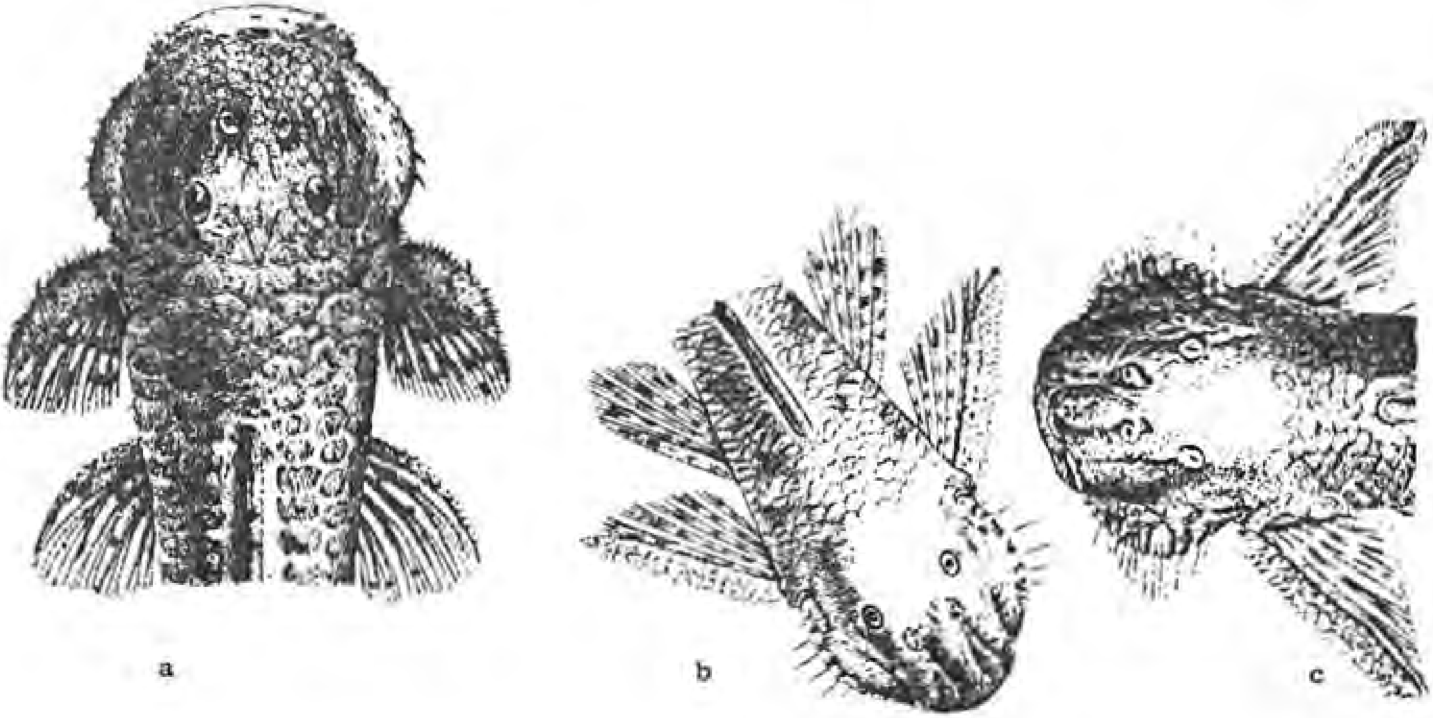


Fig. VI,9. - (a) Hemipsilichthys gobio (Lütken, 1874), holotype (after Lütken, 1874b, pl. 4 fig. 2), (b) Hemipsilichthys cameroni (Steindachner, 1907), young male, syntype, (c) H. cameroni, adult male, syntype (both after Steindachner, 1907a, pl. 1 fig. 1b, pl. 2 fig. 1a, respectively).

steindachneri, and *duseni*. The latter was designated as the type-species of *Pareiorhaphis* by Gosline (1947: 102), who re-assigned *cameroni* and *steindachneri* to *Hemipsilichthys*. *Pareiorhaphis duseni* was based originally upon 3 syntypes. Gosline (1947: 102-104) selected the lectotype and described the 2 paralectotypes as a new species, *P. alipionis*. This is all material known so far of *Pareiorhaphis*, 3 specimens, 71-80 mm standard length. The genus is said to be distinguished from *Hemipsilichthys* by the presence of scattered, embedded platelets on the abdomen and by having minute bristles on the cheek. The known species originate from the States of Paranã and São Paulo, Brazil.

Kronichthys A. de Miranda Ribeiro, 1908

This genus was erected for a single species, *Kronichthys subteres*, subsequently identified with *Plecostomus heylandi* by most authors. The respective type-material still should be compared directly before these nominal species are solidly synonymized, and provisionally I consider *subteres* as distinct from *heylandi*. Both are known from localities in the States of São Paulo and Rio de Janeiro (Gosline, 1947: 106). According to Gosline (1947: 98, key), *Kronichthys* differs from *Hemipsilichthys*, *Pareiorhaphis*, and *Pareiorhina* in having a distinctly shorter and narrower head. Regan's (1904: 221) description of *Hemipsilichthys gobio* is, apart from data stated in the original description of that species, based on the holotype of *Kronichthys heylandi*, which Regan had at hand.

Corymbophanes Eigenmann, 1909

In the key of Gosline (1947: 98), *Corymbophanes* is indicated to share the characters of *Delturus* except for the possession of 7 branched dorsal fin rays – the usual number for most Hypostomines – rather than 9 to 10 dorsal fin rays as in *Delturus*. The type-species of *Corymbophanes*, *C. andersoni*, is known only from the holotype, collected in the upper Potaro River in Guiana. *Corymbophanes bahianus* is a second species, based on 3 specimens from Ilhéus, State of Bahia. '*Corymbophanes*' *venezuelae* was recently (Isbrücker, 1980: 65) assigned to *Chaetostoma*, a genus of Ancistrinae, rather than the Hypostominae to which *Corymbophanes* belongs.

Upsilodus A. de Miranda Ribeiro, 1924

Only 2 specimens of *Upsilodus*, both *U. victori*, are known, both originating from the watershed of Rio Paraíba do Sul, maximum total length 130 mm. Gosline (1947: 98) characterized *Upsilodus* as follows: "Each tooth with two, approximately equal lobes; lateral scutes failing to meet anywhere along the middorsal line between the dorsal and the adipose, leaving a naked middorsal band nearly equal in width to an eye diameter."

Pareiorhina Gosline, 1947

Pareiorhina is a genus with a single species, *P. rudolphi*. The specific name is a substitute name for Von Ihering's (non Steindachner's) *Plecostomus microps*. It is known from the holotype from São Paulo and from 4 additional specimens from the untraceable locality Itatiaya, Mont Serrat, none of the specimens exceeding 66 mm (in total length?). According to Gosline (1947), *Pareiorhina* is closely related to *Pareiorhaphis*, from which it differs in the lack of an adipose fin, the lateral scutes meeting along the middorsal line instead of being separated by a narrow naked band, a flatter head and body, and a more elongate caudal peduncle.

Pogonopomoides Gosline, 1947

Pogonopomoides contains a single species, *P. parahybae*. Gosline (1947: 81 & 109) had 2 specimens, 355 and 340 mm in total length, the latter recorded from the Rio Paraíba do Sul. Gosline (1947: 109) stated that there seem to be 4 characters separating *Pogonopoma* from *Pogonopomoides* (1 species in each genus): a small adipose fin and cheek bristles are present in Pogonopoma, absent in Pogonopomoides; about 22 lateral body scutes in Pogonopoma and 26 in Pogonopomoides; supracleithral plate bordered posteroventrally by 4 small platelets and partly by the 1st lateral scute in Pogonopoma, by numerous platelets and not in contact with the 1st lateral scute in Pogonopomoides. In Pogonopomoides the posterior section of the air bladder is well-developed. The intestine has over 30 coils. The condition of the air bladder and intestine of Pogonopoma (and many other Loricariid genera) is not known.

Isorineloricaria Isbrücker, 1980

Isorineloricaria can be distinguished from Hypostomus (and from the other genera of Hypostominae) at once by its exceptionally elongate and slender body and caudal peduncle, and by its very spiny scutes. Contrary to Hypostomus, it shows very conspicuous secondary sexual dimorphism. This is not a condition indicating specialization in Loricariidae: putative primitive species usually show excessive growth of odontodes in mature males whereas such growth does not occur in many advanced species. Isorineloricaria males have enlarged odontodes along the margin of the head and on the body scutes, and especially on the pectoral fin spine and rays (cf. Eigenmann, 1922, pl. 34 figs. 1-2).

Awaiting a direct comparison of the respective type-material of I. spinosissima and I. festae, I treat them provisionally as distinct species, although Eigenmann (1922: 68-69) perhaps rightly has synonymized the two nominal species on the basis of numerous specimens, ranging in size from 45 to 565 mm. He concluded that I. spinosissima (including 'I. festae') undergoes marked change with growth.

Isorineloricaria only occurs along the western slope of southern Ecuador (cf. Chapter IX, fig. 4). It possesses more numerous lateral body scutes than Hypostomus species (there are 116 described Hypostomus species). The body shape and especially the pattern of odontode development is

Plate VII.

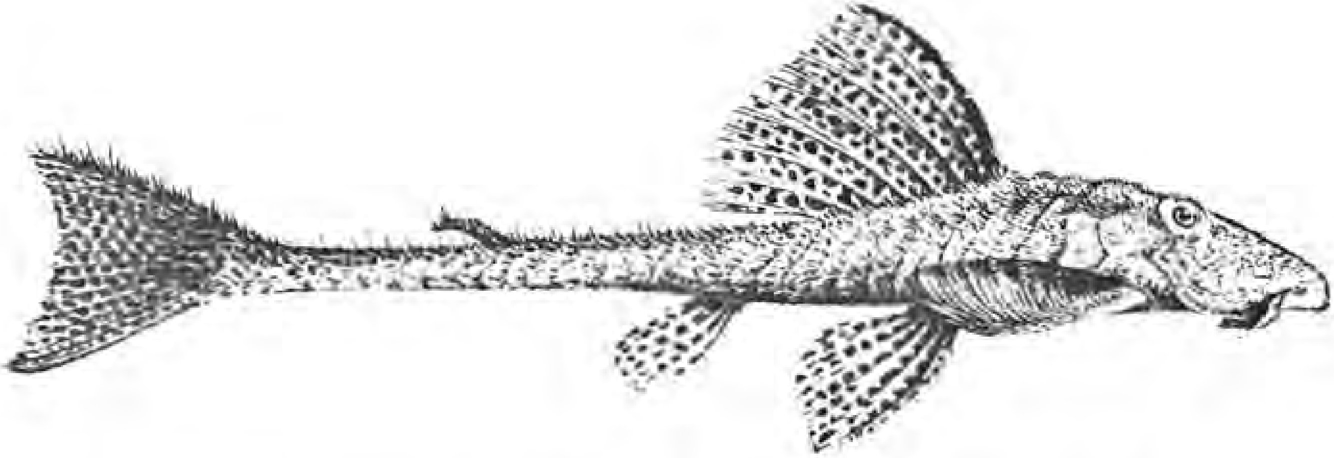


Fig. VI,10. - Isorineloricaria festae (Boulenger, 1898), syntype (after Regan, 1904, pl. 9 fig. 1).

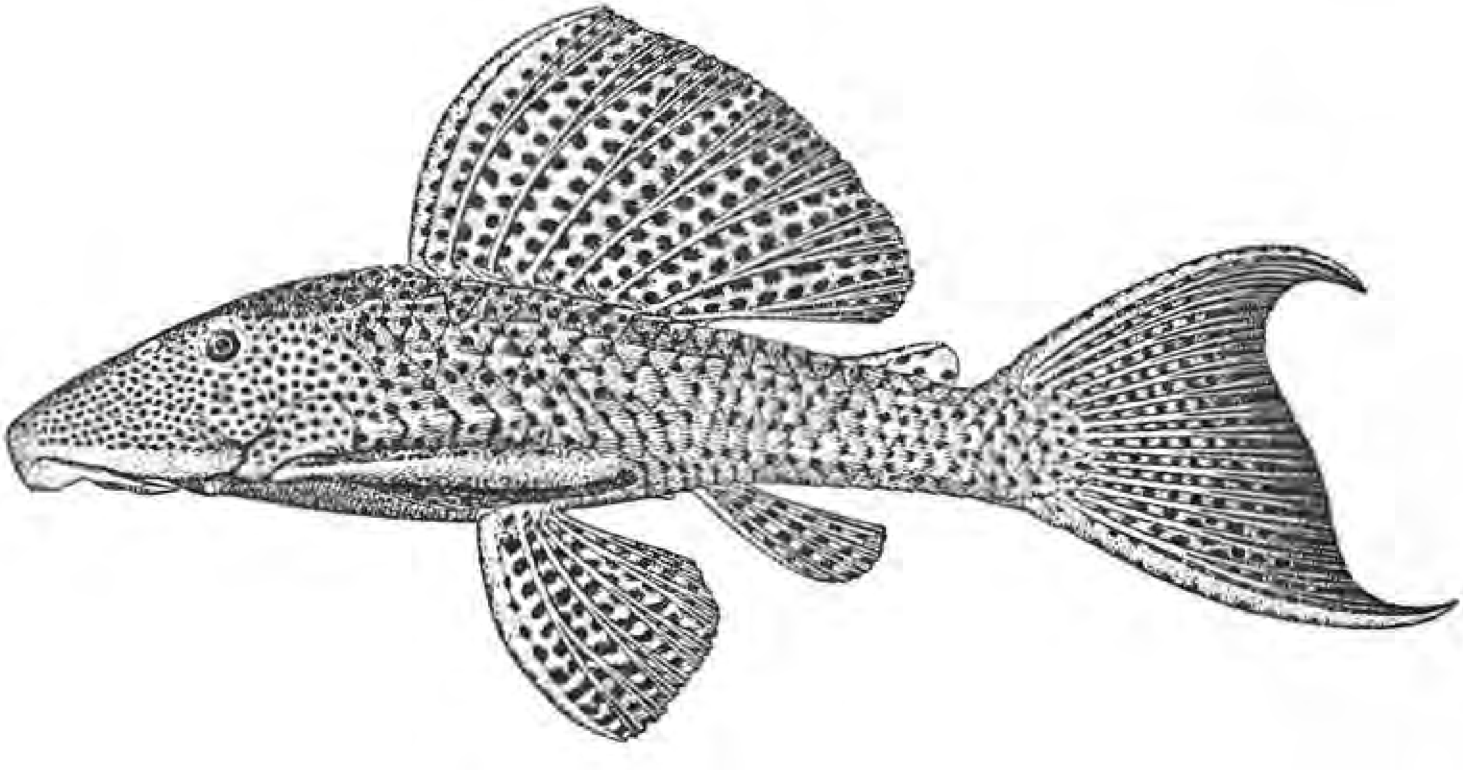


Fig. VI,11. - Hypostomus pusarum (Starks, 1913), holotype (after Starks, 1913, pl. 6).

quite reminiscent of that found in S.E. Brazilian species of Rineloricaria (e.g., R. latirostris, R. jaraguensis). Although a study on the relationships remains to be done, the characters of Isorineloricaria suggest that it is more primitive than Hypostomus on the one hand, but not at all closely related to the other allegedly more primitive genera (viz., Rhinelepis through Pogonopomoides) of the subfamily Hypostominae on the other hand. Because of its restricted occurrence, west of the Andes, together with the absence of fairly closely related forms elsewhere, Isorineloricaria may prove to be a relict.

Hypostomus La Cepède, 1803

The genus Hypostomus occurs almost everywhere in tropical and south temperate South America; unlike other Loricariidae, it even extents to southern Central America. Not less than 116 species were described and are retained in Hypostomus, several others have been referred to other genera. Unfortunately, only a – too – small number of Hypostomus species is known from a sufficiently large number of specimens and at the moment, delimitation and distinction of most species is hardly possible. However, lots of preserved Hypostomus samples are available in collections, awaiting identification until (partial) revision has been carried out. Gosline (1947) published "Preliminary material for a revision of the Southeastern Brazilian species of Plecostomus" (a well-known synonym of Hypostomus), and gave a key to some 25 species, all from a relatively small area outside the main Amazon basin. Quite a few of the species treated by Gosline are indefinitely identified, and Gosline (1947: 111, footnote) sighed: "The taxonomist trying to identify a specimen of Plecostomus will probably feel disgruntled to find himself presented with a problem rather than a name."

Boeseman (1968 & 1969) examined rich material of Hypostomus collected in some Surinam river systems. From the also relatively small area covered, 17 distinct species (and subspecies) were found. Boeseman (1968) also finally settled the problems of defining the type-species of Hypostomus, H. plecostomus (he designated the neotype), and redefined also the second described, still included species, H. watwata, for which also a neotype had to be designated.

The difficulties concerning recognition of Hypostomus forms at specific and lower level seem endless. At generic level, Hypostomus is easily recognizable: body stout, oblong or somewhat elongate; adipose fin almost always present; no marked development of odontode growth in the mature males (except perhaps on the pectoral fin spine in some species); abdomen usually covered with minute, granular platelets; numerous slender and usually bifid teeth; 7 branched dorsal fin rays.

Cochliodon Heckel, 1854

As far as known, Cochliodon differs from Hypostomus only in its peculiar dentition. The teeth are few in number (less than 20, much more than 20 in Hypostomus), short and stout, spoon-shaped, simple or with a small lobe on the outer edge of the base of each tooth. Schultz (1944a: 311) has found such a small lobe only on specimens up to 60 mm in standard length, disappearing with age, "...and the tooth wears down until it becomes cup-shaped." Six species have been described.

Pterygoplichthys Gill, 1858

Pterygoplichthys is also very close to Hypostomus, and has a similar dentition. It is distinguished from Hypostomus apparently solely by its higher number of branched dorsal fin rays, 10 to 13 in Pterygoplichthys against 7 in Hypostomus. Some of the species of Pterygoplichthys are more colourful than the average Hypostomus (although of both genera species are known which resemble each other very much in colour pattern), and several Pterygoplichthys species have a peculiar median, conspicuously elevated ridge (stronger than in most Hypostomus species) on the supraoccipital. Other Pterygoplichthys species look quite similar to 'typical' Hypostomus species: "Hypostomus sp. indet." illustrated in Isbrücker (1979b: 120, fig. 24, aquarium specimen) has 11 branched dorsal fin rays (which I overlooked), and thus is a Pterygoplichthys.

Of the 20 species I listed as valid, several have in the past been referred to the junior synonymy of various others. The perhaps exagerrated enumeration may very well demonstrate the need of revising Pterygoplichthys – a rule rather than an exception in Loricariidae.

ANCISTRINAE

All members of the Ancistrinae share the possession of a tuft of evertible interopercular odontodes. In rest, this tuft is (usually completely) withdrawn in some sort of groove posterior to its base. However, sometimes the length of the odontodes exceeds that of the groove. The odontodes in this area are usually elongate, very thin and look like fragile, glass needles. Sometimes (e.g., in Ancistrus) the odontodes are much thicker and shorter, their tips pointing outward, resembling the odontodes present on the pectoral fin spine of some Hypostominae and Loricariinae. During various activities of the fish, the tuft everts, forming a tough, brush-like organ which is used in defence and offence (protection of a territory); very likely, it also plays a rôle as a contact organ during courtship.

Numerous species are known to have these evertible interopercular odontodes, which should not be confused with the enlarged odontodes in the same area of some Hypostominae, as in the latter subfamily they are inevertible. The structure underlying the tuft, allowing the evertibility, although not being extremely complicated, has not probably evolved more than once: I believe that all Ancistrinae therefore are descendants from a shared ancestor. Various

Plate VIII.

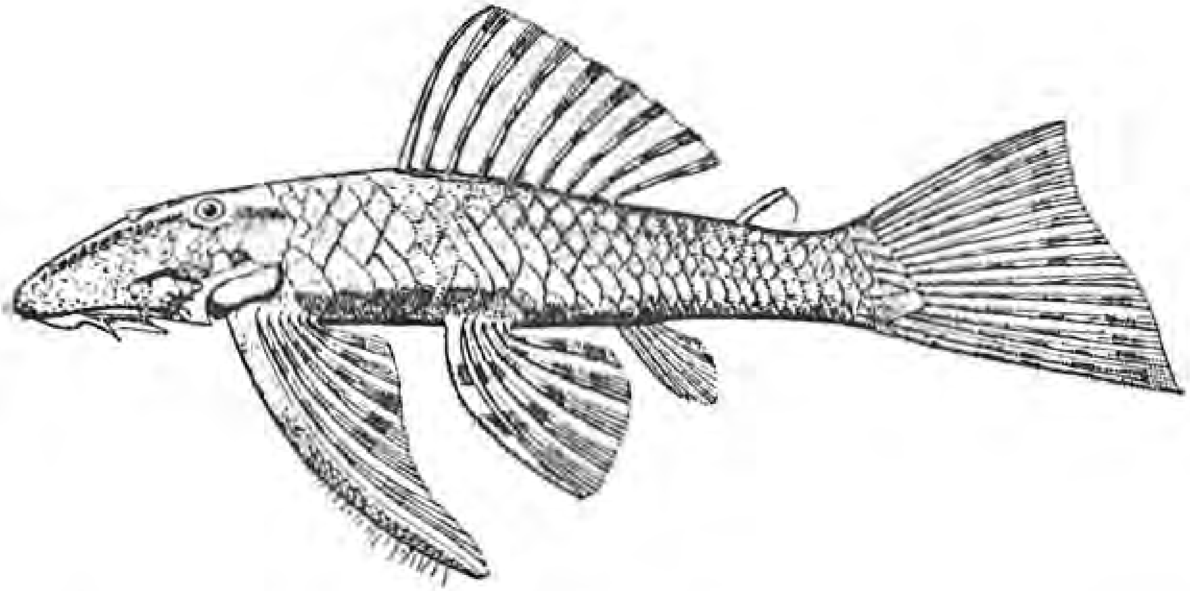


Fig. VI,12. - Lasiancistrus carnegiei (Eigenmann, 1916), holotype (after Eigenmann, 1922, pl. 10 fig. 3).

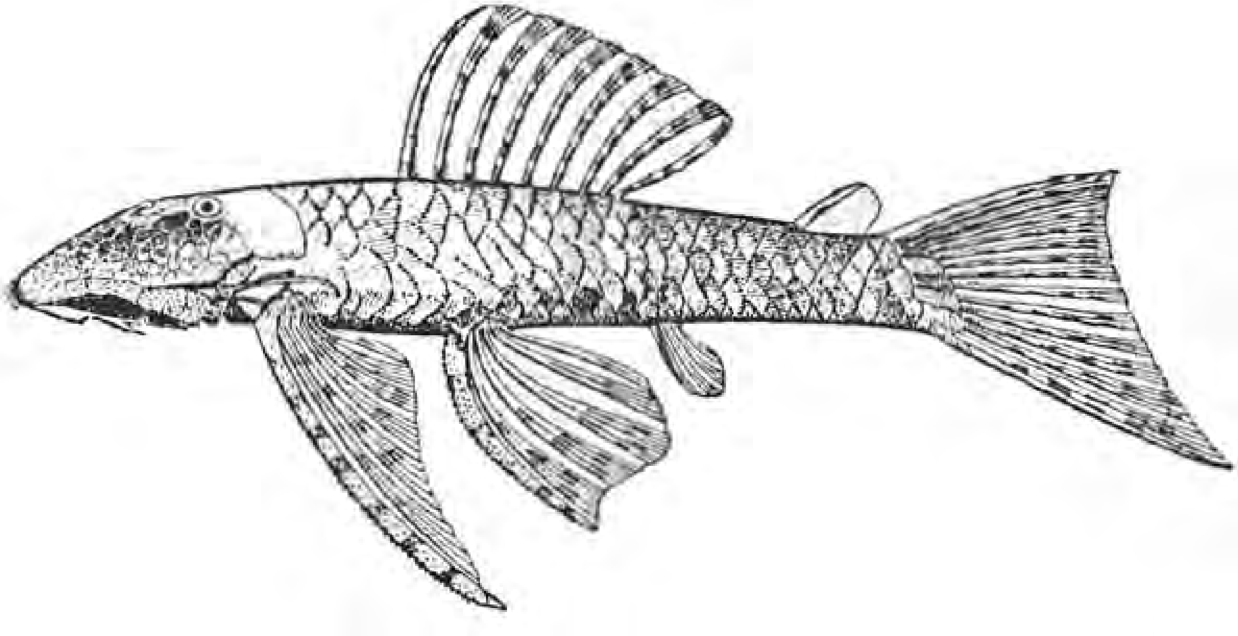


Fig. VI,13. - Dolichancistrus pediculatus (Eigenmann, 1917), holotype (after Eigenmann, 1922, pl. 10 fig. 4).

peculiar specializations have developed within the Ancistrinae. The most generalized forms are the various species of *Lasiancistrus*. The overall similarity of this genus with *Pseudancistrus* (Hypostominae; externally they virtually differ only in the presence against absence of evertible interopercular odontodes) indeed may indicate that both are rather closely related to each other, and placing them in different subfamilies might not sufficiently indicate their true affinities. However, the large number of species (178, in 18 genera) possessing the evertible interopercular odontodes, the peculiar function(s) of these odontodes, and the great diversity in the various lineages within the group has induced me to follow Boeseman (1971) to accept the Ancistrinae as a subfamily, rather than as a tribe of the Hypostominae.

ANCISTRINI

The great majority of Ancistrinae belong to the nominal tribe. They lack the extremely enlarged temporal plate (which distinguishes the Acanthicini) and have no fused premaxillae (like in the Pseudacanthicini).

Lasiancistrus Regan, 1904

Lasiancistrus has almost the same external appearance as *Pseudancistrus*, including the presence in both sexes of short, bristly odontodes along the margin of the head anterior to the opercular area, including the margin of the snout. Both *Pseudancistrus* and *Lasiancistrus* comprise species which reach a moderately large size and have a fairly depressed head and body.

In *Lasiancistrus* the interopercular tuft of evertible odontodes is well-developed. The posterior odontodes are gradually somewhat longer than the anterior ones; when everted, their tips reach about the same distance off the side of the head. Several species, up to about 200 mm.

Plate IX.

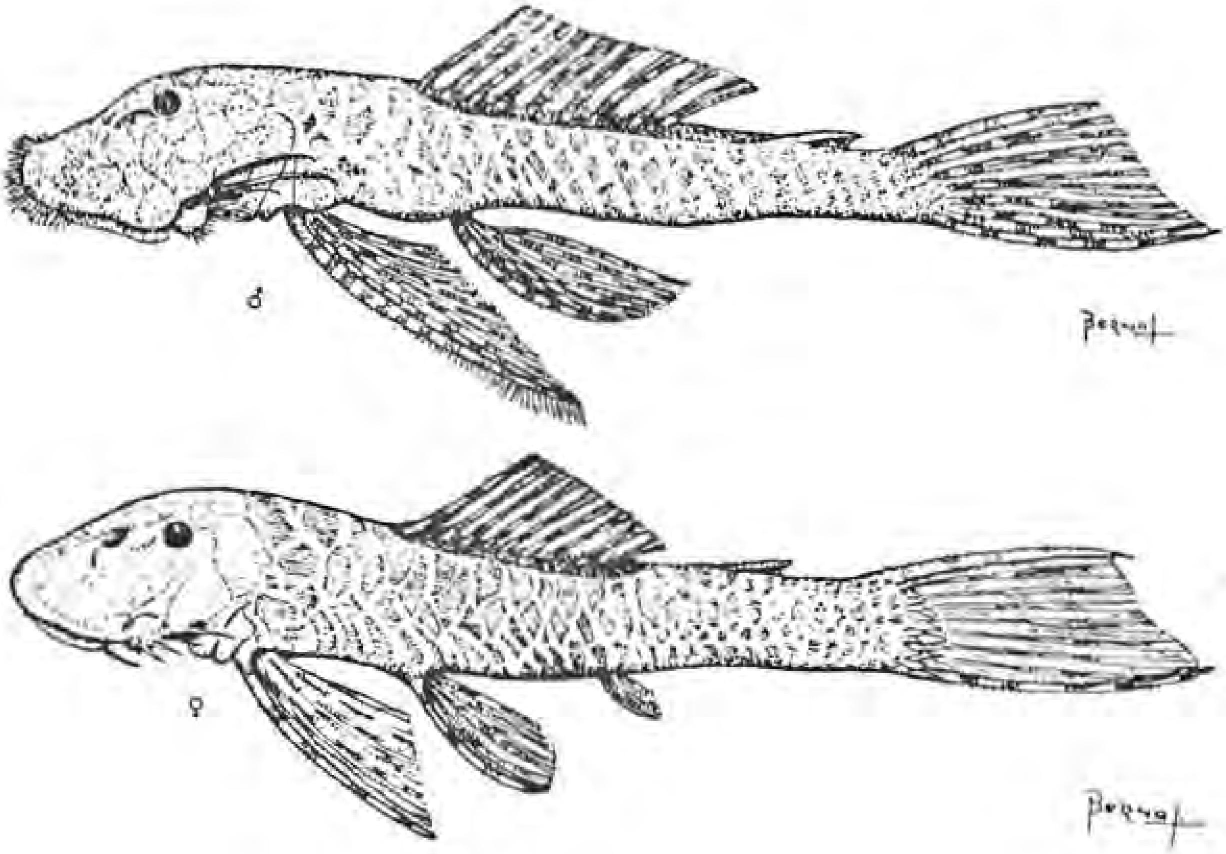


Fig. VI,14. - Dolichancistrus atratoensis (Dahl, 1960), allotype -male- and holotype -female- respectively (after Dahl, 1960: 456-457).

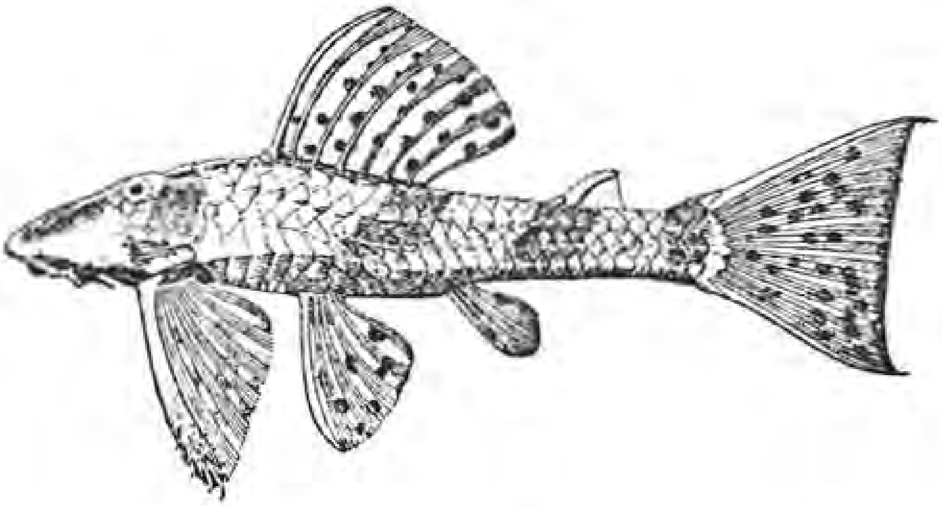


Fig. VI,15. - Hemiancistrus landoni Eigenmann, 1916, holotype (after Eigenmann, 1922, pl. 10 fig. 2).

Dolichancistrus Isbrücker, 1980

Dolichancistrus seems closely related to *Lasiancistrus*, from which it differs by the extreme length of the posterior evertible interopercular odontodes, and in the small adult size. Three species, up to 120 mm (in total length?).

Cordylancistrus Isbrücker, 1980

The single species of this genus, *Cordylancistrus torbesensis*, was originally described (and is still known only) from 175 specimens, up to 64.6 mm in standard length, including mature males and females. They were all collected from swiftly running water among boulders, rubble and coarse gravel (Schultz, 1944a: 296). The greatly depressed and very wide head remind of the head of a *Chaetostoma*; however, the short, elongate odontodes on the head which completely cover the snout (as described by Schultz, 1944a: 298) indicate that *Cordylancistrus* may actually be closely related to *Lasiancistrus*. In fact, Schultz - like several previous authors - confused *Lasiancistrus* with *Pseudancistrus*, to which latter genus *C. torbesensis* was originally asigned.

Hemiancistrus Bleeker, 1862

In general body shape, *Hemiancistrus* is reminiscent of *Hypostomus*. It has 7 to 8 branched dorsal fin rays, a broad, rounded snout, strongly carinate body scutes, about 30 evertible interopercular odontodes, strongly developed odontodes on the pectoral fin spine of large specimens, and the ventral side of the head and abdomen covered with minute granular scutelets, the extent of which increases with age. The largest specimen on record is *H. maracaiboensis*, 285 mm in standard length.

Most of the 14 species I enumerated (1980: 49-51) are placed in *Hemiancistrus* on the basis of literature data only, and at this time I am unable to distinguish the genus *Peckoltia* (see below) more clearly from *Hemiancistrus*. When

Plate X.

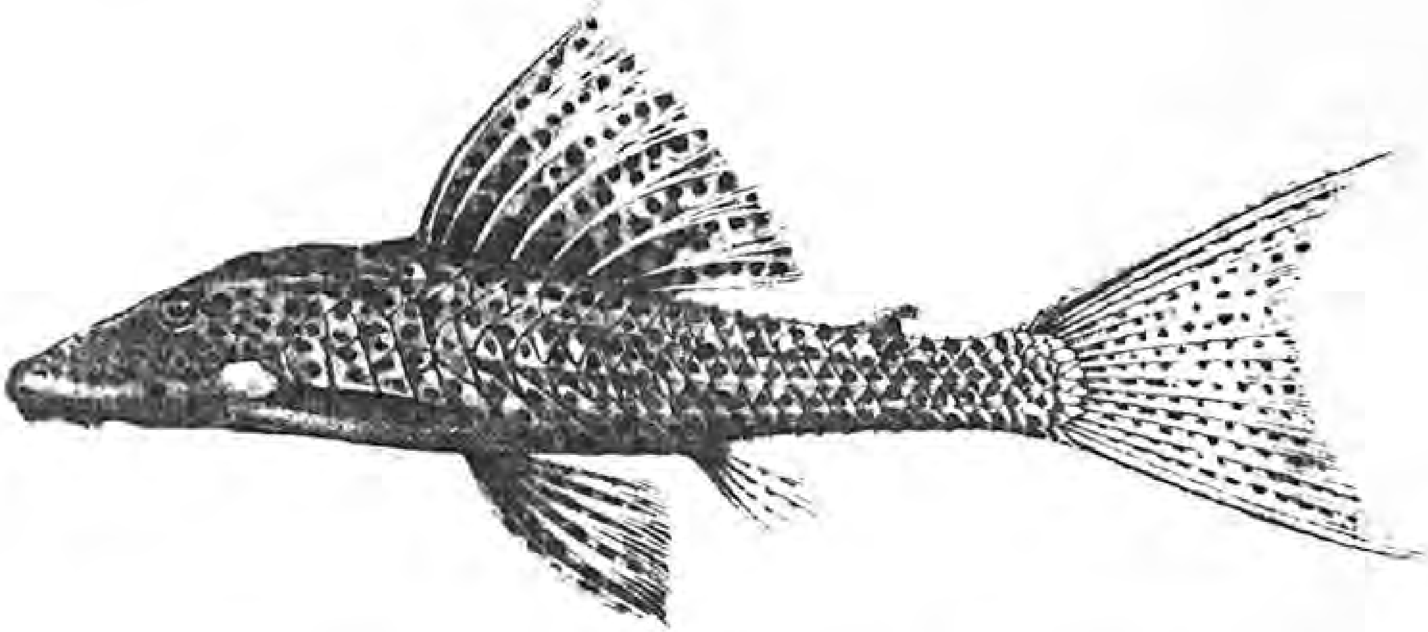


Fig. VI,16. - Hemiancistrus annectens (Regan, 1904), syntype (after Regan, 1904, pl. 11 fig. 2).

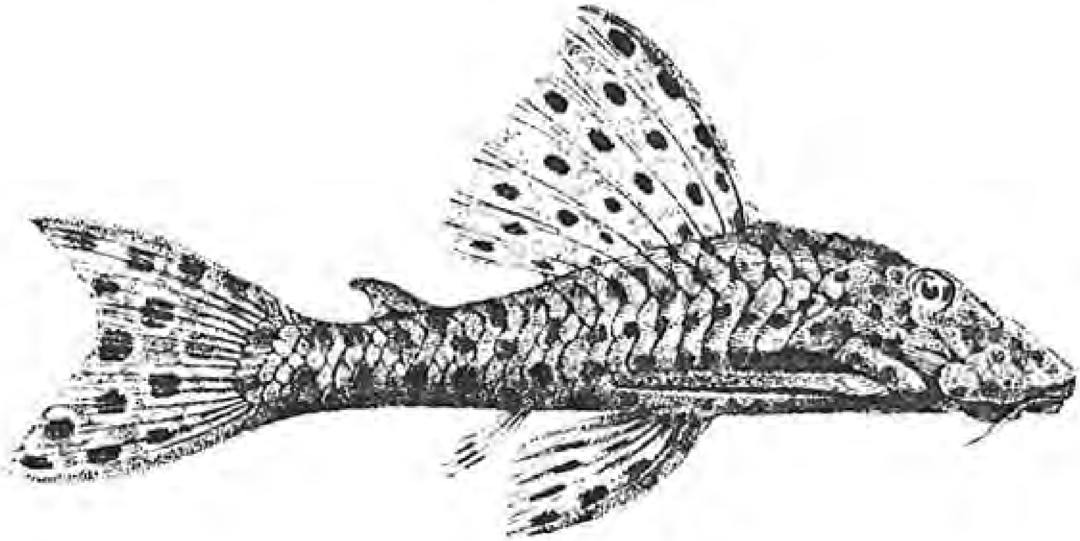


Fig. VI,17. - Peckoltia oligospila (Günther, 1864), holotype (after Regan, 1904, pl. 12 fig. 1).

a revision is being undertaken, the representatives of both Peckoltia and Hemiancistrus would profitably be considered together at one time.

Megalancistrus Isbrücker, 1980

Megalancistrus is a Hemiancistrus but for the number of branched dorsal fin rays: 10 in Megalancistrus against 7 to 8 in Hemiancistrus. In addition, the 3 nominal species of Megalancistrus are unusually large for members of Ancistrinae: one specimen is known to have reached a total length of 530 mm.

Peckoltia A. de Miranda Ribeiro, 1912

Peckoltia (19 species) is very similar to Hemiancistrus in body and head shape, but appears to differ in the more rugose posterior lateral body scutes, apparently much smaller adult size (if the recorded sizes are indicative for real maximum size is, however, doubtful); Peckoltia species usually have a characteristic colour pattern (e.g., broad dark and light stripes).

Monistiancistrus Fowler, 1940

The single holotype of M. carachama is the only known specimen of this genus. Fowler (1940a: 236) stated, after the description of Monistiancistrus: "Differs from Ancistrus Kner, 1854 chiefly in the absence of the adipose fin. The reduced dentation and unequal jaws are more as in Panaque Eigenmann & Eigenmann, 1890, in which the adipose fin is also constantly present." Monistiancistrus is perhaps incorrectly placed in the Ancistrinae: Fowler did not even mention (evertible?) odontodes in the interopercular area. If absent, M. carachama should be referred to the Hypostominae; in fact, from the description and illustrations it appears to be not very distinct from Hypostomus. At any rate, it has little in common with true Ancistrus and Panaque.

Plate XI.

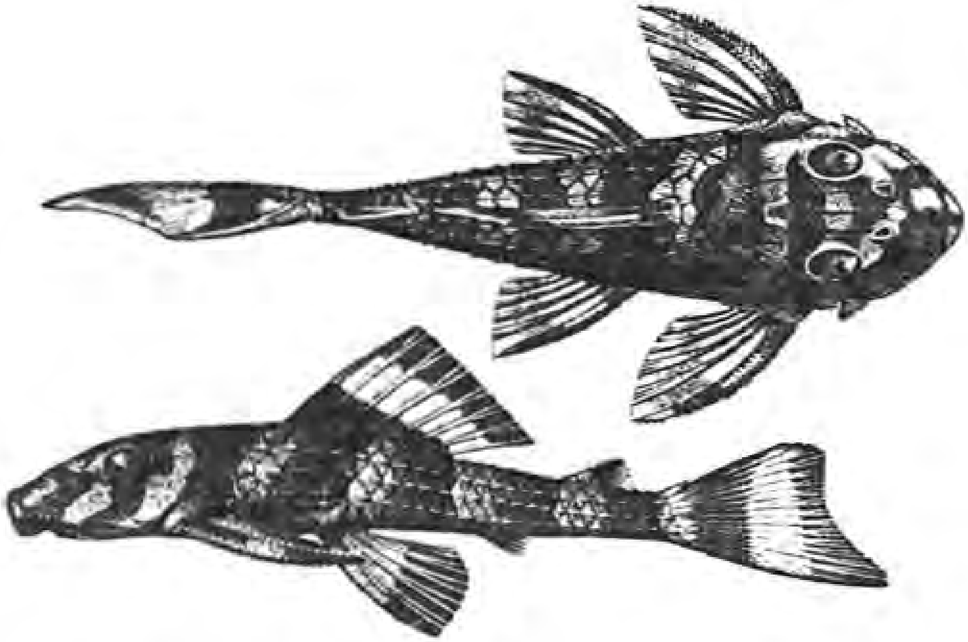


Fig. VI,18. - *Peckoltia pulcher* (Steindachner, 1915), holotype (after Steindachner, 1915c, pl. 11 figs. 1-2).

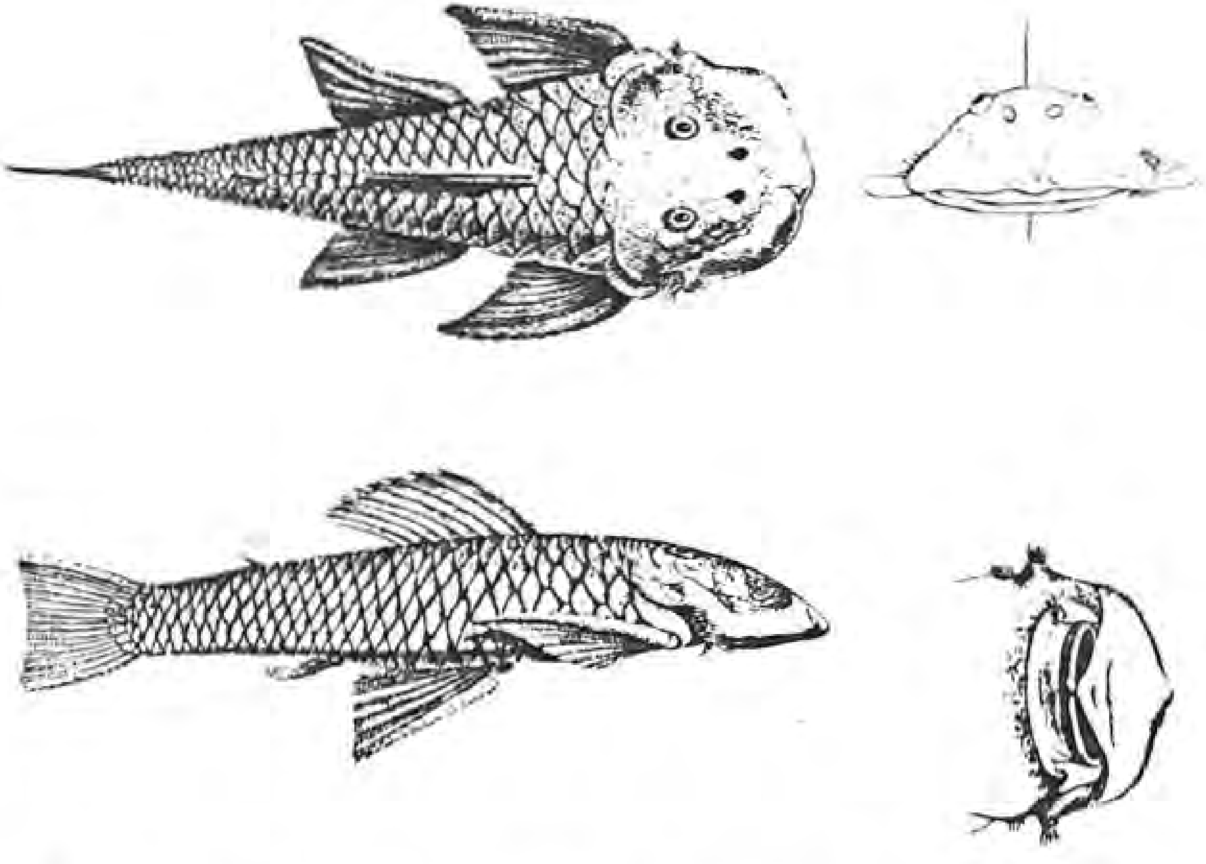


Fig. VI,19. - *Chaetostoma loborhynchos* Von Tschudi, 1845, syntype (after Von Tschudi, 1845, pl. 4 figs. 1-4).

Plate XII.

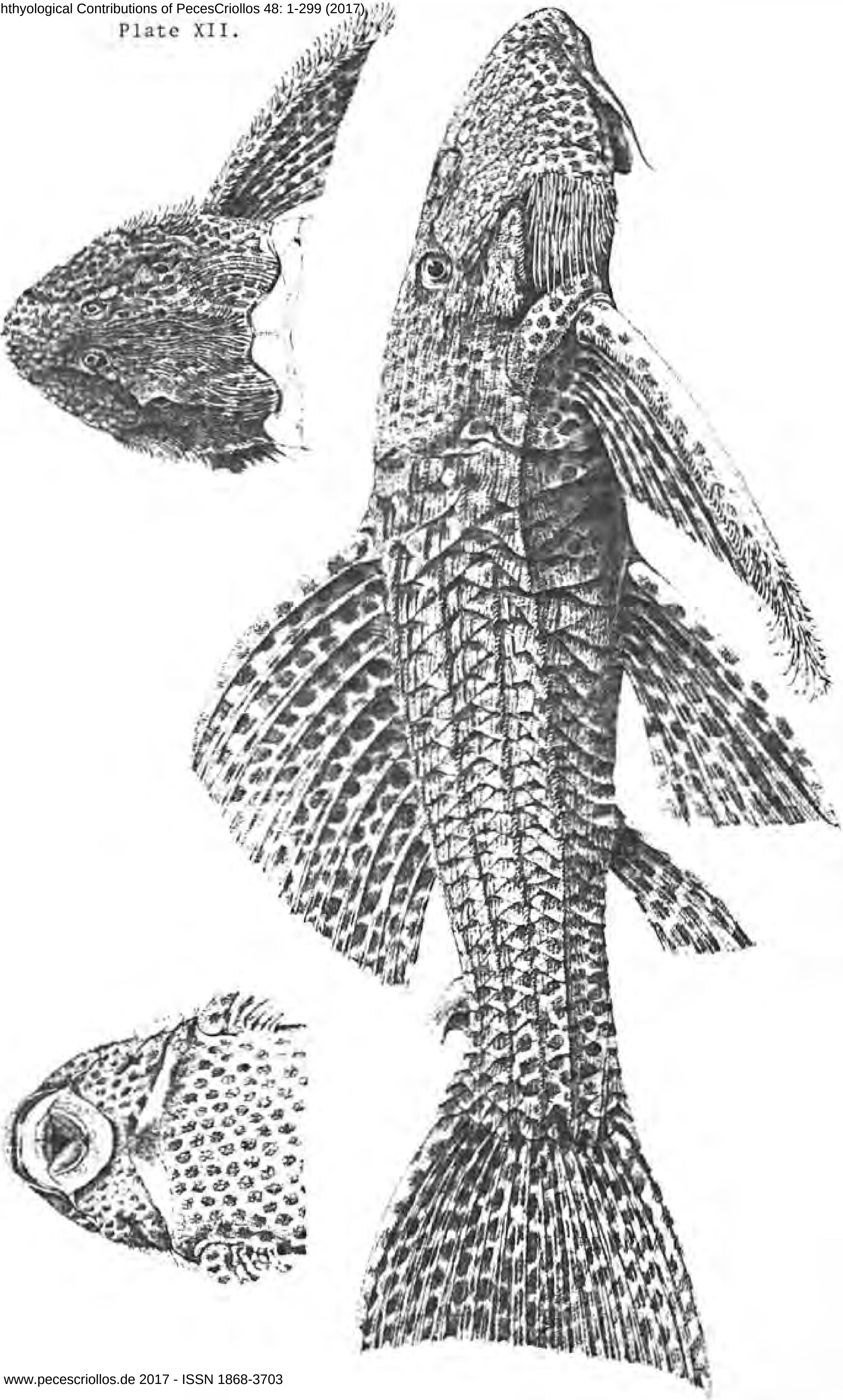


Fig. VI,20. - *Megalancistrus gigas* (Boulenger, 1895), holotype (after Boulenger, 1896, pl. 6).

Parancistrus Bleeker, 1862

Parancistrus is the only genus of Loricariidae having the dorsal fin membrane extending much beyond the last dorsal fin ray, reaching often to the adipose fin spine and at least connecting some middorsal scutes. Large (about 300 mm in total length), robust and often colourful species, none of which is well-known. The relationships to other Ancistrinae are not clear, neither.

Hypocolpterus Fowler, 1943

The characters of *Hypocolpterus* resemble those of *Chaetostoma* very much, except for the presence of a considerably larger anal fin in the former genus. A single species, *H. analis*, which is known from 3 specimens (Fowler, 1943a: 261; 1945c: 123), the largest being 320 mm (in total length?).

Chaetostoma Von Tschudi, 1845

Chaetostoma is the first described genus of the subfamily Ancistrinae. It contains almost 40 species, which collectively are easily recognizable by their extremely wide mouth, smooth head, and their naked – often swollen – margin of the snout. The number of branched dorsal fin rays varies from 7 to 10. *Chaetostoma* is abundantly collected from fast running mountain streams. They occur at unusually high altitudes for a mailed Loricariid.

Leptoancistrus Meek & Hildebrand, 1916

Leptoancistrus are small, *Chaetostoma*-like fishes, with the odontodes in the interopercular area in two forms, viz., relatively short (about 10) odontodes anteriorly, and conspicuously longer (1 to 7) ones posteriorly. The longest odontodes may extend as far as to the middle of the pectoral fin spine. No adipose and no anal fin. Two species: *L. canensis*, known from 52 specimens, up to 75 mm, and *L. cordobensis* (listed in an addendum in Isbrücker, 1980: 181), of which 3 specimens, up to 37 mm are known; they were des-

Plate XIII.

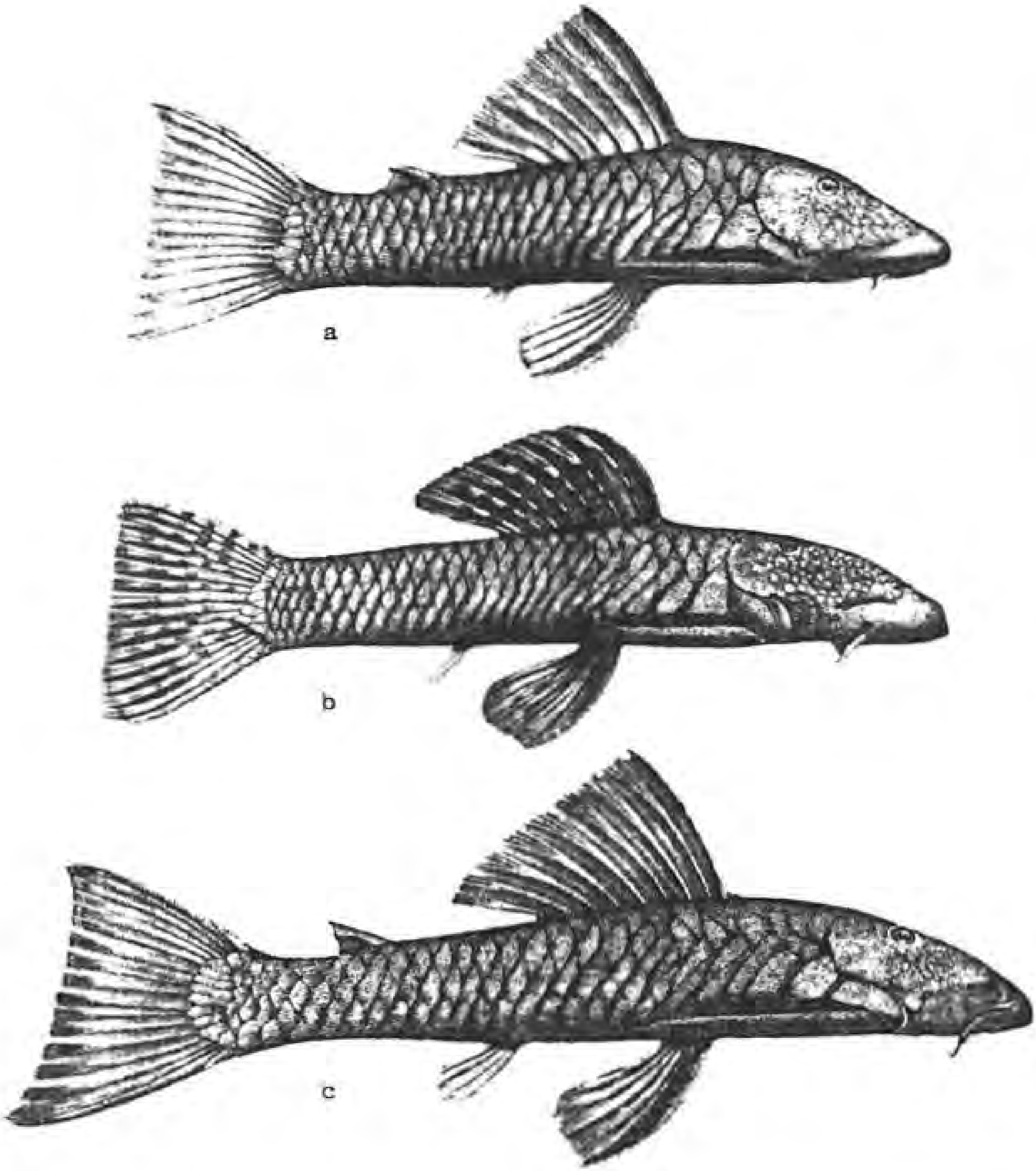


Fig. VI,21. - (a) *Chaetostoma breve* Regan, 1904, syntype; (b) *Chaetostoma anomalum* Regan, 1903, syntype; (c) *Chaetostoma marginatum* Regan, 1904, syntype (after Regan, 1904, pl. 13 figs. 3, 2, and 1, respectively).

cribed from Panama (L. canensis) and Colombia (L. cordobensis), respectively.

Lipopterichthys Norman, 1935

Like Leptoancistrus, Lipopterichthys lacks an adipose fin and the anal fin. The only described species of Lipopterichthys, L. carrioni reaches a total length of 78 mm, has the "Interoperculum with a few spines of moderate length" (Norman, 1935), and is known from 5 specimens from Ecuador. Mr Howes (pers. comm.) drew attention to the desirability that Lipopterichthys becomes directly compared with the Leptoancistrus spp., which indeed are resembled most closely and may prove to be not distinct.

Ancistrus Kner, 1854

This singular genus most probably includes Xenocara as a junior synonym. It is the only known genus in which the males have fleshy, bifid and simple tentacles and barbels on the middle of dorsum of the (naked part of the) snout, arranged into an Y-like configuration. Often there are additional small barbels along the snout margin as well, not rarely in both sexes, although in mature males these are much more conspicuous than in juveniles and in females.

Panaque Eigenmann & Eigenmann, 1889

This genus can be immediately recognized by its dentition; the number of teeth is reduced, the teeth are short, thick, with a cup-like crown, reminiscent very much of the teeth possessed by the Hypostomine genus Cochliodon. The odontodes in the interopercular area are well-developed, increasing in length with age, and excessively long in some (probably only the male) specimens. Most species are very colourful. They are robust in general body shape and may reach a length of up to 390 mm, as far as we know them.

ACANTHICINI

Plate XIV.

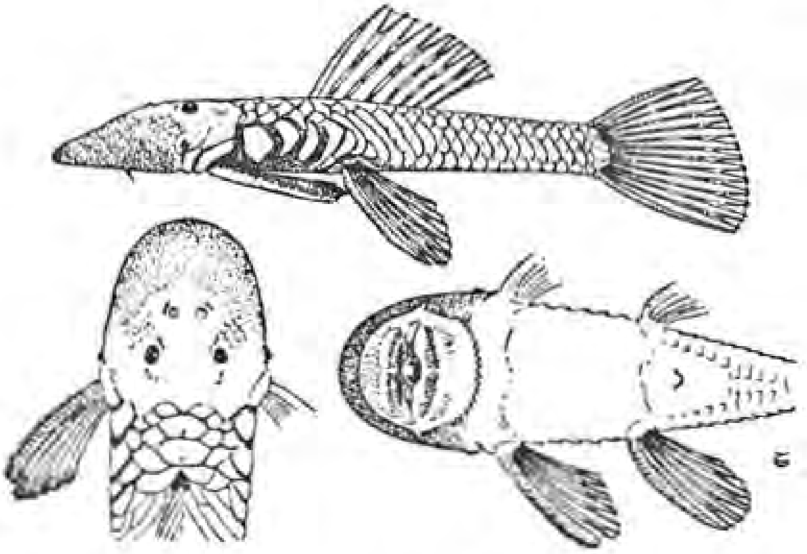


Fig. VI,22. - Lipopterichthys carrioni Norman, 1935, holotype (after Norman, 1935: 628).

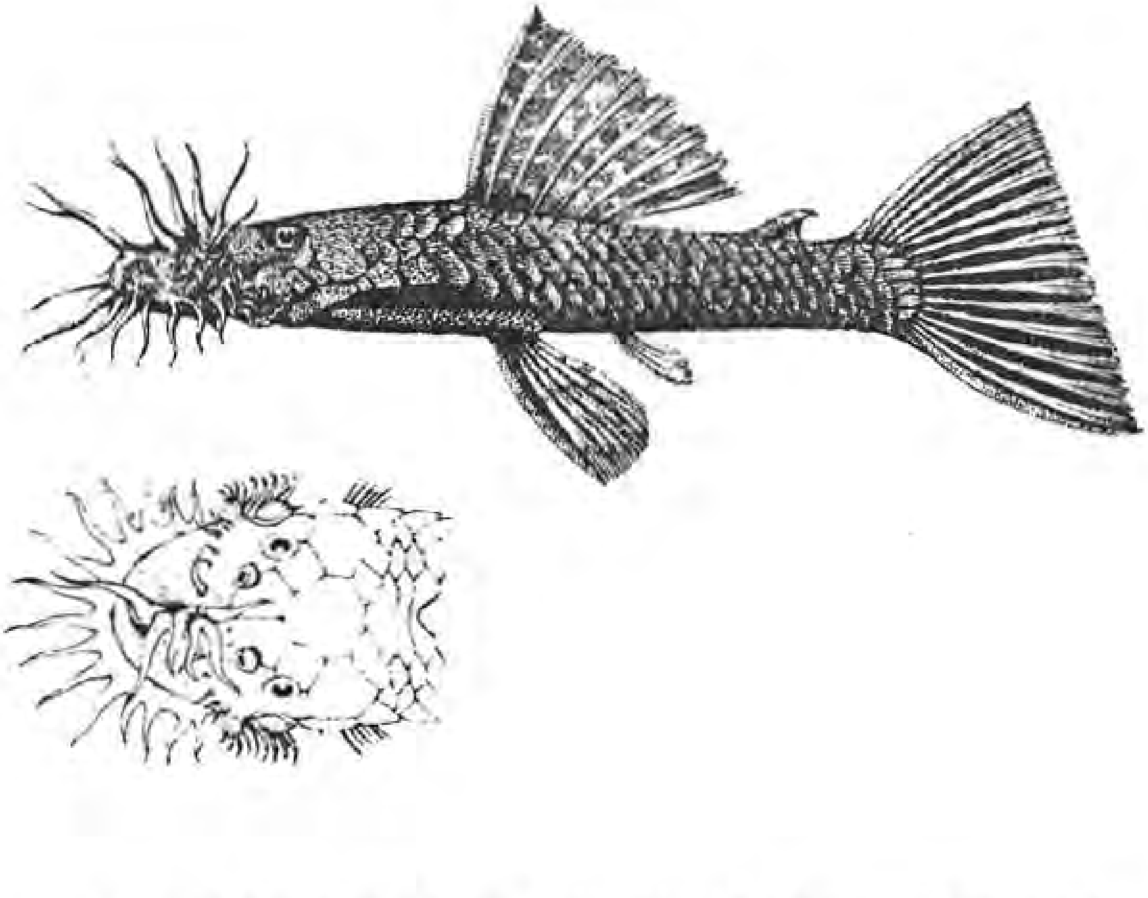


Fig. VI,23. - Ancistrus occidentalis (Regan, 1904), male, syntype (after Regan, 1904, pl. 14 figs. 5, 5a).

Plate XV.

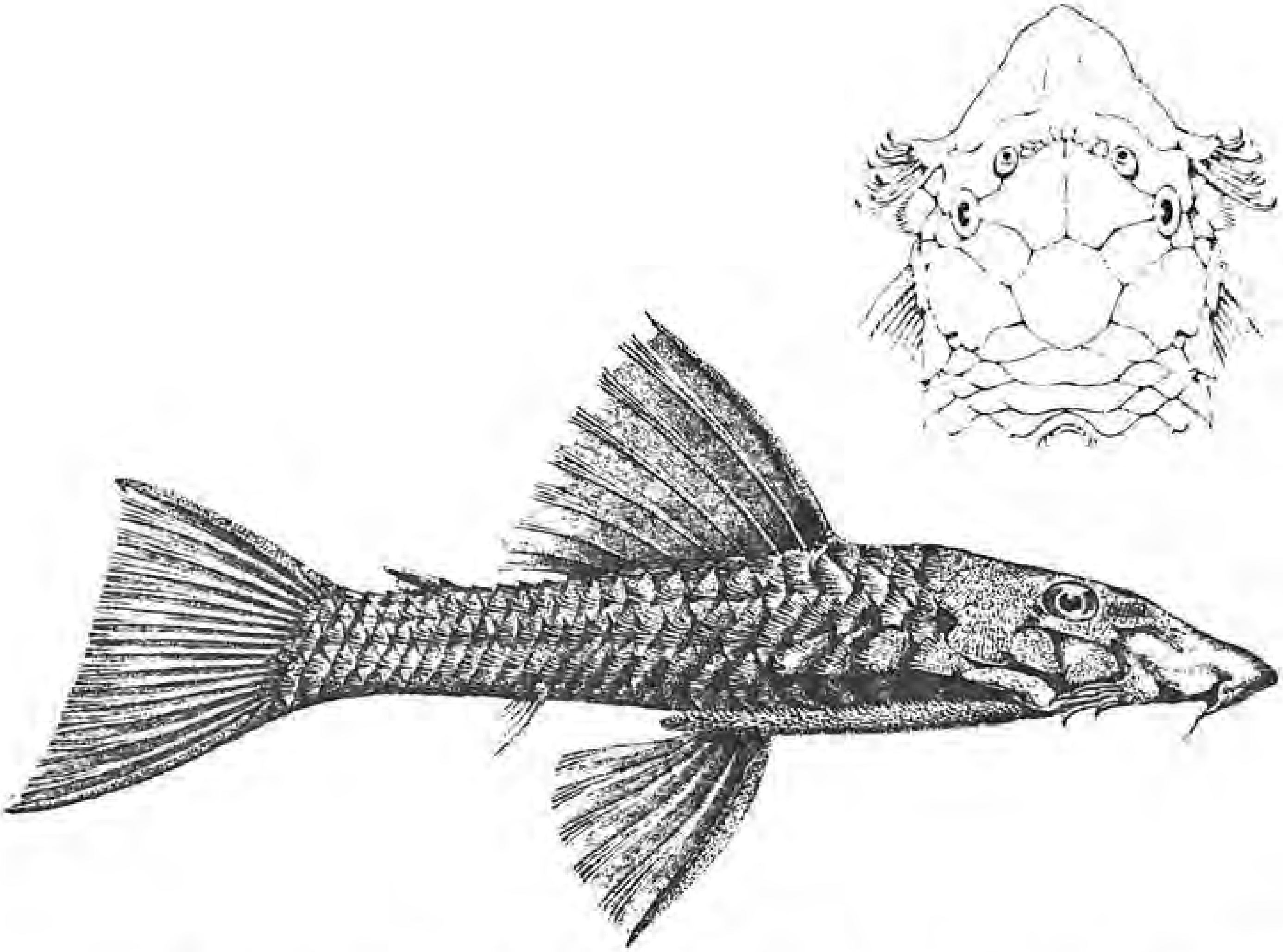


Fig. VI,24. - Ancistrus latifrons (Günther, 1869), holotype (type-species of Xenocara); (after Regan, 1904, pl. 15 fig. 1).

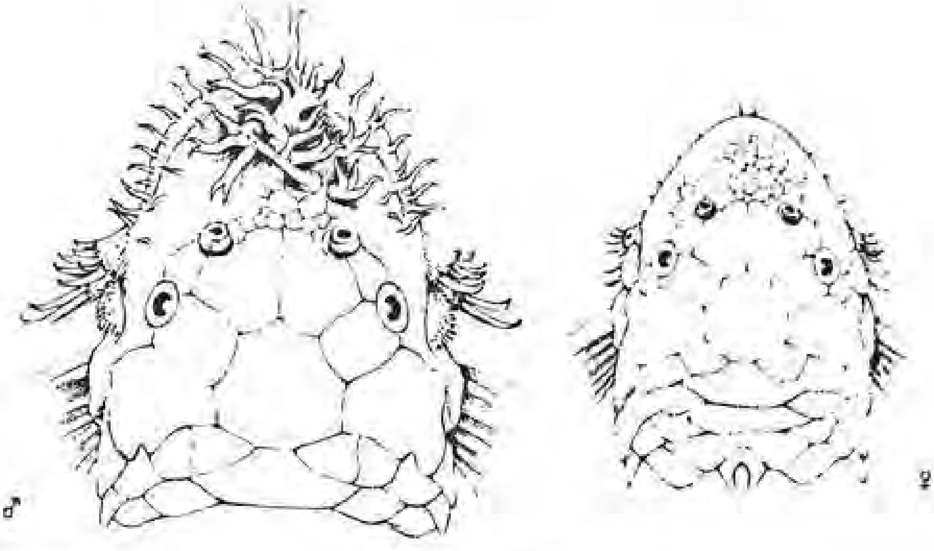


Fig. VI,25. - Ancistrus chagresi Eigenmann & Eigenmann, 1889, syntypes, male and female (after Regan, 1904, pl. 14 fig. 7).

Bleeker (1862: 2-3) established the Acanthicini, including the genera Acanthicus, Rhinelepis, and Pseudorinelepis. The tribe may stand, however, excluding the latter two genera.

Acanthicus Von Spix, 1829

Acanthicus differs from all other Loricariidae by the possession of an extremely large temporal plate. It agrees with the Ancistrini in having the premaxillae separated from each other, and like these, Acanthicus possesses a moderately high number of teeth in both the upper and lower jaws.

PSEUDACANTHICINI

This tribe differs from all other Ancistrinae in having the premaxillae partly firmly fused. The lips form a round rather than a more or less strongly oval adhesive disk, with a short maxillary barbel at either side. Pseudacanthicus is superficially quite reminiscent of Acanthicus because of the mutually very conspicuously developed odontodes, but it differs at once from that genus in the much smaller (more normal) size of the temporal plate, and in the reduced number of teeth.

PSEUDACANTHICINA

Pseudacanthicus Bleeker, 1862

Pseudacanthicus (the only genus of the subtribe) includes species reaching a fairly large body size (P. histrix with a recorded total length of 760 mm is the largest known member of the entire family), with a deep body and very spinose dermal ossifications: the odontodes are well-developed and at least in some species known to be involved in most conspicuous secondary sexual dimorphism.

LITHOXINA

This subtribe contains 2 genera of small species (not exceeding a total length of 86 mm) with a depressed body and head

Plate XVI.

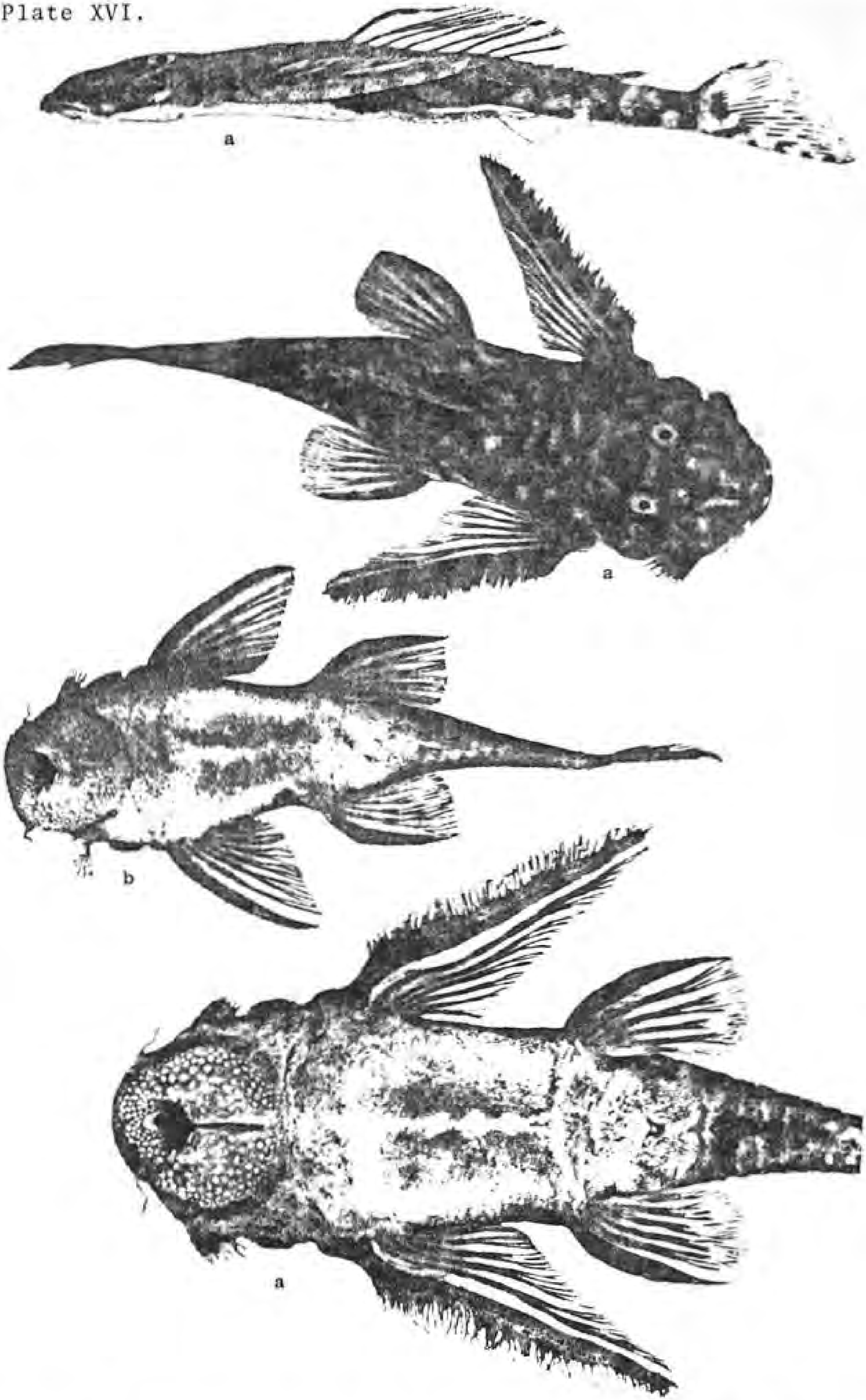


Fig. VI,26. - Lithoxus lithoides Eigenmann, 1910, (a) holotype, male, (b) paratype, female (after Eigenmann, 1912a, pl. 29).

and no conspicuous odontodes on dermal ossifications, except for those on the pectoral fin spine in mature males. Compared to the Pseudacanthicina, Lithoxina are therefore comparatively very smooth fishes. The tail of Lithoxina looks not unlike the tail of various Loricariinae.

Lithoxus Eigenmann, 1910

Lips provided with a maxillary barbel at either side only, the margin almost continuous, without barbels.

Exastilithoxus Isbrücker & Nijssen, 1979

This is the only genus of the subfamily Ancistrinae having the lips provided with marginal barbels, those on the lower lip more numerous and longer than the barbels on the upper lip. Barbels (in addition to the single maxillary barbel present at either side of the mouth in all Loricariidae) otherwise only occur in some of the subtribes of the Loricariini, subfamily Loricariinae.

HYPOPTOPOMATINAE

This subfamily appears to be very closely related to the Hypostominae (it may prove to be a specialized offshoot), but its members are easily recognizable by their exposed lower transverse part of the cleithrum, scapula and coracoid (cf. Gomes, 1955), the snout being not extremely produced (as in the Acestridiini of the subfamily Loricariinae, which also have the lower part of the girdle exposed). The anterior ventral margin of the snout is provided with a series of strong, recurved, spine-like odontodes. None of the Hypoptopomatinae reaches a large body size.

The Hypoptopomatinae are currently being revised by Dr H. A. Britski of São Paulo.

OTOCINCLINI

In my 1980 paper, the 44 members of the tribe Otocinclini were assigned to the genera Parotocinclus (13 species, al-

Plate XVII.

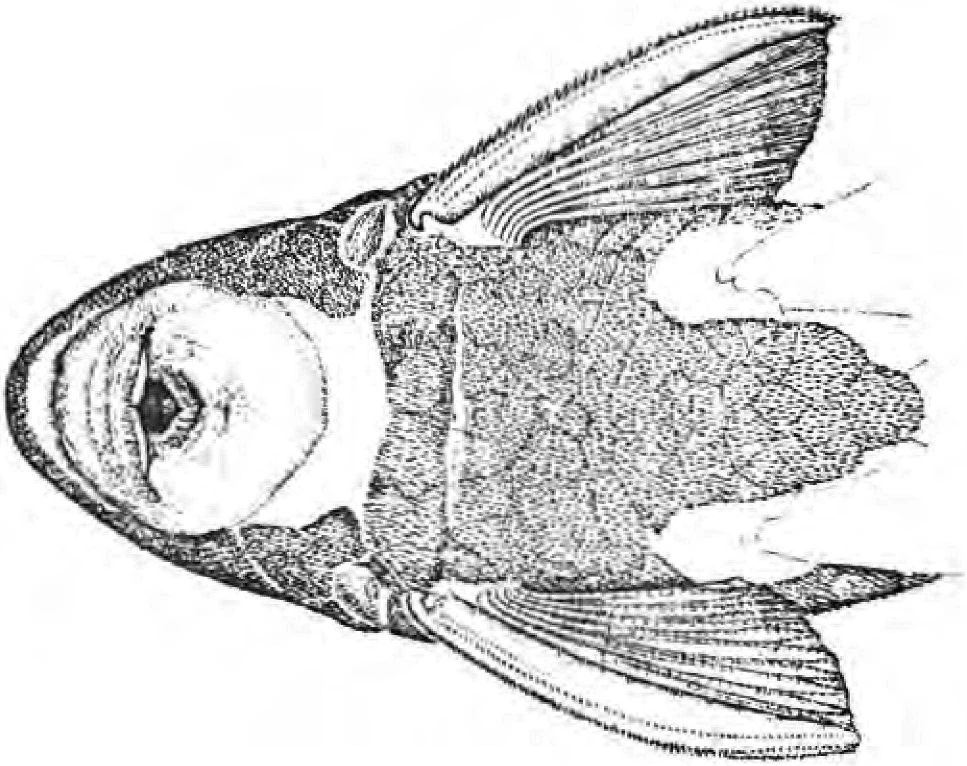


Fig. VI,27. - Parotocinclus britskii Boeseman, 1974, schematized (after Boeseman, 1974, fig. 2).

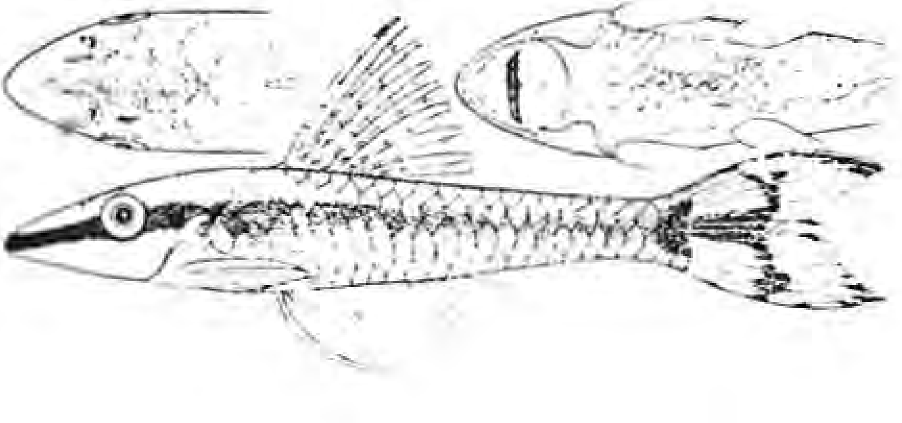


Fig. VI,28. - Otocinclus mariae Fowler, 1940, holotype (after Fowler, 1940b, figs. 41-43).

most wholly upon Garavello's – 1977 – revision of the genus, which was made under supervision of Dr Britski), Otocinclus (27 species), Othothyris (1 species), 2 unnamed genera, Britski MS (1 species in each), and to Pseudotocinclus (2 species). Hisonotus and Microlepidogaster were referred to the synonymy of Otocinclus.

The Otocinclini are distinguished from the Hypoptopomatini clearly by the shape of body and head; this shape is rather reminiscent of the more primitive genera of the Hypostominae: higher and broader than in the Hypoptopomatinae. In addition, Otocinclini reach a significantly smaller adult size than the Hypoptopomatini, whereas their eyes are relatively much smaller and in a relatively high dorsolateral position as compared to the Hypoptopomatini. In my opinion, Otocinclini are more closely related to some Hypostominae than are the Hypoptopomatini.

Recently (autumn 1980), I had the great pleasure of meeting Dr Britski in Amsterdam, and he pointed out to me that at least Microlepidogaster is a valid genus (quite distinct from Otocinclus, including several species), and also that in my 1980 enumeration several species of Otocinclini were incorrectly assigned to the various genera involved. Rather than 'quoting' extensively herein Dr Britski's very kind personal information, I prefer to await publication on this difficult subject by this expert himself.

Parotocinclus Eigenmann & Eigenmann, 1889

According to Boeseman (1974: 267): "The genus Parotocinclus appears to be characterized by having the temporal not perforated, the abdomen covered with 3-5 series of scutes, the possession of an adipose fin, the slightly depressed head with dorsolateral eyes, which are not visible in ventral view." Twelve or 13 species.

Plate XVIII.

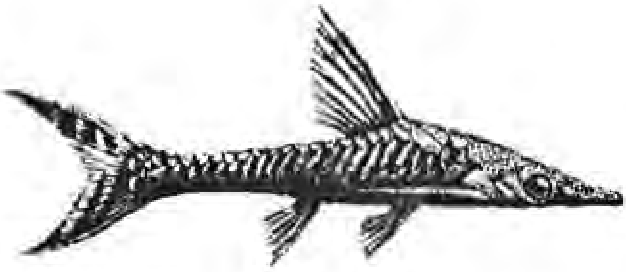


Fig. VI,29. - Hypoptopoma guentheri Boulenger, 1895, syntype (after Regan, 1904, pl. 15 fig. 2).

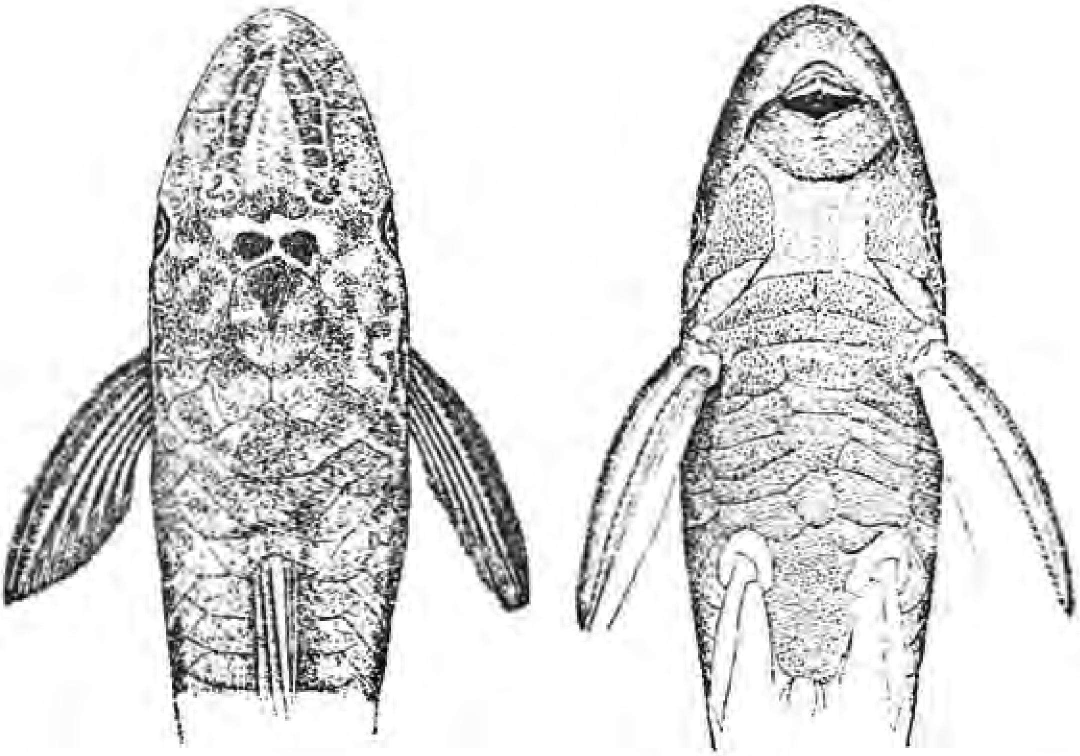


Fig. VI,30. - Hypoptopoma guianense Boeseman, 1974, schematized (after Boeseman, 1974, fig. 1).

Microlepidogaster Eigenmann & Eigenmann, 1889

Several species. See p. VI,22.

Otocinclus Cope, 1871

Several species. See p. VI,22.

Othothyris Myers, 1927

One species. See p. VI,22.

Unnamed genus A, Britski MS

One species. See p. VI,22.

Unnamed genus B, Britski MS

One species. See p. VI,22.

Pseudotocinclus Nichols, 1919

Two species. See p. VI,22.

HYPOPTOPOMATINI

Hypoptopoma Günther, 1868

This appears to be the only genus of this tribe, although the poorly defined Oxyropsis Eigenmann & Eigenmann, 1889 might prove to be valid (Dr Britski, pers. comm.). For the present, I follow Boeseman (1974: 258-267), who published the most recent comparison of the 12 nominal species of Hypoptopoma.

The tribe Hypoptopomatini (and its only included genus) differs from the Otocinclini by their spatula-shaped head (especially the snout), by reaching distinctly larger adult sizes, and by the relatively large eyes, which can be seen as clear from above as from below on account of their remarkable lateral position.

LORICARIINAE

All members of the subfamily Loricariinae are distinguished from the other subfamilies particularly by having the caudal peduncle (usually strongly) depressed, except in the Farlowellini and Acestridiini, where the caudal peduncle is oval or roundish in transverse view, as a result of the extremely narrow caudal peduncle when seen in dorsal or in ventral view.

The caudal peduncle is covered by a single median series of scutes (the left and right components of each of these scutes are medianly tightly fused) posterior to the dorsal and the anal fin, except for a few azygous scutelets in front of the caudal fin origin.

The area between the posterior scutes on the caudal peduncle and between the anterior series of dorsal and ventral (thoracic) scutes is fully bridged by the well-developed, firmly connected longitudinal body scutes. Each lateral body scute is provided with a (usually bifurcate) lateral line canal situated below each transverse series of scutes.

A pectoral pore is found in many species, and probably can be found in well-preserved material of all species. The function of this pore is unknown. When the pectoral fin spine of a spread fin in a preserved specimen is pressed along the body, the pectoral pore releases fluid.

A mostly inconspicuous, naked area just posterior to the temporal plate is present in front of the lateral body scutes.

Fusion lines are visible in the scutes just dorsal and ventral to the lateral line. The number of transverse scutes plus the parts divided by fusion lines at one side of a member of the subfamily Loricariinae is 5, agreeing with the number of transverse scutes at one side of the average member of the other subfamilies.

Contrary to the condition in the great majority of other Loricariidae, an adipose fin is absent in the entire subfamily Loricariinae. The presence or absence of an adipose fin was proven to be a weak character to distinguish between certain genera (and even between some species) of Loricariidae. Apart from being functional to disappear after the members of the Loricariinae gradually became more streamlined than their ancestors, the complete absence of the adipose fin might indicate that the subfamily evolved from a lineage which already lost the adipose fin – there are several genera of Hypostominae without adipose fin.

HARTTIINI

The Harttiini are distinguished from the other Loricariinae by having: a) the origin of the dorsal fin about opposite to the origin of the pelvic fins, b) 6 branched dorsal fin rays, the last one split to its base, and c) 12 (rarely 11) branched caudal fin rays.

The orbital rim is round or slightly oval, never provided with a posterior notch.

The subsidiary branches of the fin rays all stem from one side of the main (anterior) branch, except where the subsidiary branches are very long: then only a single dichotomous branching occurs distally.

The outer surface of the upper lip is provided with minute dermal scutelets.

Secondary sexual dimorphism apparently is always present, although not all the species are already known from mature specimens of either sex. Prominent odontodes develop along the sides of the snout and on the dorsum of the pectoral fin rays (particularly conspicuously on the spine) in nuptial males.

The buccal cavity of Harttiini is very similar to that of the members of the subfamilies Hypostominae (perhaps also of the Neoplecostominae), Ancistrinae, and Hypoptopomatinae. It contains a smooth upper and lower oral valve membrane, the former often with a small to quite conspicuous fleshy protuberance in the middle.

HARTTIINA

This subtribe is characterized by its dentition and by the shape of the lips, which are virtually of the same structure as the dentition and lips usually present in the Hypostominae (with few exceptions), the Ancistrinae (with few exceptions), and in the Hypoptopomatinae.

There are numerous long, filiform teeth with a strongly bend, bilobate crown pointing towards the buccal cavity. The teeth are arranged into one (rarely into two).row(s) in each half of the jaws, together forming an usually oval series. The jaws (as in most other Loricariidae) are at the symphysis separate (independently movable in the living fish), of a cupuliform structure, with a weak bony wall, almost as thin as paper. Replacement of the teeth seems to occur regularly. The functional teeth are along the outer margin of the jaw; posterior to this series in the upper jaw and anterior to the functional teeth in the lower jaw are some series of replacement teeth present, usually all of these are entirely hidden in the 'gums.'

The papillose part of the upper lip is very narrow, forming just a narrow free margin anterior to the teeth. The lower lip is short, most of the posterior part of it is free from the ventral surface of the mouth. Both lips together form a perfectly adhesive device. There is a short maxillary barbel at each rictus. Sometimes this rictal barbel does not extend beyond the lips, but its presence is always clearly visible as a narrow strip devoid of papillae.

Low papillae are otherwise present all over the lower surface of the lips, as a large number of smooth, fleshy, small 'cushions.' The margin of the lips is smooth, or is fringed with very short papilla-like extensions and/or minute flattened flaps.

On account of the trends towards increase of adult size (standard length), decrease of predorsal length, increase of postdorsal plus postanal caudal peduncle length, together with some increase of the body depth and decrease of the body width, the genera of the Harttiina can be arranged as follows: Harttiella → Harttia → Cteniloricaria → Pterosturi-

soma & *Lamontichthys* → *Sturisomatichthys* → *Sturisoma*. This sequence might essentially show an almost straight lineage from the most generalized towards the most specialized genus. As a matter of fact, all these genera are obviously gradually closely related to each other. Therefore, it is rather difficult to draw sharp lines of distinction between several of the recognized genera. An alternative would be the treatment of all Harttiina species as the representatives of far less genera, which would considerably expand the limits of *Sturisoma*, the first described genus. Regan (1904) adhered to such a point of view, and assigned all species known to him to *Oxyloricaria*, a junior synonym of *Sturisoma*. Another possibility is the concession to treat all genera (except *Lamontichthys* and *Harttiella*) as subgenera of *Sturisoma*. However, the genus-concept is largely subjective. The very same characters which serve to distinguish between genera of the one student are equally significant if another student argues that these same taxa have to be considered subgenera, or perhaps only species-groups. For two reasons, I find the present generic arrangement within the Harttiina the most satisfying. One reason is that I recognize a much more archaic condition in *Harttiella* and in *Harttia* than in the highly specialized *Sturisoma*, and placing a variety of forms as assembled in the Harttiina into one, two, or three genera, does not satisfactorily express their relationships. The second reason is the existence of the genus *Lamontichthys*, clearly a genus of Harttiina, unique among them and among all other mailed Loricariidae by its higher number of pectoral fin rays. In general appearance, *Lamontichthys* is particularly reminiscent of *Pterosturisoma*, but I doubt whether these two genera are really so close to one another.

Species which show characters that bridge the gap between *Harttiella* and *Harttia* on the one hand and *Sturisoma* on the other hand can be put into three groups of genera: the more primitive group is *Harttiella* plus *Harttia*, together with the apparently slightly more specialized Ctenilоricaria, the intermediate group is a pair consisting of Pterosturisoma and Lamontichthys, while the most specialized group is the pair formed by Sturisomatichthys and Sturisoma.

Although I admit that to some of us the present series of genera may seem to suffer from oversplitting, I can imagine a hardly more satisfying alternative.

Harttiella Boeseman, 1971

Harttiella was originally established for two species, previously known as Harttia crassicauda Boeseman, 1953 (the type-species) and as Canthopomus montebelloi Fowler, 1940b, respectively. As already stated (this chapter, p. 6), Canthopomus is a junior synonym of Pseudorinelepis (Hypostominae). I have re-examined the holotype (and still only known specimen) of C. montebelloi and quite to my surprise found that it is a member of the genus Ixinandria (subtribe Rineloricariina of the Loricariini). It differs only very slightly from the few known specimens of I. steinbachi, the type-species of Ixinandria. The holotype and 14 paratypes of Harttiella crassicauda were also examined.

Harttiella crassicauda is an intricate species in several respects. It was collected only once, from a small creek, apparently a tributary of the Marowijne River in Surinam, near the top of the Nassau Mountains. The Nassau Mountains reach a maximum height of 570 m and are plateau-shaped. Fifteen specimens of H. crassicauda were collected in 1949. The largest specimen (holotype) is a nuptial male, in my opinion an adult, only 48.1 mm in standard length, 58.8 mm in total length. The largest paratype is also a nuptial male, 41.1 mm in standard length. Six paratypes have standard lengths between 28.4 and 38.4 mm; they may all be females, but likely they are mixed with males which are unrecognizable as such by the lack of apparent secondary sexual dimorphism. The remaining 7 paratypes are

Plate XIX.

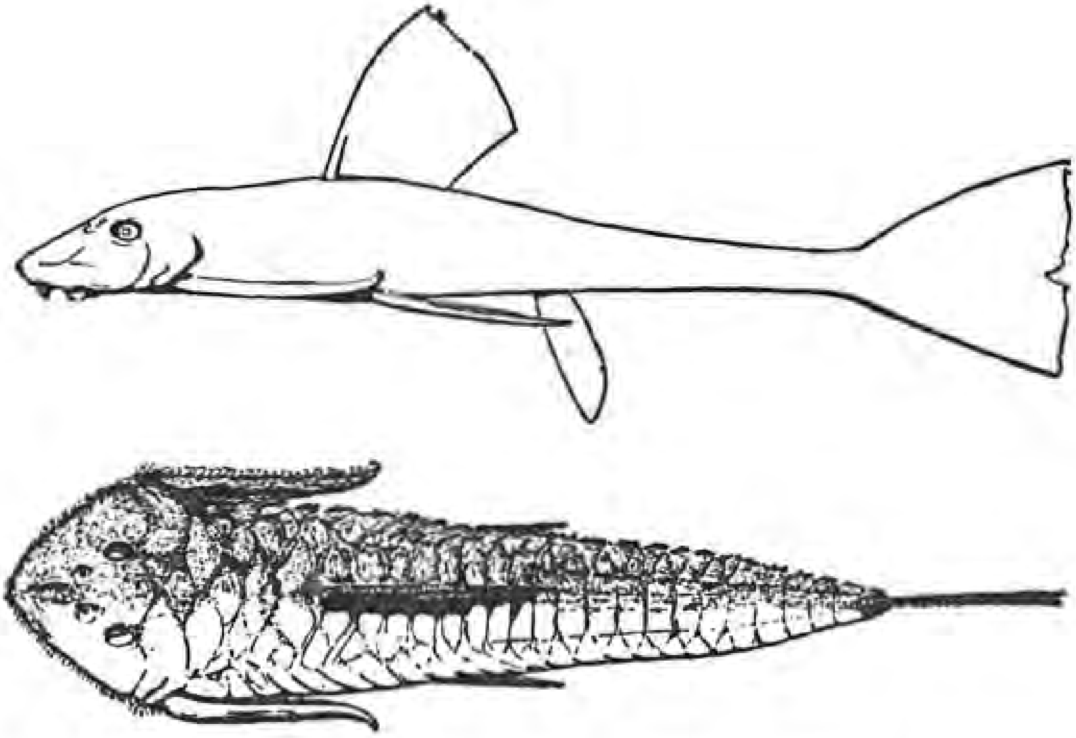


Fig. VI,31. - Harttiella crassicauda (Boeseman, 1953), holotype (after Boeseman, 1953, figs. 2a-b).

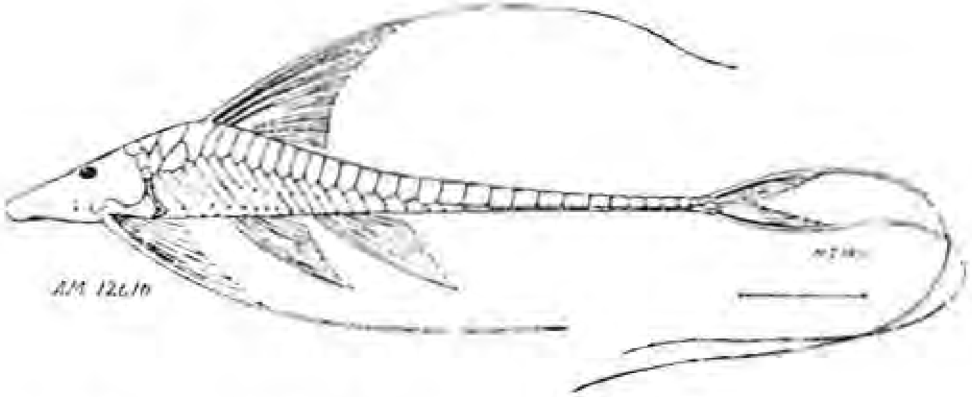


Fig. VI,32. - Lamontichthys filamentosus (La Monte, 1935), holotype (after La Monte, 1935, fig. 4).

juveniles with standard lengths from 11.2 to 16.7 mm; in general appearance they are very reminiscent of the tadpoles of some European frog or toad.

Boeseman (1971: 27) described the colour pattern: "The specimens are now rather dark brownish, with a lighter ventral surface. Especially the lower snout tip is intensely dark, and there appear to be some slight indications of transverse bands and a dusky caudal base." The holotype has minute brown pigmentation spots on dorsum of body and head, and on dorsum of pectoral fin.

Harttiella crassicauda is the smallest species of the subfamily Loricariinae known so far. To what extent this small adult size accounts for the apparently primitive characters is difficult to say. It seems to me that this species is the most generalized of the entire subfamily. At any rate, it has not a really depressed caudal peduncle (the holotype has the caudal peduncle depth and width both 4.2 in head length, whereas other Harttiina have a caudal peduncle depth of at least 9.0 in head length and a width of at least 5.1), proportions which are more in agreement with several species of the Hypostominae (primitive genera), of various Ancistrinae, and of the Hypoptopomatinae rather than with the average Loricariinae. If not the characteristic posterior mediodorsal and medioventral scutes had been present (although not as sharply shaped as in other Harttiina), and if more than the 12 branched caudal fin rays, usual for Harttiina had been present, then H. crassicauda could quite easily have been assigned to the Hypostominae. In the British Museum (Natural History), London, there is a small specimen of an unidentified genus and species of primitive Hypostominae, from Bolivia (?), Rio de Janeiro, waterfall of Tinna (locality not traced), Titicaca Expedition 1937, 31.4 mm in standard length (BMNH 1969.1.27:47). It has an adipose fin and 14 branched caudal fin rays, and in all characters this specimen is clearly a member of the Hypostominae, but it is more than anything else remarkably reminiscent of

Harttiella.

Harttiella crassicauda has a naked abdomen, and a very low number of lateral body scutes (usually 27, rarely 28; possibly, Boeseman neglected the middle scute on the caudal fin base in his counts). Unlike most other Loricariinae, the coalescing scutes (about 20) are hard to tell from the parallel ones. Tip of the snout naked.

Harttiella shows a number of morphometric characters which distinguish it from all other Harttiina: the postanal caudal peduncle length is 2.7-2.9 in standard length, up to 2.5 in all other Harttiina; its pelvic 'spine' is 3.9-4.3 in standard length against 4.3 or more in its relatives. Its comparatively broad interorbital area (2.8-2.9 in head length) otherwise occurs in distantly related genera, such as Lamontichthys, Sturisomatichthys, and Sturisoma, only.

Secondary sexual dimorphism. - Nuptial males develop conspicuous, recurved odontodes, the more prominent ones on dorsum and sides of the head (also around the nostrils and around the orbital rim) and in several rows on dorsum of the pectoral fin spine. Enlarged odontodes are also present on the dorsum and the sides of the body, decreasing gradually in size posteriorly. In this respect, Harttiella reminds of Isorineloricaria of the Hypostominae, and also strikingly of Ixinandria of the Loricariinae (Loricariini, Rineloricariina).

If Boeseman's (1971: 6, 7, 9, 28) assumption – which I share – that Harttiella crassicauda represents the most archaic form known of the Loricariinae proves to be correct, its restricted distribution is of interest. Likely, the genus is more closely related with Harttia than with any other genus of this subtribe, but no direct link to Harttia is obvious. The resemblance of Harttiella to Ixinandria (which latter I believe to be the most primitive genus of the tribe Loricariini) is a point of interest to trace the affinities both of and within the subfamily Loricariinae (see pp. 77-79).

Harttia Steindachner, 1876

Harttia appears to be a more specialized genus than Harttiella, but compared to the remaining genera of the subtribe it is the least specialized.

The delimitation of Harttia has been largely unstable until quite recently. Harttia itself was synonymized with Oxyloricaria (= Sturisoma) by Regan (1904), but subsequently was almost always accepted as a valid genus.

In short, 6 species were originally described in Harttia which are now assigned to 5 different genera: filamentosa (now in Lamontichthys), filamentissima (probably a junior synonym of Lamontichthys filamentosus), microps (now in Pterosturisoma), caquetae (now in Sturisomatichthys), crassicauda (now in Harttiella), and nijsseni (now in Metaloricaria).

In addition, 4 species have at some time been referred to Harttia but likewise are now included in another 2 different genera: platystoma, fowleri, and maculata (these 3 are now in Cteniloricaria), whereas brevirostris is now known as a species of Sturisoma.

At this time, 5 species are retained in Harttia, 4 of which dwell around in S.E. Brazil (H. loricariformis, H. kronei, H. carvalhoi, and H. rhombocephala; the exact locality of the latter could as yet not been traced), whereas the 5th species was about 10 years ago described from abundant specimens from Surinam (H. surinamensis).

Of these 5, I have examined 3 species, H. loricariformis, H. kronei, and H. surinamensis. Harttia carvalhoi and H. rhombocephala are known only from their original descriptions and illustrations. Harttia rhombocephala is apparently most closely related to H. loricariformis, while H. carvalhoi is reminiscent very much of H. kronei. As indicated by Boeseman (1953, 1971), his Harttiella crassicauda (see above) appears to be comparatively close to Harttia kronei. In my opinion, H. kronei and H. carvalhoi indeed are both more ge-

Plate XX.

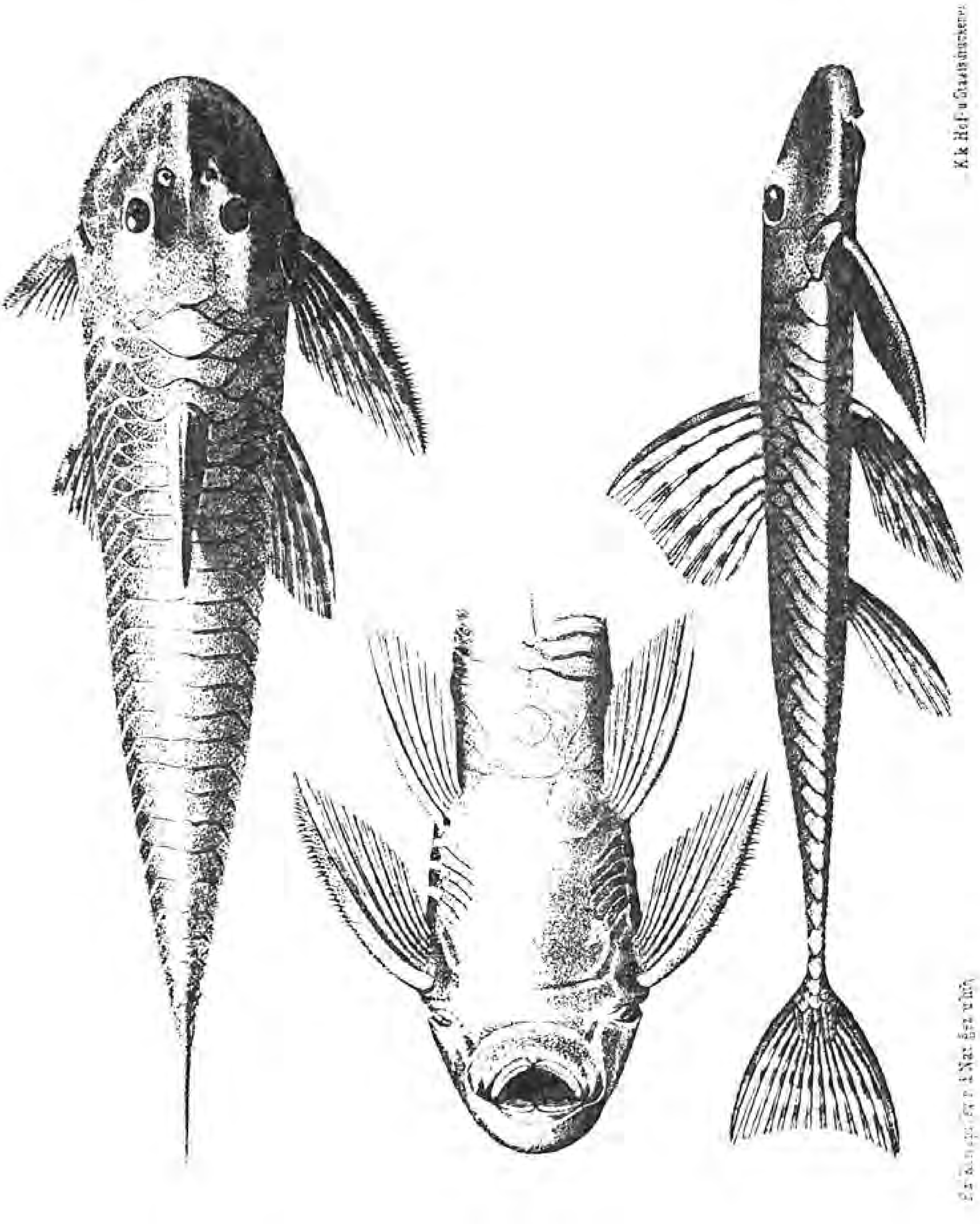


Fig. VI,33. - Harttia loricariformis Steindachner, 1876, likely the now lectotype (after Steindachner, 1876c, pl. 6 figs. 2, 2a-b).

neralized as compared to H. loricariformis plus H. rhombocephala, whereas H. surinamensis shows relatively specialized characters. In various characters, Harttia surinamensis is even quite reminiscent of Cteniloricaria.

The S.E. Brazilian Harttia spp. reach a standard length of about 130 mm (Eigenmann & Eigenmann's (1890: 387) record of H. loricariformis of 230 mm needs confirmation), have a broad, rounded and depressed head, a much depressed and relatively broad body (body depth at dorsal fin origin is 2.0-3.2 in head length); a short, slightly emarginate or moderately furcate caudal fin when spread; they have a naked abdomen, or the abdomen covered irregularly with minute, weak scutelets. The head is comparatively large (3.6-4.0 in standard length); predorsal comparatively long (2.6-2.9 in standard length); and postdorsal and postanal caudal peduncle relatively short (1.9-2.0 and 2.4-2.5, respectively, in standard length); the lower lip is not quite narrow (4.0-6.8 in head length). Lower surface of the upper lip is covered with small, rugose scutelets.

Harttia surinamensis differs from the S.E. Brazilian species by its longer standard length (up to about 190 mm), by having the abdomen in adults completely covered with minute scutelets – similar to those in the S.E. Brazilian species –, by its distinctly more furcate caudal fin, its smaller head (4.1-4.5 in standard length), relatively shorter predorsal (2.9-3.1 in standard length), by its somewhat longer postdorsal and postanal caudal peduncle length (1.8 and 2.1-2.2, respectively, in standard length), and finally, by its narrower interorbital (4.1-4.7 in head length, against 3.8-4.1 in the S.E. Brazilian species). In all these characters, H. surinamensis tends to approach the Cteniloricaria species. As a matter of fact, on account of their general similarity I have placed (1975) – now – Cteniloricaria maculata together with H. surinamensis in Harttia. Harttia surinamensis has the largest number of teeth (125 in the upper jaw of adults) known in species of Harttiina.

In all Harttia spp., the tip of the snout is apparently naked.

Secondary sexual dimorphism. - In Harttia loricariformis, the odontodes along the head and snout margin, as well as those on the dorsum and outer side of the pectoral fin spine are in nuptial males conspicuously longer than in females.

Harttia kronei obviously is the most rugose species of the genus; all examined specimens are similarly rugose because of the presence of numerous slender but not exceptionally long odontodes on the dorsum of head, body, and pectoral fin, and along the side of the head; I figure that all specimens I have seen could be males.

Harttia carvalhoi was illustrated (P. de Miranda Ribeiro, 1939a, pl. 2 figs. A-B) after 2 specimens. The fish in pl. 2 fig. A is more slender, has relatively longer pectoral fins and a thicker pectoral fin spine, and a somewhat broader head than the specimen in pl. 2 fig. B, in my opinion indicating A as a male, B as a female.

No secondary sexual dimorphism is apparent in the single known specimen of H. rhombocephala.

Boeseman (1971: 30) noted for Harttia surinamensis: "The pectoral spine is strong, slightly curved, in all specimens but one merely slightly rough, but in the single exception [in ZMA], presumably a male, with long stiff bristles on the outer apical two-thirds, the bristles reaching a length almost equal to eye diameter."

Cteniloricaria Isbrücker & Nijssen, 1979

Cteniloricaria comprises 3 species, all occurring in the Guianas only: C. platystoma, C. fowleri, and C. maculata. The genus is evidently closely related to Harttia, from which it differs firstly in the more conspicuous development of abdominal scutelets. These are not only less numerous (and

Plate XXI.

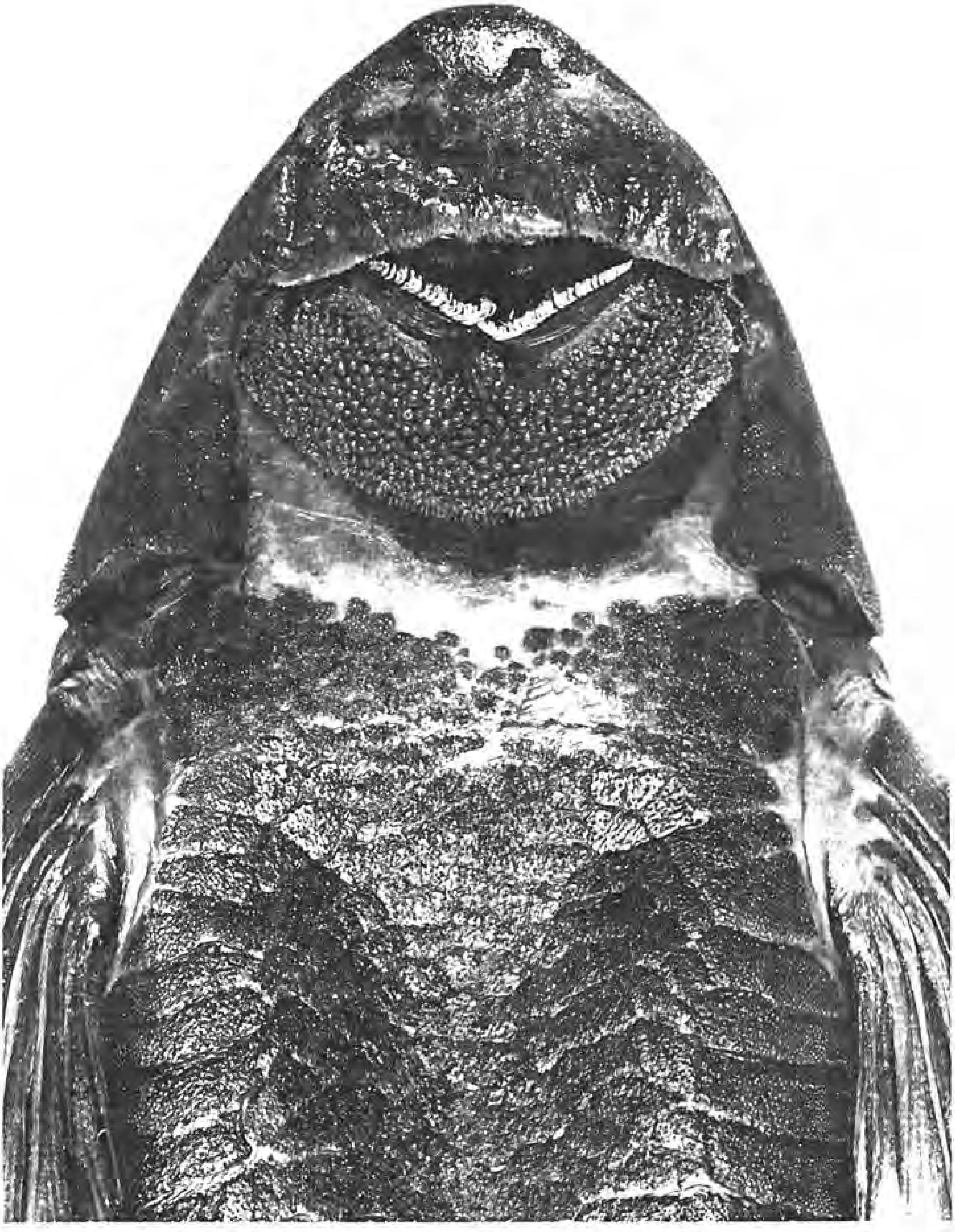


Fig. VI,34. - Cteniloricaria platystoma (Günther, 1868), detail of the lectotype, ventral view (photo L. A. van der Laan, ITZ, Amsterdam).

consequently, larger), but also begin to develop at a distinctly earlier stage in life than in those Harttia spp. which possess an abdominal cover.

Secondly, Cteniloricaria has a narrower and more acute snout and head than Harttia spp., C. fowleri still being relatively broad, C. platystoma being the most slender species, and C. maculata being intermediate in this respect.

Thirdly, Cteniloricaria has longer pectoral, dorsal, and caudal fins than Harttia - the latter fin clearly is comparatively deeper furcate.

The following dimensions may illustrate the differences of Cteniloricaria with the Harttia spp. from S.E. Brazil (data given in this order): maximum standard length is 190 against about 130 mm; the head is shorter (4.0-5.4 in standard length against 3.6-4.0); predorsal shorter (3.1-3.7 in standard length against 2.6-2.9); postdorsal and postanal caudal peduncle is longer (1.6-1.8 and 1.9-2.2, respectively, in standard length against 1.9-2.0 and 2.4-2.5); the dorsal fin 'spine' (= unbranched ray) and the first branched dorsal fin ray are longer (2.8-4.7 and 3.2-4.3, respectively, in standard length against 4.3-5.0 and 4.6-5.4); the upper caudal fin 'spine' is longer (4.2-5.9 in standard length against 5.7-7.0); the interorbital area is narrower (4.1-4.8 in head length against 3.8-4.1); the head tends to be narrower (1.1-1.3 in its own length against 1.0-1.1); the caudal peduncle is lower (depth 14.0-19.5 in head length against 10.2-13.2) and finally, tends to be narrower (width 6.9-9.8 in head length against 5.8-7.3).

These same dimensions are in Harttia surinamensis: standard length about 190 mm; head length 4.1-4.5; predorsal length 2.9-3.1; postdorsal and postanal caudal peduncle length 1.8 and 2.1-2.2, respectively; dorsal fin spine length and length of the first branched dorsal fin ray 3.7-4.6 and about 4.1, respectively; upper caudal fin spine about 7.2; interorbital width 4.1-4.7; head width 1.0-1.2; depth and width caudal peduncle 12.8-18.5 and about 7.1, respectively. These data are brought ahead here just in case Harttia surinamensis would prove to become assigned preferably to Cteniloricaria.

Like in Harttiella and in Harttia, Cteniloricaria has the tip of the snout naked.

Secondary sexual dimorphism. - In spite of rich material available from Surinam (C. maculata) and from the Oyapock River in French Guiana (C. fowleri), including adults, none of the specimens shows secondary sexual dimorphism, neither in the development of their odontodes nor in another way. Specimens displaying such features are, however, to be expected.

* * *

The relationships of the three genera of the subtribe Harttiina defined above (all species being much depressed and having the tip of the snout naked) – for convenience they may be informally referred to as the Harttia-group of genera (Harttiella, Harttia, and Cteniloricaria) – are further discussed under the subtribe Metaloricariina (p. 46). The four remaining genera (defined below) of the Harttiina are gradually more compressed and have no naked snout tip; they may be informally referred to as the Sturisoma-group.

* * *

Pterosturisoma Isbrücker & Nijssen, 1978

Pterosturisoma contains a single species, P. microps, originally described after 5 specimens, 2 of which seem now to be lost. They were collected together about 60 years ago in the Peruvian Amazon, Iquitos; the largest is 161 mm in standard length. While establishing the genus, Nijssen and I have redescribed and illustrated this species.

Plate XXII.

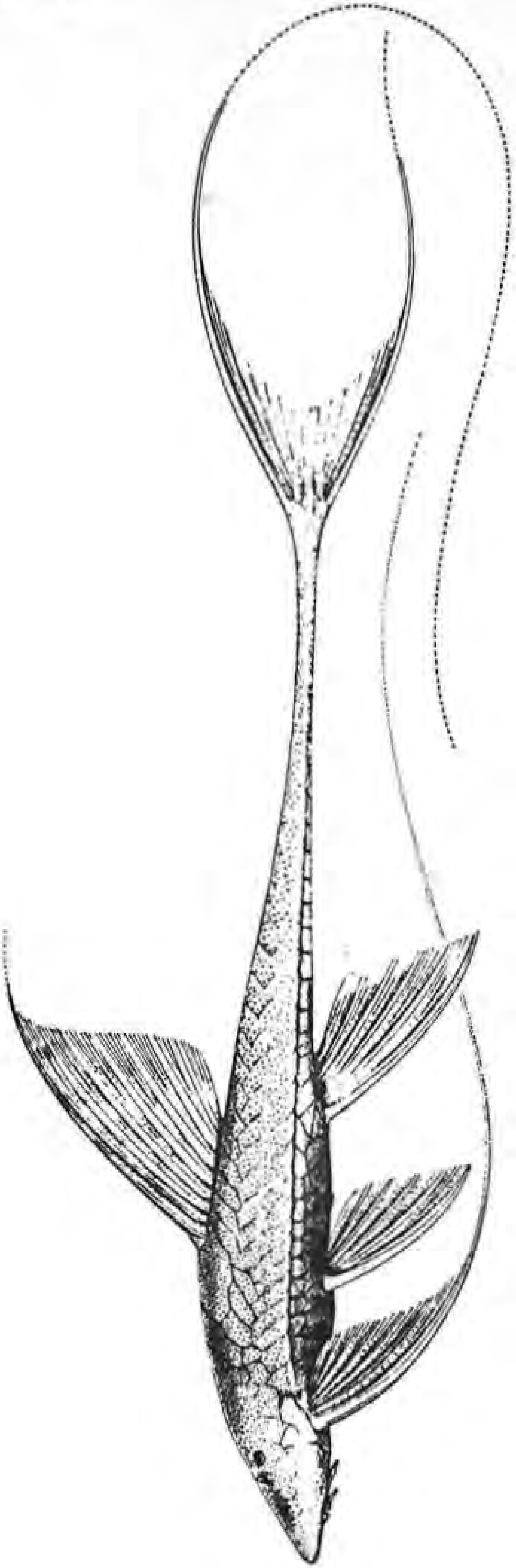


Fig. VI,35. - Pterosturisoma <u>microps</u> (Eigenmann & Allen, 1942), paralectotype (after Eigenmann & Allen, pl. 9).

Pterosturisoma microps first of all differs from its relatives by its extremely small eyes (maximum orbital diameter 11.1-12.8 in head length against at least 7.6 – in *Lamontichthys stibaros* – in all other species of Harttiini). It is unique also for the extremely long, filamentous pectoral fin 'spine', which is comprised 1.1 times in standard length. *Lamontichthys filamentosus* also has extremely long pectoral fin spine filaments, but a similarly filamentous dorsal fin spine as well. *Pterosturisoma* shares a filamentous upper and lower caudal fin spine (up to 310 mm!) with the other genera of the *Sturisoma*-group; such extensions are absent in the representatives of the *Harttia*-group. Together with the following genera of this subtribe, *Pterosturisoma* further differs from the *Harttia*-group by having no naked tip of the snout, a higher body at the origin of the dorsal fin (1.5-1.6 in standard length in *Pterosturisoma* against 1.8-3.2 in the *Harttia*-group), and finally, it is distinguished by its wider body at the origin of the anal fin (1.2 in standard length against 1.4-2.2).

Pterosturisoma shares various characters with and is superficially most reminiscent of *Lamontichthys*; therefore, its additional distinguishing characters are given in comparison with that genus. Secondary sexual dimorphism is still unknown.

Lamontichthys P. de Miranda Ribeiro, 1939

Lamontichthys is known from 13 specimens, belonging to 2 (circum-Amazonian) species; it differs from all other Loricariidae (presumably also from all other mailed Loricariidae) by its number of branched pectoral fin rays: 7 instead of 6 as in all other members of at least the subfamily (2 out of 179 species).

Gosline (1947: 80-81, 91, 92) recorded 9 to 12 branched pectoral fin rays in *Astroblepus* and 8 in *Lithogenes*. Together with diverse additional arguments, Gosline emphasised that the presence of more than 6 branched pectoral fin rays supports the indication of a highly primitive character for a Loricariid. He therefore included *Astroblepus* and *Lithogenes* within the Loricariidae as the representatives of the most primitive subfamily (Astroblepinae) and the next to most primitive subfamily (Lithogeneinae). It is beyond the scope of the discussion of *Lamontichthys* to establish the status of subfamilies ascribed to the Loricariidae.

The 7 branched pectoral fin rays of *Lamontichthys* are, however, not likely an indication for a retained primitive character. To me it seems more plausible to assume that in *Lamontichthys* the '7th' ray was secondarily attained, perhaps while adapting to its – not specifically known – habitat, or maybe simply as some variation on the stereotyped 6 rays.

Lamontichthys was treated by Nijssen and the present author (1978), including 2 species: *L. filamentosus* and *L. stibaros*. *Lamontichthys filamentosus* has extremely long, filamentous extensions of the dorsal and pectoral fins; the outer (unbranched) caudal fin rays likewise are remarkably long, but this is no exception in this group of genera. *L. stibaros* is closely related to *L. filamentosus*, but lacks filamentous extensions of the pectoral and dorsal fins, whereas it differs from *L. filamentosus* in a number of other details. *Lamontichthys filamentosus* slightly reaches over 167 mm in standard length, *L. stibaros* 242 mm.

Peculiar for the genus is the lack of odontodes on the surface of the mediodorsal scutes posterior to the dorsal fin and on the surface of the medioventral scutes posterior to the anal fin, except for the presence of odontodes only along the posterior edge of each 'naked' scute. The lateral line is scarcely visible externally. Dorsum of the cleithrum is broad. Median predorsal scutes are curved in transverse view.

As offered under *Pterosturisoma* above, a comparison of that genus with Lamontichthys is given here. Pterosturisoma (in agreement with almost all Loricariidae) has odontodes all over its externally ossified parts. The lateral line has well-developed external (bifurcate) tubes. The median predorsal scutes have a horizontal flattening.

The following morphometric and meristic trends and differences may help to tell Lamontichthys (first-mentioned data) from Pterosturisoma: standard length up to 242 mm against 161 mm; predorsal length 3.2-3.8 in standard length against 3.1-3.2; pectoral fin spine length 1.2-4.0 in standard length against 1.1; thoracic length 1.0-1.2 in head length against 1.2-1.3; maximum orbital diameter 5.6-7.6 in head length against 11.1-12.8; interorbital width 2.8-3.6 in head length against 3.9-4.1; cleithral width 0.9-1.0 in head length against 1.1; width caudal peduncle 5.8-8.5 in head length against 5.1; 32-34 lateral body scutes against 35; up to 86 teeth in either (left or right) 'half' jaw against up to about 55 in each of the upper and up to about 47 in each of the lower jaw halves.

Secondary sexual dimorphism. - So far, this is known only in L. filamentosus (cf. Isbrücker & Nijssen, 1978b: 64, figs. 5 and 7 of males, figs. 1-4 of either females or specimens unrecognizable as males). Nuptial males gradually develop 'bristles' (large, protuberant odontodes) on part of the dorsum of the pectoral fin spine. The largest specimen available (sl 167.3 mm, USNM 167913) is a male with fully developed 'bristles' and the following notes are based on this specimen. The length from the ventroanterior base of the pectoral fin spine to the tip of the first branched ray is 37.3 mm. The anterior odontodes occur at 13.8 mm from the ventroanterior base. The entire denticulate area is 19.2 mm long, whereas the distal end of the spine is naked at a distance of 5.9 mm from the tip of the first branched ray. The bristled area is covered with a layer of thick, mucous tissue forming a rather long shaft enclosing the base of the odontodes. The long odontodes (about 3.3 mm long) look like translucent needles with the tip bending slightly towards the head. The tip of these odontodes is light yellowish. (This section taken from our 1978 description).

Sturisomatichthys Isbrücker & Nijssen, 1979

Sturisomatichthys is closely related to Sturisoma, from which it differs particularly in lacking a distinctly produced rostrum. The tip of the ossified snout margin, however, curves up in front of the upper lip, showing a similar degree of variability as found in some Rineloricaria spp.; e.g., Rineloricaria phoxocephala is in this character strongly reminiscent of Sturisomatichthys spp. This snout margin was measured as if it were a produced rostrum, present in Sturisoma, for comparison. In Sturisomatichthys it is contained 8.8-15.2 times in head length against the ventrorostral length of Sturisoma which is contained 2.1-7.3 times in head length. Usually, the produced snout of Sturisoma is much less than 7.3 times in head length; the specimen in which this ratio was found is a paralectotype of S. frenatum, 179.7 mm in standard length.

Sturisomatichthys consists of 4 species, occurring in N.W. South America, from the upper Amazon north up to Panama, and in the Rio Magdalena basin. Except for S. citurensis, I have examined these species, including the type-material. The standard lengths of the species examined are mentioned below.

Compared to Pterosturisoma and Lamontichthys together, Sturisomatichthys has a tendency towards a longer head, although the respective ratios show considerable overlap: head length is 4.3-5.8 in standard length in Sturisomatichthys against 5.0-6.1 in Pterosturisoma plus Lamontichthys. The dorsal fin spine and its first branched ray are shorter in Sturisomatichthys (3.8-4.3 and 3.9-5.2, respectively, in standard length against 1.3-3.5 and 2.6-3.9 in Pterosturisoma & Lamontichthys). The anal fin spine tends to be shorter in

Plate XXIII.

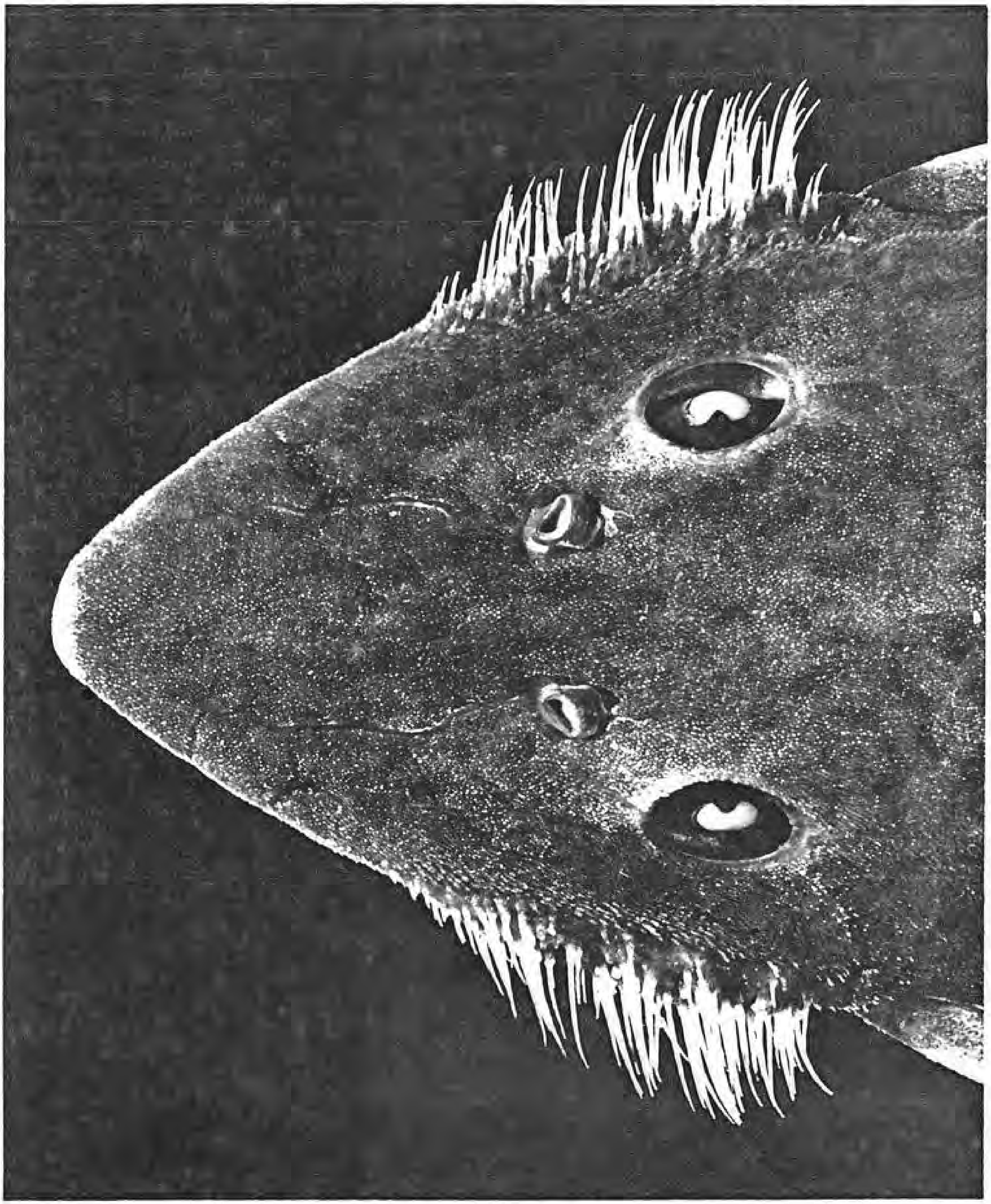


Fig. VI,36. - Sturisomatichthys tamanae (Regan, 1912), male in BMNH 1914. 5.18:74 (photo L. A. van der Laan, ITZ, Amsterdam).

Sturisomatichthys (4.6-5.5 in standard length against 4.0-5.0 in Pterosturisoma and Lamontichthys together). In Sturisomatichthys the pectoral fin spine is much shorter (4.7-5.5 in standard length, compared to 1.1-4.0 in the two other genera), just like the pelvic fin spine (5.8-6.3 in standard length against 4.7-5.4).

The thoracic length tends to be shorter in Sturisomatichthys than in Pterosturisoma and Lamontichthys combined: 1.2-1.6 in head length against 1.0-1.3; similar tendencies are true for the abdominal length (1.3-1.9 in head length against 1.1-1.3); cleithral width (1.1-1.5 in head length against 0.9-1.1); supracleithral width (1.3-1.8 in head length against 1.2-1.5); head width (1.1-1.5 in its own length against 1.0-1.2); head depth (2.0-2.5 in its own length against 1.8-2.0); body depth at dorsal fin origin (1.5-2.2 in head length against 1.3-1.6); body width at dorsal fin origin (1.2-1.8 in head length against 1.0-1.2); body width at anal fin origin (1.5-2.2 in head length against 1.2-1.4); and finally, width caudal peduncle (6.8-9.4 in head length against 5.1-8.5 in Pterosturisoma & Lamontichthys).

The caudal peduncle is distinctly narrower in Sturisomatichthys than in the other two genera: 13.9-18.2 in head length against 9.1-13.1. The number of coalescing lateral scutes is 14-16 in Sturisomatichthys, which falls within the range of variability in Lamontichthys (14-21, same as in Sturisoma), but is slightly less than in Pterosturisoma (17-18).

The abdominal scutelets of Sturisomatichthys may briefly be characterized as being perfectly intermediate in number (correlation with the size of these scutelets) between Pterosoma and Lamontichthys on the one hand, and Sturisoma on the other hand.

Compared to Sturisoma, Sturisomatichthys tends to have a longer head as well (see comparison to Pterosturisoma and Lamontichthys): 4.3-5.8 in standard length against 5.2-6.4 in

Plate XXIV.

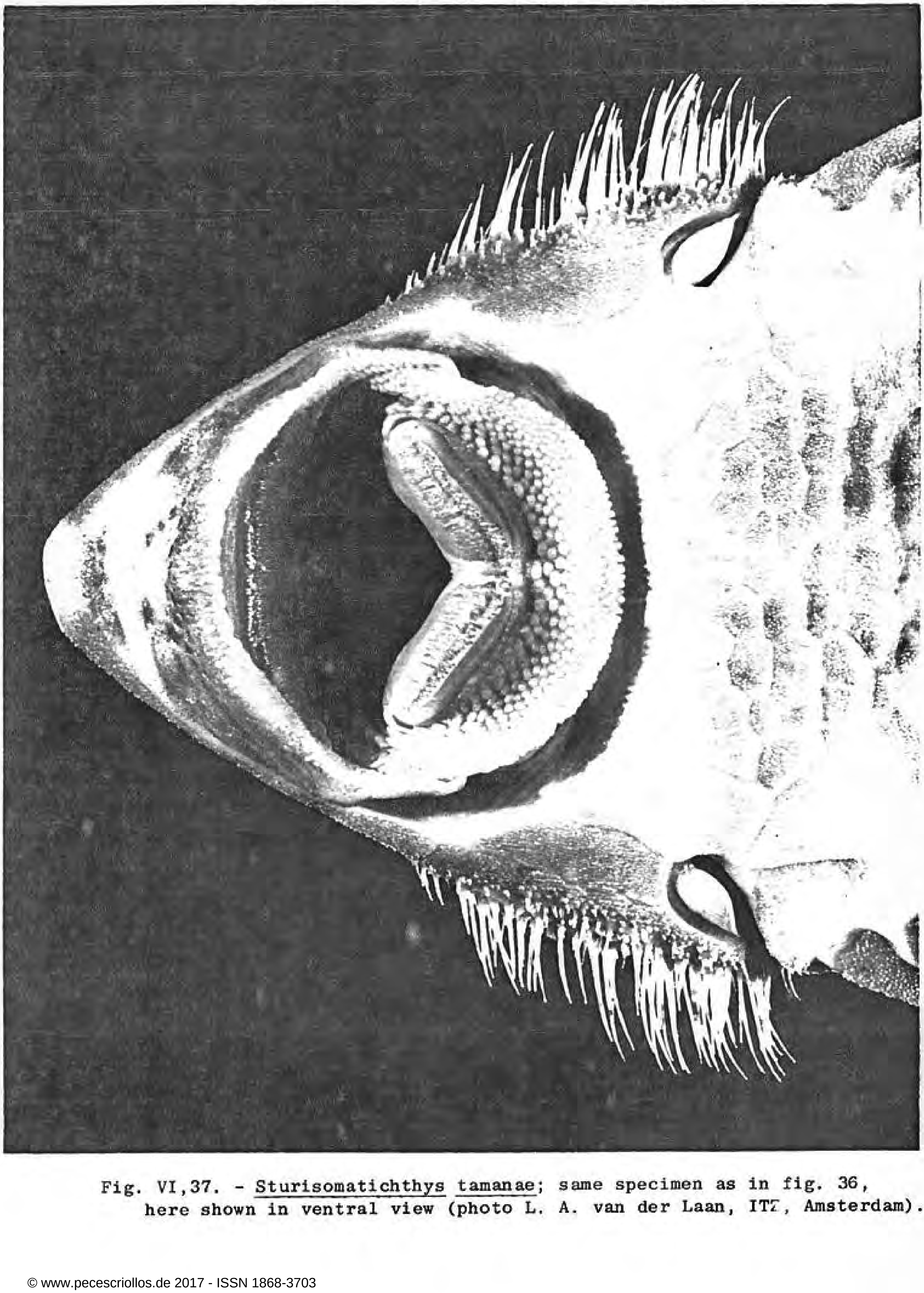


Fig. VI,37. - Sturisomatichthys tamanae; same specimen as in fig. 36, here shown in ventral view (photo L. A. van der Laan, ITZ, Amsterdam).

Sturisoma; the snout (excluding the ventrorostral length of *Sturisoma*, thus enabling a better comparison) tends to be longer in *Sturisomatichthys* (1.5-1.8 in head length) than in *Sturisoma* (1.7-2.2). Thoracic length is 1.2-1.6 in head length in *Sturisomatichthys*, 0.9-1.3 in *Sturisoma*.

Sturisomatichthys citurensis is known to me only from the descriptions by Meek & Hildebrand (1913: 82; 1916: 262-263), notes and an illustration by Eigenmann (1922: 96-97, pl. 16 fig. 3; in key on p. 94), and from a note by Hildebrand (1938: 243), neglecting the mere listing of this species in catalogues etc. It seems to occur in the Bayano and Tuira Rivers of the Pacific slope of Panama only. It reaches up to 250 mm (total length?) and is said to be rather closely related to *S. tamanae*. *S. citurensis* has 30 or 31 lateral body scutes, 15-16 coalescing scutes, and 5-8 rows of scutelets on the abdomen.

Sturisomatichthys leightoni (type-species) and *S. caquetae* reach a standard length of 112.6 mm (adult female, aquarium specimen, now in ZMA, leg. Dr W. Foersch; the lectotype is only 57 mm in standard length) and 91.5 mm, respectively. Both are more closely related to each other than to *S. tamanae*, of which I examined specimens up to 207 mm in standard length. *Sturisomatichthys caquetae* and *S. tamanae* have I,12,I caudal fin rays, except for a single specimen of the latter species, which has 11 branched caudal fin rays. *S. leightoni* has always I,11,I caudal fin rays, which is quite exceptional for a member of the tribe Harttiini.

Besides reaching a considerably larger standard length, *S. tamanae* differs from *S. leightoni* and *S. caquetae* in several morphometric and meristic data. These characters are given here for *S. tamanae* first, followed by those in comparison with *S. leightoni* and *S. caquetae* together. Ratios of morphometric characters expressed in standard length are: head length 5.5-5.8 against 4.3-4.6; predorsal length 3.3-3.6

against 3.0-3.1; postdorsal caudal peduncle length 1.5-1.6 against 1.7; and anal fin spine length 4.6-5.2 against 5.5.

Ratios of measurements expressed in head length show the following differences: snout length 1.5-1.6 against 1.7-1.8; thoracic length 1.2-1.3 against 1.6; abdominal length 1.3-1.4 against 1.6-1.9; maximum orbital diameter 5.7-6.3 against 6.9-7.4; cleithral width 1.1-1.2 against 1.3-1.5; supracleithral width 1.3-1.4 against 1.5-1.8; head width 1.1-1.2 against 1.4-1.5; head depth 2.0-2.2 against 2.5; body depth at dorsal fin origin 1.5-1.8 against 2.2; body width at dorsal fin origin 1.2-1.4 against 1.6-1.8; body width at anal fin origin 1.5-1.7 against 2.1-2.2; and depth caudal peduncle 13.9-14.7 against 16.5-18.2. Finally, Sturisomatichthys tamanae has 33-34 lateral body scutes, whereas there are 31 lateral body scutes in S. leightoni and S. caquetae.

Morphometric data obtained from specimens raised in tanks are omitted from the comparison above.

Secondary sexual dimorphism. - Meek & Hildebrand (1913: 82) noted in the original description of Sturisomatichthys citurensis: "...sides of head without bristles or with very short ones.", and in their (1916: 263) subsequent description of the same species stated: "...snout...margin granular, with short bristles on sides in male, ..."

A male of Sturisomatichthys leightoni protecting eggs was illustrated and mentioned by me (1979b: 113, figs. 18-20), and a male and presumably a female (the lectotype) of S. tamanae in an earlier publication (1979a: 113, figs. 5-7). The holotype of S. caquetae also is a male. In male specimens with well-developed equipment, an elongate patch of fixed (or 'immovable', if nobody tries hard), conspicuous long, almost straight odontodes are present in an erect position along the posterior half or so of the snout margin. The complete absence of similarly developing odontodes on the pectoral fin (like such are present in other genera of Harttiini) in Sturisomatichthys is worthy of mention.

Sturisoma Swainson, 1838

Sturisoma comprises 15 described species, inhabiting various areas within an altogether huge range of localities: the genus occurs in all but one of the faunistic regions (the exception being the E. Brazilian region) recognized in South America (see chapter IX, p. 3 and 7, figs. 1 and 14).

In addition to specimens without type-status, I have examined primary type-material of Sturisoma barbatum (type-species of Oxyloricaria), S. brevirostre (type-species of Parasturisoma), S. festivum, S. frenatum, S. guentheri, S. kneri, S. lyra, S. monopelte, S. nigrirostrum, S. panamense, S. robustum, and S. tenuirostre. I am looking for a specimen to become designated as the neotype for Sturisoma rostratum (type-species of the genus). The holotype of Sturisoma aureum could not be traced – it may be lost – but the species was adequately described and illustrated. After examination of the holotype of S. dariense a detailed comparison of all the described species can be made, as a basis for a revision of this interesting genus.

Sturisoma is distinguished from other genera of Harttiini especially by its – often much – produced rostrum (obviously a successful adaptation, within the tribe evolved to such an extent only in this genus). Sturisoma further differs in its well-developed abdominal cover, consisting of well-defined, large and relatively few scutelets. Moreover, most Sturisoma species possess more numerous lateral body scutes than the average Harttiine. Boeseman (1971: 11) records 31-37 scutes in longitudinal series, whereas I found 34-38, including in my count the small triangular scutelet on the caudal fin base. There is an unusual large range of variability in the number of coalescing lateral body scutes: 14-21.

The pattern of predorsal scutes is in Sturisoma more complex than in the other Harttiini (and most other Loricariinae). Therefore, 'the' number of these scutes can vary according to

Plate XXV.

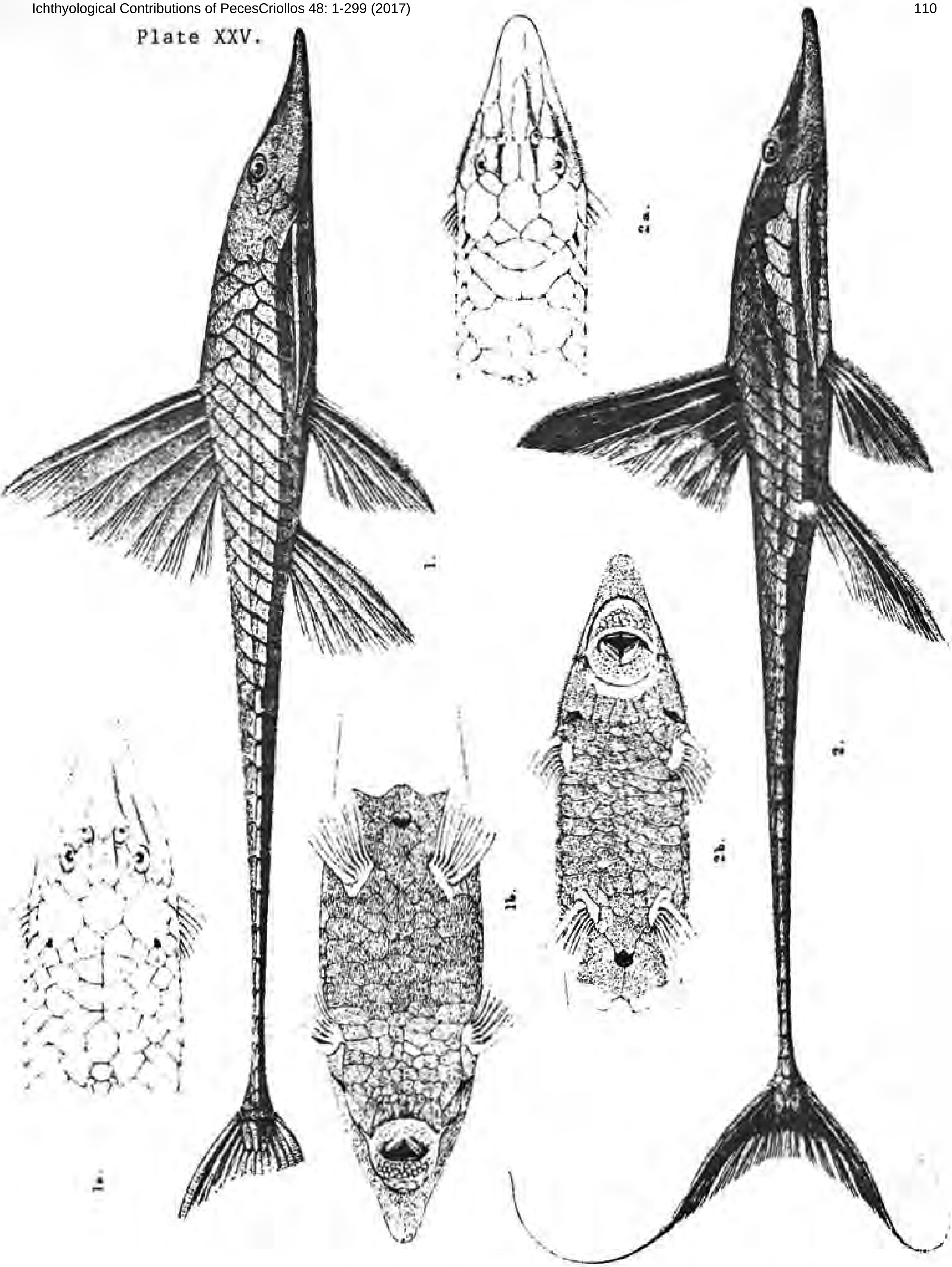


Fig. VI,38. - Sturisoma guentheri (Regan, 1904), holotype, and Sturisoma frenatum (Boulenger, 1902), one of the syntypes (figs. 1 and 2, resp., after Regan, pl. 18).

any definition. Boeseman (1971: 11) records 3-4 predorsal scutes.

Between the supraoccipital and the origin of dorsal fin spine, the following median series is usually present:

a) two relatively small transverse scutes meeting each other medianly and both meeting along the tip of the supraoccipital process, followed by

b) a single median scute (with a median suture) of medium size, with anterior and posterior convex edges, followed by

c) a transverse scute (with a median suture), slightly larger than the preceding one, anterior with a concave and posterior with a convex edge, followed by

d) a tightly fused complex of scutes covering a considerable area in front of the dorsal fin origin. The complex consists of a more or less hexagonal central scute (without suture). Anteriorly this scute is enclosed by a pair of rather small scutes bridging the space between the scute indicated under (c) and the central scute, which further posteriorly is enclosed by a double pair at either side, the posterior pair of which surrounds the relatively minute predorsal plate. This predorsal plate is movable and attached to the base of the dorsal fin spine, being part of the complex dorsal fin spine locking mechanism.

In Boeseman's (1971: 11) recent diagnosis of Sturisoma ranges of morphometric characters (compiled from published descriptions and illustrations) are given, which in some detail differ from the range I obtained for the same characters, as follows (mine added in parentheses): predorsal length 2.7-3.4 (3.1-3.7) in standard length; postdorsal length 1.6-1.9 (1.5-1.7) in standard length; postanal length 1.7-2.3 (1.6-2.0) in standard length; width of head 1.4-1.8 (1.1-1.6) in its own length.

A comparison of some morphometric differences between Sturisoma and Sturisomatichthys has already been made above (pp. 39 and 40-41)

Plate XXVI.

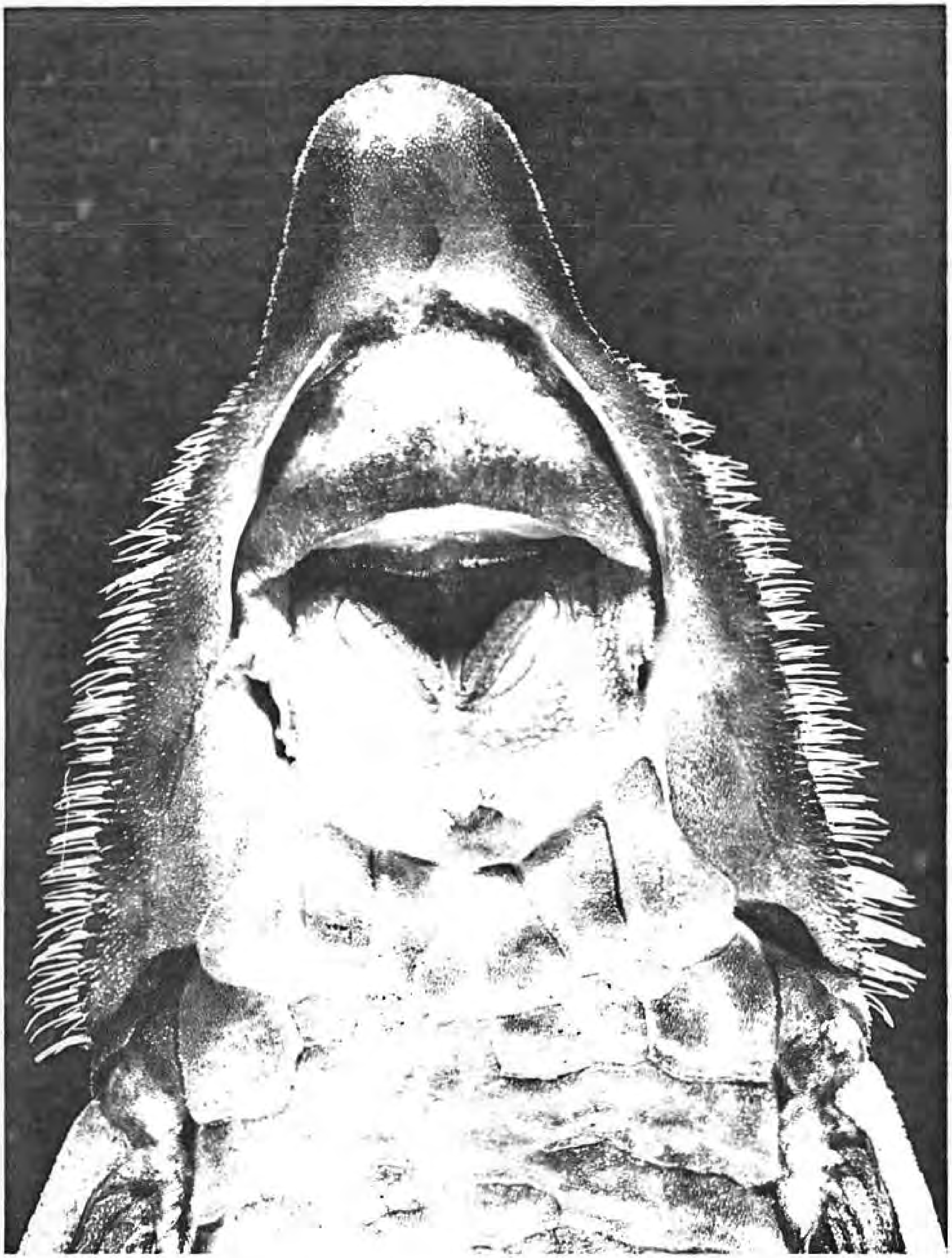


Fig. VI,39. - Sturisoma frenatum (Boulenger, 1902), lectotype, a male (photo L. A. van der Laan, ITZ, Amsterdam).

In some species of *Sturisoma*, the colour pattern is remarkably similar on the one hand to that of certain *Rineloricaria* species (e.g., *Rineloricaria lanceolata* and *R. heteroptera*; see my 1979b paper, figs. 7, 8, and 9, published also in my 1973a and Nijssen & mine paper of 1976a), on the other hand the colour pattern reminds equally of that in certain populations of *Loricaria simillima* and of an unidentified species of *Loricaria* known thus far only from some juvenile specimens (Isbrücker, unpublished, 1978: II,49-50, figs. 20 and 27). For example, all share a pale (bright yellowish or whitish) median stripe running in front of the eyes between rather broad dark brown stripes with an irregular inner margin on the head, together with conspicuous, rather broad, dark stripes running obliquely down anterior to the dorsal fin origin.

Some species of *Sturisoma* possess a conspicuous dark longitudinal stripe on the lateral body scutes, a detail of the colour pattern which closely agrees with that encountered in many *Farlowella* species.

Secondary sexual dimorphism. - Kner (1854a, pl. 5 figs. 1-3) illustrated the holotype of *Sturisoma barbatum*, a male showing moderately elongated odontodes on part of the pectoral fin spine, in addition to conspicuous odontodes along the posterior snout margin. In the actual holotype of *S. barbatum* the pectoral odontodes are somewhat shorter than indicated in the otherwise accurate illustrations; the more conspicuous odontodes may have fallen off. However, the location of the pectoral rugosity is reminiscent of the same as described and illustrated in our time for *Lamontichthys filamentosus*. I have not encountered other *Sturisoma* specimens with such odontodes on the pectoral fin, in spite of excessive development of odontodes on the snout in various males. The male of *S. barbatum* has fragile, long odontodes along the margin of the head, weakly curving in a posterior direction.

In *Sturisoma*, the male of only a relatively small number of species is known.

The male of *Sturisoma frenatum* has fragile, long, well-developed erect (only slightly curved) odontodes which in the opercular area are the longer, anteriorly gradually decreasing in length, extending to a point just beyond a transverse line from about the anterior margin of the rugose upper lip, somewhat beyond the beginning of the produced rostrum.

Eigenmann (1922: 94-95, pl. 16 figs. 4-6) illustrated 3 adults, as *Sturisoma panamense* (their specific identity needs confirmation). The specimen in his fig. 4 no doubt is a male, the one in fig. 5 is recorded to be a female, whereas the fish in his fig. 6 is not sexually determined by Eigenmann. This specimen could be a male at the onset of masculine odontode development, since a few of such odontodes are visible in the illustration at the right side of the posterior head margin. Maybe, development of the long odontodes commences in that area (at both sides). The odontode development in the available males of *Sturisoma* is usually reminiscent of that in *Sturisomatichthys*, although the affected area tends to extend somewhat more anterior in *Sturisoma*.

Reference may be made at this point to a recently discovered (still unnamed) genus of Farlowellini, showing characters seemingly rather intermediate between *Sturisoma* and the Farlowellini. As a matter of fact, Boeseman (1971) included the genus *Farlowella* in his subfamily Harttiinae; the new genus here referred to might support the idea of a more close relationship between Harttiini and Farlowellini even more than the genus *Farlowella* (see p.59).

METALORICARIINA

Metaloricaria Isbrücker, 1975

The subtribe Metaloricariina consists of a single genus with two species. It differs from the Harttiina in the shape and number of teeth, in the relative size of the jaws, and in the shape and structure of the lips.

Plate XXVII.

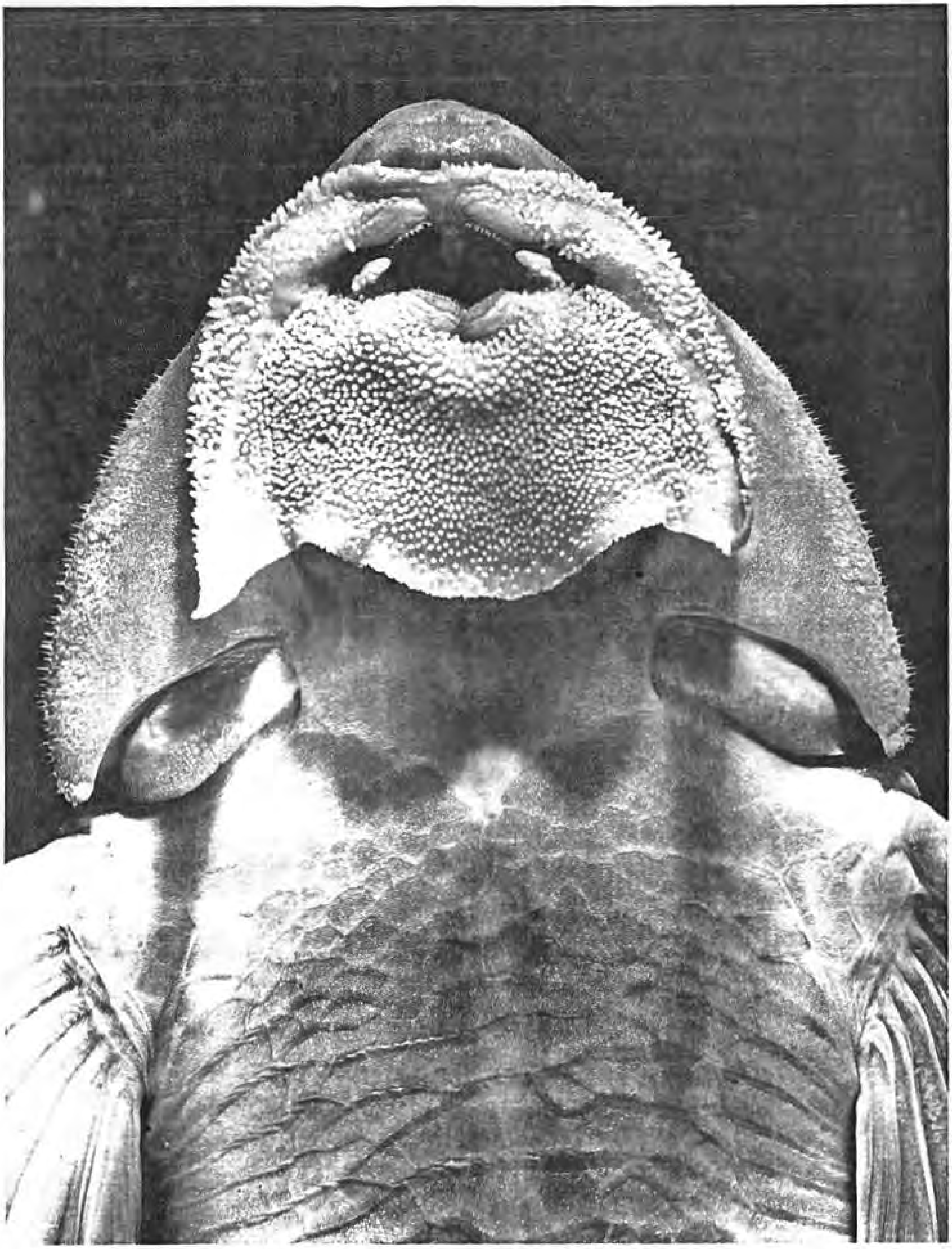


Fig. VI,40. - Metaloricaria paucidens Isbrücker, 1975, holotype (photo L. A. van der Laan, ITZ, Amsterdam).

Metaloricaria has relatively much shorter and clearly less slender teeth than any Harttiina species. Each tooth is considerably less bend near its tip in Metaloricaria than in other genera of Harttiini, which latter in addition possess on each tooth a strongly bilobate (bifurcate) crown, both lobes being about equally large. Metaloricaria also has bilobate crowns, but with a distinctly smaller outer lobe than inner lobe, the outer lobe originating much lower along the tooth than in Harttiina (Isbrücker, 1975a: 8, fig. 4).

Metaloricaria has a maximum of 27 teeth; the number of teeth increases with size, from 5 or 7 in specimens of about 80 mm in standard length to 26 or 27 in specimens of about 270 mm. Other genera of the tribe have at least 40 teeth in each jaw (e.g., Harttiella crassicauda, in an adult specimen of 41.1 mm in standard length; cf. Boeseman, 1971: 27, table 2), up to 120 or 125 in each jaw (e.g., Harttia surinamensis, in an adult specimen of 188 mm in standard length; cf. Boeseman, 1971: 31-32, table 4).

The premaxillae of Metaloricaria do not meet at the "symphysis" as invariably in Harttiina, there being a considerable large gap. The premaxilla and dentary of Metaloricaria are much shorter in transverse line than in other members of the Harttiini; jaws and dentition of the present genus are reminiscent of the structure usually suggestive of such genera as Rineloricaria & Dasyloricaria (Rineloricariina) and Pseudoloricaria & Limatulichthys (Pseudoloricariina) - all Loricariini – rather than of any genus of the Harttiini.

The papillose anterior and lateroventral side of the upper lip is conspicuous and broad as compared to the other genera of the tribe. The lower lip particularly tends to be long and broad (median length 3.1-5.2 times in head length against 4.0-13.4 in all other Harttiini), while the maxillary barbels are distinctly longer than in its relatives (2.0-3.1 in head length against 5.0-10.7 in the Harttiina). The lower lip posteriorly has the margin convex in the middle and concave at either side towards the maxillary barbel. Upper and lower lips together are more or less horse-shoe-shaped in outline (oval to roundish in Harttiina), a shape not found in any other mailed Loricariid. On the surface of the lip inside the buccal cavity, between the outer sides of the premaxilla and dentary, there is a large fleshy, papillose flap. The upper oral valve membrane is in the middle provided with a conspicuous membranaceous elongate extension, which in Metaloricaria is several times larger than in other Harttiini.

Secondary sexual dimorphism. - The holotype of Metaloricaria paucidens (as well as one of the paratypes, standard length 234.5 mm) is a mature male, 270 mm in standard length. Elongate odontodes originate from a layer of thick, mucous tissue confined to the approximately two-thirds of the posterior margin of the snout. The skin in this area is rougher than on other parts of the body and head. In the holotype (largest specimen known), these odontodes are up to about 1 mm long, very slender, straight and erect, with a curved, yellowish tip. No similar odontodes occur in the predorsal area, nor on the pectoral fin.

Boeseman (1976, pl. 8) records the holotype of Metaloricaria nijsseni to be a male as well, stating (1976: 173) that there is "...an area of more developed bristles on the cheeks and the upper surface of the pectoral spine in adult males."

Discussion. - Boeseman (1971) established the Harttiini (as a new subfamily, Harttiinae, splitted from the Loricariinae), including Harttiella, Harttia, Parasturisoma (with Lamontichthys as a junior synonym), Sturisoma (syn.: Oxyloricaria), and Farlowella, correctly (1971: 5 & 6) "...omitting Acestridium as a problematical genus, ..."

Harttiella was subsequently found to include one (out of two) species, presently assigned to the genus Ixinandria (at that time not yet established; it belongs to the Loricariinae sensu Boeseman, 1971 = tribe Loricariini in the present sense). Boeseman's Harttia included 'Oxyloricaria' fowleri, which is now included in the genus Cteniloricaria; perhaps Harttia surinamensis should also be assigned to this genus.

Parasturisoma sensu Boeseman (1971) is now split as follows: brevirostris is a Sturisoma, citurense, leightoni, and tamanae are in Sturisomatichthys, filamentissima and filamentosa in Lamontichthys, maculata and platystoma in Cteniloricaria, and finally, microps is in Pterosturisoma.

Farlowella was subsequently again allocated in the tribe Farlowellini, proposed by Fowler (1958) as a substitute name for Bleeker's (1862) tribal name Acestrini.

Subsequent to this very useful publication by Boeseman, Dr Nijssen and I saw a rich and nicely preserved, unidentified and quite new collection of freshwater fishes from French Guiana while visiting the Institute Royal des Sciences Naturelles de Belgique at Brussels. It housed a series of 14 specimens of a large species of Loricariinae, indefinitely reminiscent of 'some' Pseudoloricaria laeviuscula, and of 'some' larger Rineloricaria spp. such as R. latirostris or R. jaraguensis, and even of 'some' (now Dasyloricaria) filamentosa.

These latter forms all have a posterior orbital notch, 10 branched caudal fin rays, and distinctly different lip shapes and structures, whereas the then still unidentified fish has no orbital notch, 12 branched caudal fin rays, etc.; it certainly did not bear any close relationship to Pseudoloricaria, Rineloricaria and Dasyloricaria (which latter at that time was, however, not yet split off from Loricaria sensu lato) on the one hand, nor to Harttia and Parasturisoma sensu Boeseman, 1971 on the other hand, so bingo: Metaloricaria was erected for the fish we encountered in Brussels, representing a previously undescribed species.

In the original description it was very briefly stated that Metaloricaria is related to Harttia; a further study was still being carried out on their affinities at a larger scale.

Metaloricaria paucidens from French Guiana was compared to Harttia surinamensis and "Harttia" maculata, both being described recently from rich Surinam material by Boeseman (1971); the latter species was originally named Parasturisoma maculata.

Boeseman (1976: 168 and 170) subsequently stated: "In a previous paper (Boeseman, 1971), I omitted any record of several specimens, clearly of a Harttia-like aspect, feeling some doubt about their systematic allocation on account of the relatively limited numbers of teeth, especially in young examples. Since then, I have come to the conclusion that these specimens, which evidently represent a new species [Harttia nijsseni], should indeed be allocated to the genus Harttia on account of ..." (followed by 5 characters). Boeseman (1976: 170) also noted: "The smaller number of teeth in juveniles, not unexpected in this group, evidently is of little systematic or phylogenetic importance." and continued, after introducing Metaloricaria [and its 'not' distinguishing characters] that: "These few features, however, form a single functional unit with presumably a considerable adaptability and therefore probably without sufficient importance to warrant generic distinction from Harttia Steindachner."

So, Metaloricaria was synonymized with Harttia by Boeseman (1976), an action which I fail to understand, considering, apart from the characters displayed by this genus, (a) Boeseman's previous (1971) omission of this species (now Metaloricaria nijsseni) from his quite diverse subfamily Harttiinae, in spite of the specimens available at the time: Boeseman (1976: 170-171, list of material) had collected Metaloricaria nijsseni already on 28th December 1963; and (b) the evidently much closer relationship between two species which Boeseman previously (1971), very likely correctly preferred to place into two different genera: Harttia (surinamensis) and into Parasturisoma (maculata), although these two species are generically clearly less distinct from each other than both are from Metaloricaria.

It may be noticed in passing, that the first published record of a Metaloricaria is an unidentified photograph in a popular account of Surinam freshwater fishes by Nijssen (1970: 13) with the simple caption: "Zuigbek van harnasmeerval", Dutch,meaning "Sucking mouth of a mailed catfish". I completely overlooked this article and moreover was unaware of the possible occurrence of Metaloricaria in Surinam. Nijssen's entire collection of Surinam Loricariinae (except for 2 specimens of Loricaria cataphracta and 2 of Loricariichthys maculatus which were retained for my studies), including several Metaloricaria specimens, was on loan at Boeseman's disposal from 1970-1976. This material will be described in a forthcoming paper.

Metaloricaria might be regarded as a highly advanced genus which evolved more likely from an ancestor shared with the genera of the Harttia-group (see p. 35) rather than with those of the Sturisoma-group.

In addition to the already mentioned characters, the following tendencies in and distinctions of morphometric and meristic characters are listed here for comparison:

(1) Metaloricaria comprises larger species (up to 273 mm in standard length) than Harttia (S.E. Brazilian spp. up to slightly over 127 mm, the Surinam species up to slightly over 189 mm) and Cteniloricaria (up to 190 mm).

The following dimensions are expressed as ratios of standard length:

(2) the head length of Metaloricaria (4.4-5.1) is more similar to Cteniloricaria (4.0-5.4) than to Harttia surinamensis (4.1-4.5) or than to Harttia spp. from S.E. Brazil (3.6-4.0);

(3) predorsal length is 3.2-3.8 in Metaloricaria, 3.1-3.7 in Cteniloricaria, 2.9-3.1 in H. surinamensis, and 2.6-2.9 in S.E. Brazilian Harttia spp.;

(4) postdorsal length is relatively larger gradually in Metaloricaria (1.5-1.7) than in Cteniloricaria (1.6-1.8), in

H. surinamensis (1.8), or in *Harttia* spp. from S.E. Brazil (1.9-2.0);

(5) the same tendency is found in the postanal length: 1.8-2.0 in *Metaloricaria*, 1.9-2.2 in *Cteniloricaria*, 2.1-2.2 in *H. surinamensis*, while in the S.E. Brazilian *Harttia* spp. it is considerably shorter: 2.4-2.5. In these dimensions (2-5), *Metaloricaria* more closely approaches *Cteniloricaria* rather than *Harttia surinamensis*, contrary to Boeseman's (1976: 170 & 171-173) conclusion, who reached his conclusion without comparing his new species with his *Parasturisoma maculata*;

(6) in *Metaloricaria*, the dorsal fin 'spine' is contained 4.0-6.2 times in standard length, 2.8-4.7 in *Cteniloricaria*, 3.7-4.6 in *H. surinamensis*, 4.3-5.0 in *Harttia* spp. from S.E. Brazil;

(7) the first branched dorsal fin ray is 4.2-6.0 in *Metaloricaria*, 3.2-4.3 in *Cteniloricaria*, 4.1 in *H. surinamensis*, 4.6-5.4 in S.E. Brazilian spp. of *Harttia*;

(8) anal fin 'spine' length in *Metaloricaria* is 5.8-8.0, 6.2-7.4 in *Cteniloricaria*, 7.0-8.4 in *H. surinamensis*, and 6.4-9.0 in S.E. Brazilian *Harttia* spp.;

(9) the pectoral fin spine length is 4.6-6.4 in *Metaloricaria*, 3.0-4.9 in *Cteniloricaria*, 3.5-4.3 in *H. surinamensis*, and 3.7-4.8 in *Harttia* spp. from S.E. Brazil;

(10) similar tendencies are in the length of the pelvic 'spine', which is 5.3-8.5 in *Metaloricaria*, 4.3-5.8 in *Cteniloricaria*, 4.8-5.5 in *H. surinamensis*, and 4.4-5.9 in S.E. Brazilian spp. of *Harttia*;

Three dimensions expressed as ratios of the head length are:

(11) thoracic length 1.5-1.8 in *Metaloricaria*, 1.2-1.4 in *Cteniloricaria*, 1.3 in *H. surinamensis*, and 1.3-1.4 in *Harttia* spp. from S.E. Brazil;

(12) interorbital width 4.6-5.9 in *Metaloricaria*, 4.1-4.8 in *Cteniloricaria*, 4.1-4.7 in *H. surinamensis*, and 3.8-4.1 in the S.E. Brazilian spp. of *Harttia*; and

(13) head width 1.1-1.3 in *Metaloricaria* and in *Cteniloricaria*, 1.0-1.2 in *H. surinamensis*, and 1.0-1.1 in *Harttia* spp. from S.E. Brazil;

(14) *Metaloricaria* has 33-36 lateral body scutes, *Cteniloricaria* 31-32, *H. surinamensis* 30-31, *Harttia* spp. from S.E. Brazil 30-35;

(15) of these lateral body scutes, finally, 20-25 are coalescing in *Metaloricaria*, 19-22 in *Cteniloricaria*, 20-22 in *H. surinamensis*, and 20-24 in S.E. Brazilian spp. of *Harttia*.

FARLOWELLINI

The Farlowellini are distinguished from the other Loricariinae by having: a) the origin of the dorsal fin about opposite to the origin of the anal fin, b) almost always 5 branched dorsal fin rays, the last one split to its base.

Very rarely, there are 4 or 6 branched dorsal fin rays; usually there are 5 branched pelvic fin rays as in all other genera of Loricariinae, but often there are only 4 of such rays in *Farlowella* (as further specified under "Unnamed genus C" below). Farlowellini usually have 10-12 branched caudal fin rays, very rarely even 13 (in mutilated specimens less than 10 branched caudal fin rays are present), which is a most unusual variability for a genus of Loricariinae. The contrasting number of fin rays (especially of those in the dorsal, pelvic and caudal fins) is indicated clearly when shown in tabulated comparison with the other Loricariinae (table VI,i, p. 54). See also the spefications of frequency on pp. 63-64.

The pectoral and pelvic fins are relatively short, compared to Harttiini and Loricariini, whereas the dorsal and anal fins are in some species quite long; the branched rays have the (few) subsidiary branches quite distally situated.

All Farlowellini are extremely slender, elongate fishes, almost always with the snout considerably produced, and with the unbranched caudal fin rays with a very long, filamentous extension, easily breaking off in preserved material.

The orbital rim is round, not provided with a posterior

Table VI,i.- Review of the fin-ray counts in the Loricariinae.

	D		A	P_1		P_2		C			
	5	6	4	6	7	4	5	10	11	12	13
Loricariinae	x	x	x	x	x	x	x	x	x	x	x
Harttiini											
Harttiina											
Harttiella	.	x	x	x	.	.	x	.	.	x	.
Harttia	.	x	x	x	.	.	x	.	.	x	.
Cteniloricaria	.	x	x	x	.	.	x	.	.	x	.
Lamontichthys	.	x	x	.	x	.	x	.	.	x	.
Pterosturisoma	.	x	x	x	.	.	x	.	.	x	.
Sturisomatichthys	.	x	x	x	.	.	x	.	x	x	.
Sturisoma	.	x	x	x	.	.	x	.	.	x	.
Metaloricariina											
Metaloricaria	.	x	x	x	.	.	x	.	.	x	.
Farlowellini											
"*A. m.*"	x	.	x	x	.	.	x	.	x	.	.
Farlowella	x	.	x	x	.	x	x	x	x	x	(x)
Acestridiini											
Acestridium	.	x	x	x	.	.	x	x	.	(x)	.
Loricariini											
Rineloricariina											
Ixinandria	.	x	x	x	.	.	x	x	.	.	.
Rineloricaria	(x)	x	x	x	.	.	x	x	.	.	.
Dasyloricaria	.	x	x	x	.	.	x	x	.	.	.
Spatuloricaria	.	x	x	x	.	.	x	x	.	.	.
Ricolina											
Ricola	.	x	x	x	.	.	x	x	.	.	.
Loricariina											
Paraloricaria	.	x	x	x	.	.	x	x	.	.	.
Loricaria	.	x	x	x	.	.	x	x	.	.	.
Brochiloricaria	.	x	x	x	.	.	x	x	.	.	.
Crossoloricaria	.	x	x	x	.	.	x	x	.	.	.
Pseudohemiodon	.	x	x	x	.	.	x	x	.	.	.
Rhadinoloricaria	.	x	x	x	.	.	x	x	.	.	.
Planiloricariina											
Planiloricaria	.	x	x	x	.	.	x	x	.	.	.
Reganellina											
Reganella	.	x	x	x	.	.	x	x	.	.	.
Pseudoloricariina											
Limatulichthys	.	x	x	x	.	.	x	x	.	.	.
Pseudoloricaria	.	x	x	x	.	.	x	x	.	.	.
Loricariichthyina											
Loricariichthys	.	x	x	x	.	.	x	x	.	.	.
Hemiodontichthyina											
Hemiodontichthys	.	x	x	x	.	.	x	x	.	.	.

"(x)" means that the count incidentally occurs.

notch.

The outer surface of the upper lip is provided with minute dermal ossifications, covered with minute odontodes.

The buccal cavity is very similar to that described above (p. 25) of the Harttiini.

Apart from the usually long snout, the Farlowellini are distinguished from most other Loricariidae in having the external lateral side of the soft mouth parts to a very large extent free from the inner wall of the ossified mouth.

Farlowellini in addition differ from both Harttiini and Loricariini greatly by their increased number (7-10 against 4 or less, see under Sturisoma, p. 43) of predorsal scutes, each being conspicuous, rather squarish and arranged into a longitudinal mediodorsal series.

The abdomen is completely covered, either only by the prominent thoracic scutes, which may meet in the middle of the belly, or are separated by hardly more than a single longitudinal row of rather small scutelets. The abdominal cover extends anteriorly as gradually smaller scutelets, reaching to about the posterior margin of the lower lip.

Secondary sexual dimorphism in Farlowella is manifest in mature males (as far as they are known), which develop elongate odontodes along the snout margin in the short-snouted species, or on and along the sides mainly of the produced part of the snout in the longer-snouted species.

In many characters, the Farlowellini are most reminiscent of the Acestridiini (the two tribes are further compared under the latter, p. 67), no doubt because of several convergencies in their respective evolution. The Farlowellini are in various characters also to a great extent similar to the genus Sturisoma of the Harttiini. The differences between these two latter, however, in my opinion are too great to visualize the Farlowellini simply as a direct continuation of Sturisoma or any other genus of Harttiini, the similarities perhaps express-a convergent development rather than a close affinity. It is interesting to note that the area of distribution of *Sturisoma* agrees with the same of the Farlowellini.

Farlowella Eigenmann & Eigenmann, 1889

Farlowella contains (except for the genus *Rineloricaria* of the Loricariini) the largest number of described species of the subfamily Loricariinae: 37 species (including several described originally as subspecies), most of which appear to be perfectly valid in spite of the often poorly defined (and definable) discriminating characters.

Farlowella occurs in a very large area in South America, being represented by various Amazonian as well as by numerous circum-Amazonian species.

The largest specimen of *Farlowella* I have seen has a standard length of 222 mm. I have examined numerous specimens, including type-material of *Farlowella acus*, *F. amazona*, *F. carinata*, *F. curtirostra*, *F. gladiolus*, *F. gladius*, *F. gracilis*, *F. henriquei*, *F. knerii*, *F. nattereri*, *F. oxyrryncha*, *F. parvicarinata*, *F. pseudogladiola*, *F. reticulata*, *F. rugosa*, *F. schreitmuelleri*, *F. scolopacina*, and *F. smithi*: a revision is in preparation.

Within the tribe, *Farlowella* is distinguished by its quite low number of teeth (about 20 in each jaw section), by its less numerous coalescing scutes (10-20), and by its narrower lower lip (6.8-11.2 times in head length without ventrorostral length). Further comparative morphometric and meristic data of *Farlowella* are given below, together with those of *Sturisoma* and of "Unnamed genus C."

A conspicuous feature of *Farlowella* is its sometimes extremely long rostrum: it may be up to 0.6 times in the head length, which is defined as the total head length minus ventrorostral length (see below).

The scutes of the different *Farlowella* species show

Plate XXVIII.

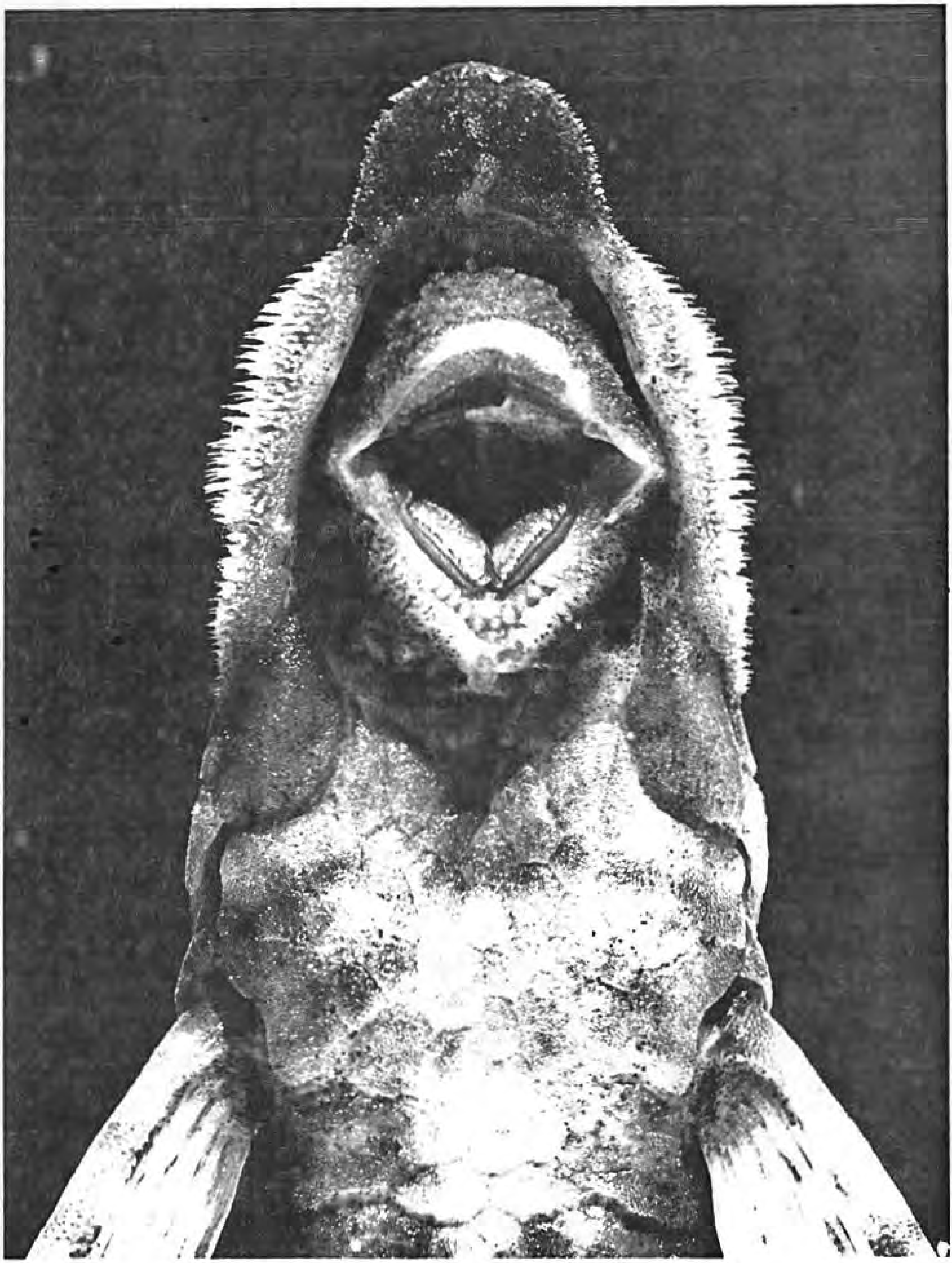


Fig. VI,41. - Farlowella cf. curtirostra Myers, 1942, male, aquarium specimen imported from Colombia (photo L. A. van der Laan, ITZ, Amsterdam).

Plate XXIX.

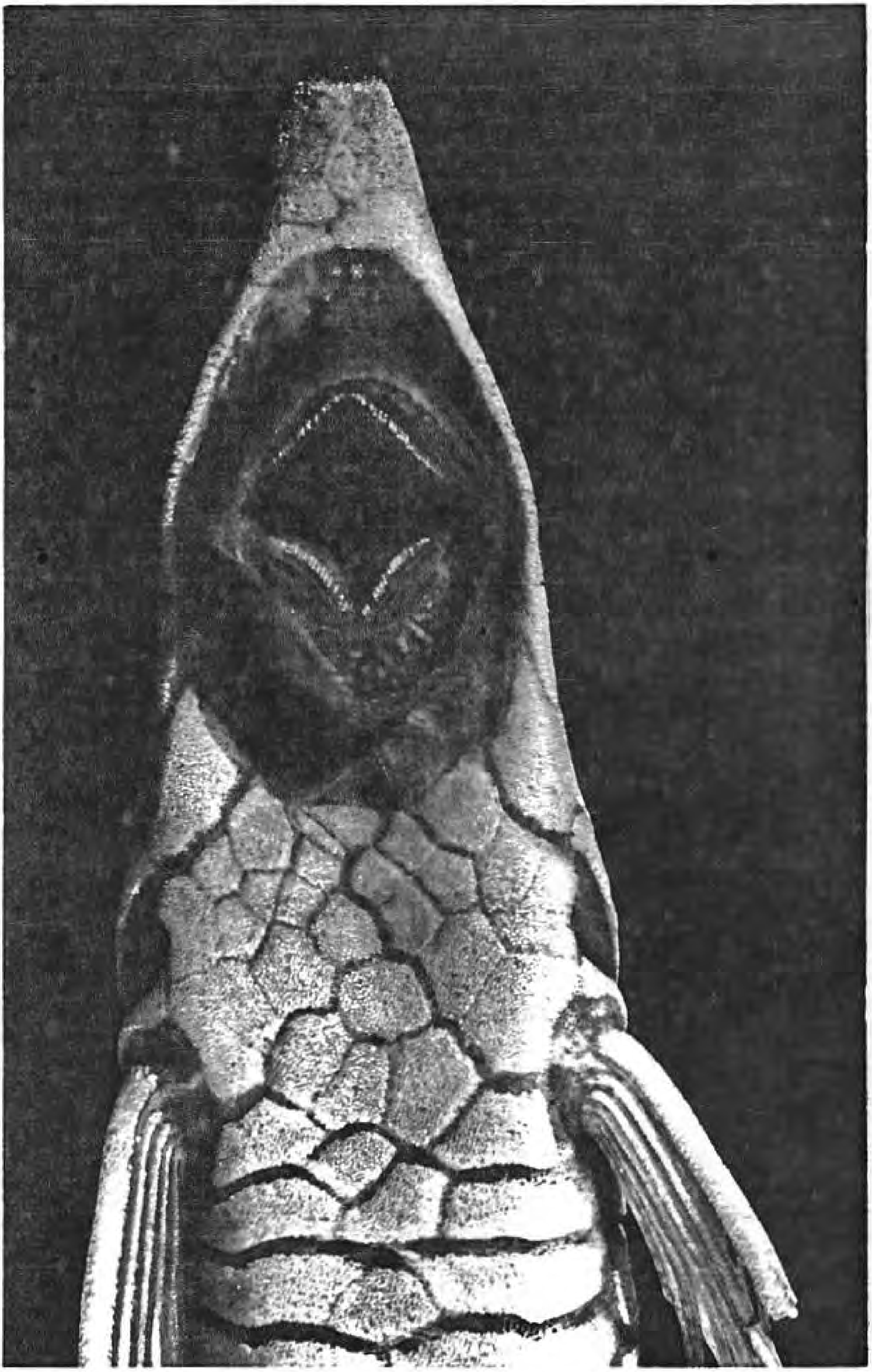


Fig. VI,42. - Farlowella curtirostra Myers, 1942, holotype (photo L. A. van der Laan, ITZ, Amsterdam).

Plate XXX.

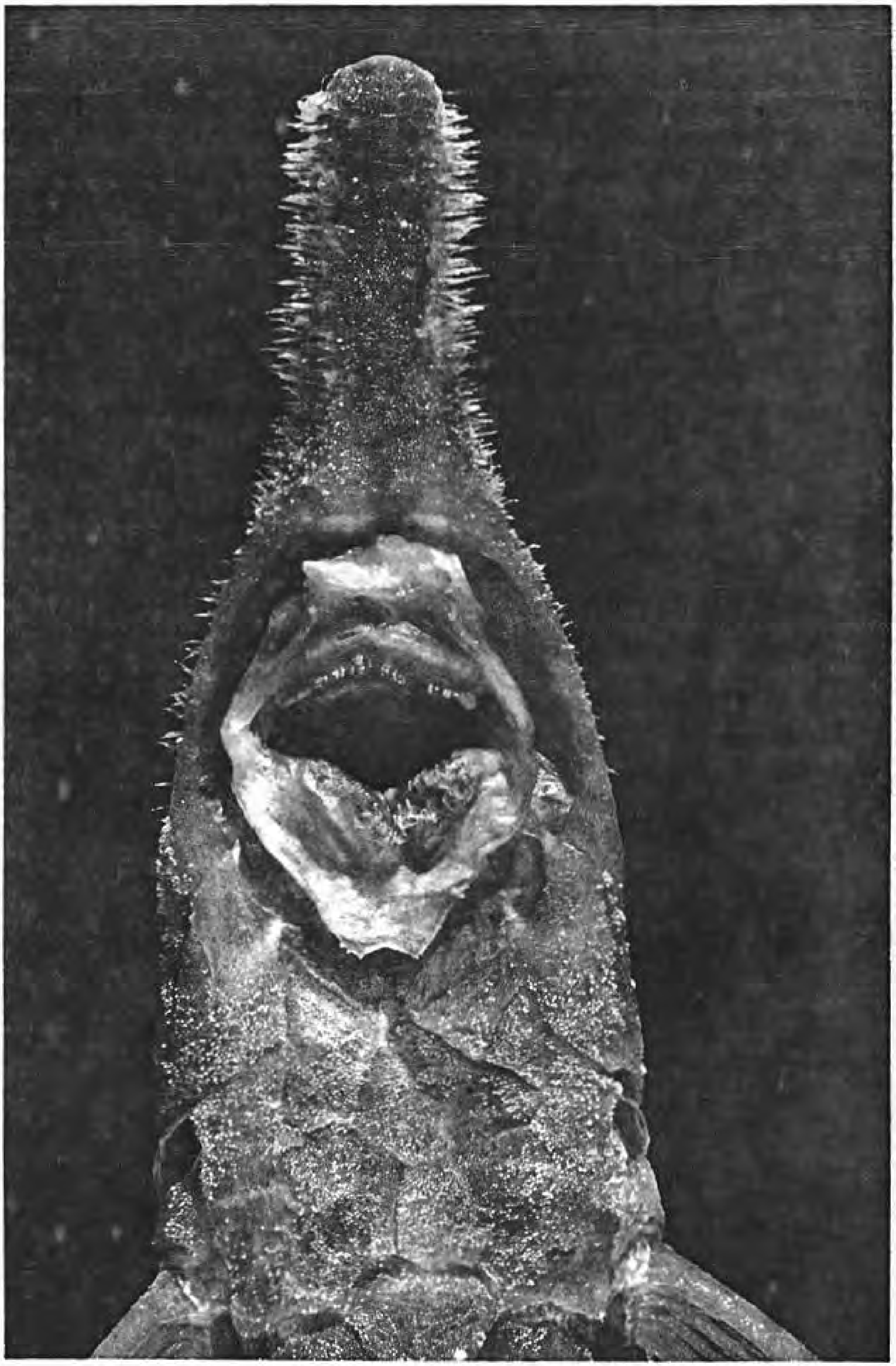


Fig. VI,43. - Farlowella acus (Kner, 1854), holotype, male (photo L. A. van der Laan, ITZ, Amsterdam).

Plate XXXI.

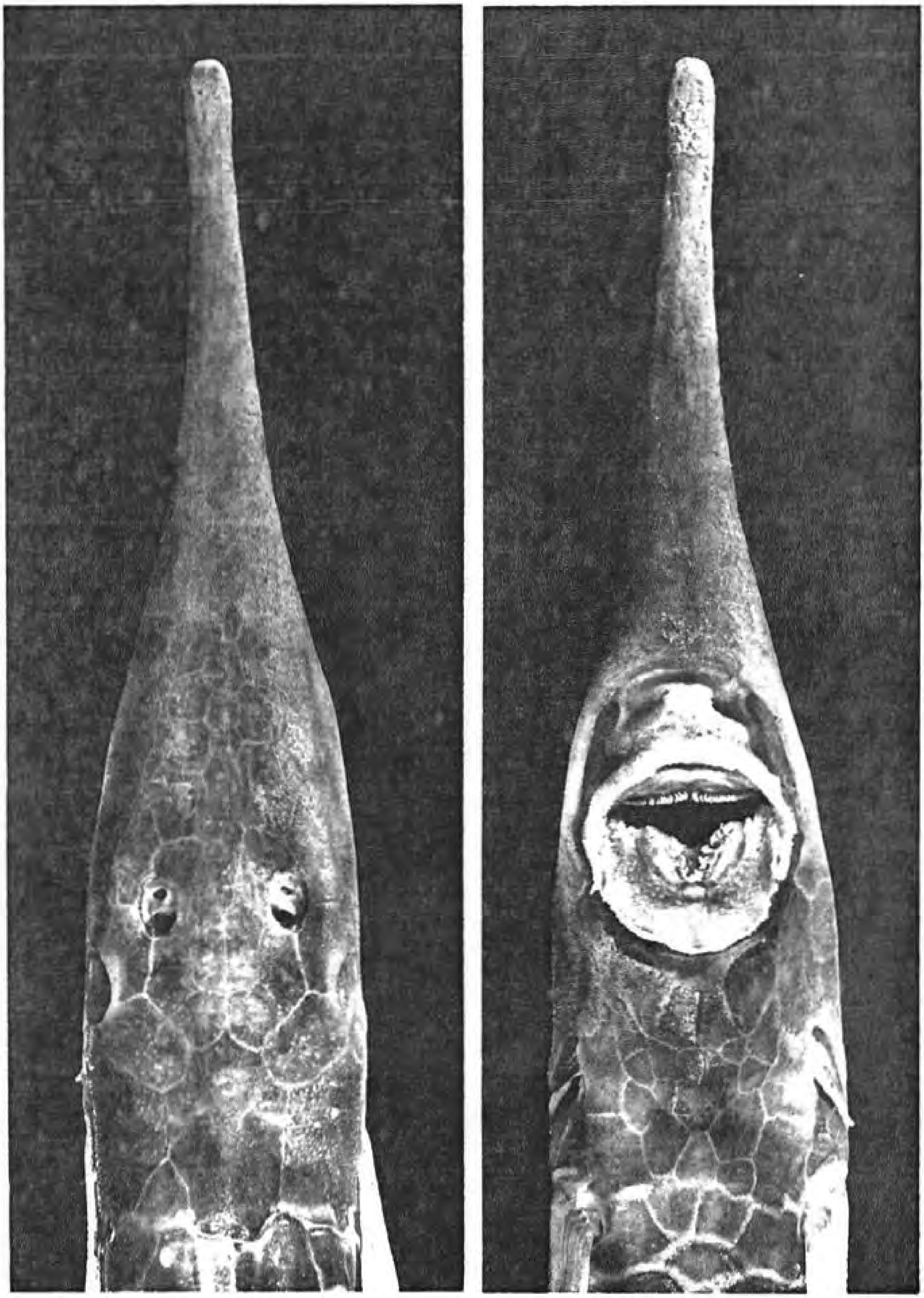


Fig. VI,44. - Farlowella oxyrrhyncha (Kner, 1854), holotype, head in dorsal and ventral view (photo L. A. van der Laan, ITZ, Amsterdam).

Plate XXXII.

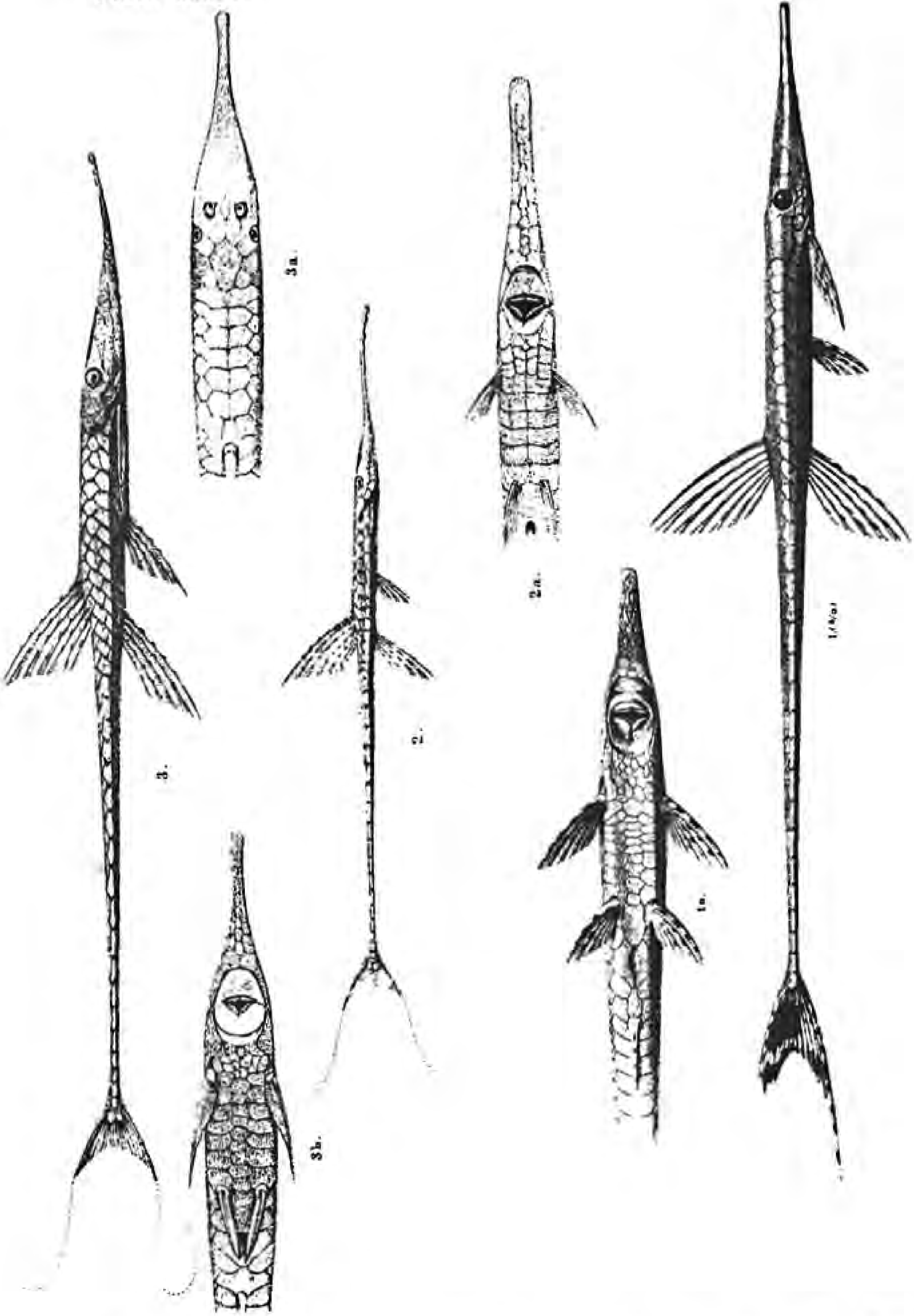


Fig. VI,45. - *Farlowella knerii* (Steindachner, 1883), syntype (1, after Steindachner, 1883b, pl. 7 figs. 1, 1a), *F. gladiolus* (Günther, 1864), syntype (2, after Regan, 1904, pl. 20 fig. 2), and *F. gracilis* Regan, 1904, holotype (after Regan, 1904, pl. 20 fig. 3).

different degrees of rugosity, caused by the presence of weaker or stronger (secondary sexually dimorph?) odontodes and by an either almost entirely smooth surface against the presence of granular, irregularly uneven ossification. This variation is especially present on the cover of the head and snout: in some species it is remarkably smooth in one extreme, whereas in another extreme there are species which clearly show conspicuous, relatively large and well-defined scutelets.

There is also great variation in the different shapes of head and snout. In *Farlowella curtirostra*, the produced snout is short and resembles that of a short-snouted *Sturisoma*. We have aquarium specimens, imported from Colombia (Rio Meta?), which may be *F. curtirostra* or a related species, which have the snout not more produced than a *Sturisomatichthys* or than some *Rineloricaria* spp. (that is, hardly or not at all produced), and all these have a rather broad, roundish snout tip in dorsal or ventral view.

Farlowella scolopacina and *F. acus* have an already much more elongate, produced snout tip with the sides concave and with a roundish tip. *Farlowella knerii* has the snout relatively still longer, but rather depressed dorsally and straight in dorsal and ventral view, anteriorly a little tapering gradually, and with a rather blunt tip. *Farlowella gladiolus* and *F. gracilis* are a step further beyond *F. knerii*, having 'fragile', still longer and narrower ventrorostral extensions. *Farlowella acestrichthys* is another species with an extremely long and quite acute snout, which towards its tip gently curves up; a similarly elongate snout is characteristic for *F. oxyrryncha*, which likewise may have the snout tip relatively acute. The ultimate snout length on record is that of *Farlowella carinata*, resembling the snout of *F. knerii* in general shape, but being much longer and more rugose. A specimen of *F. carinata* with a standard length of 221.4 mm looks like a real living Pinocchio, being provided with a ventrorostral length of 44 mm.

Farlowella species usually have not yet been available from sufficiently large samples which clearly represent one and the same species. In the few cases where such good samples were available, however, the variability in various dimensions is frequently considerable, rendering a solid evaluation of the many described species very difficult for the time being. Several forms may prove to be endemic. I have an impression that Farlowella is presently still rapidly evolving and believe to have seen both extreme forms as well as numerous nicely intermediate samples.

As already noted under Sturisoma (p. 45), many species of Farlowella have a dark brown longitudinal stripe along the lateral body scutes, similar to the stripe found in a number of Sturisoma spp. It is possible that such a colour pattern is a useful adaptation to their habitat, but in addition it could be indicative of (remote...?) relationships.

Some of the Farlowella spp. have the tip of the snout naked, in others it is covered with the same granular dermal ossification also present all over the snout and head.

Secondary sexual dimorphism. - Short-snouted species have in the mature male a horizontal, elongate patch of slender, fragile and rather long odontodes covering partly the margin of head and snout, at the height of the posterior margin of the lower lip, anteriorly running almost to the medioanterior ventral rim of the ossified mouth, where the ventrorostral extension begins. These odontodes are relatively short anteriorly and posteriorly, the middle being the longer.

Mature males of long-snouted species have such odontodes particularly concentrated on the produced rostrum, the most conspicuous of these being present along the sides, although a few of them may occur on the dorsum of the produced rostrum as well as along the margin of the head. Some long-snouted species have males with an apparently more rugose dermal cover on head and snout than present in females.

To enable direct comparison and avoiding a mere repeat of data, Farlowella is compared below with Sturisoma (Harttiini) and with the following genus:

Unnamed genus C, Isbrücker, Britski, Nijssen & Ortega, MS.

This genus was most recently discovered and recognized, almost simultaneously, both at institutions in São Paulo and in Amsterdam: Dr H. A. Britski of São Paulo & Dr H. Ortega of Pucallpa, Dr H. Nijssen and I will publish a joint paper with a description, illustrations and formal naming of this genus, which is represented by a single, likewise unnamed species. Herein, it may be reffered to as "A.m.," being the initials of the name we have in mind.

The fish occurs near the eastern Andes of Peru, department of Loreto, district Coronel Portillo, Río Huacamayo, a tributary of Río Aguaytia near Aguaytia, 08°04' S, 74°39' W. The first 4 specimens now in Amsterdam were collected by Dr P. de Rham & Dr H.-J. Franke; 22 additional specimens (coll. Ortega) are now on loan from São Paulo in Amsterdam for examination.

A.m. is particularly interesting, for in general appearance it is remarkably reminiscent of some Sturisoma species. Because of the position of the dorsal versus anal fin origin, the rather short fins in comparison with most Sturisoma spp., its number of branched dorsal and caudal fin rays, and because of its single row of abdominal scutelets between the two series of well-developed thoracic scutes, however, it must be included in the Farlowellini, it being most closely related to Farlowella. In several respects, A.m. partly bridges the gap between particularly Sturisoma on the one hand and Farlowella (and therefore, the tribe as well) on the other hand, whereas it possesses some features shared with neither Farlowella nor Sturisoma. As stated already (pp. 55-56), I believe that the Farlowellini are not only distantly related to the Harttiini (*Sturisoma*-group of genera). Admittedly, the present genus – although not really intermediate – is superficially more similar to *Sturisoma* than to any other genus, seemingly supporting Boeseman's (1971) view on the relationships between *Sturisoma* and *Farlowella*. The still existing distinctions between *Harttiella* through *Sturisoma* on the one hand and *Farlowella* plus *A.m.* on the other, are in my opinion clearly sufficient to retain both the Harttiini and the Farlowellini.

After measuring specimens with a produced rostrum, in order to obtain better results for comparison, the length of the ventrorostral extension is subtracted from those measurements otherwise influenced by this length: standard length, predorsal length, preventral length, and snout length. In the comparison between *Sturisoma*, *A.m.*, and *Farlowella* below, I used data from all available specimens; of *A.m.* 4 specimens were examined, of *Farlowella* 130. For practical simplicity, the methods to compare species of Harttiini used to differ in various details from the methods to compare Farlowellini, although of course, each stated character was measured and counted in the same way. However, in the course of the examination, various measurements were found to be either not useful or superfluous and abandoned. Initially, a full set of measurements of 54 specimens of *Farlowella* for example, were taken and subsequently judged to be ignorable in quite some detail.

In the following comparison, data of the genus *Sturisoma* are mentioned first, followed by the same of *A.m.*, and finally by those of *Farlowella*:

(1) standard length (ventrorostral length not subtracted) is up to 260 mm in *Sturisoma*, up to 154 mm in *A.m.*, and up to 222 mm in *Farlowella*.

The first set of data are expressed as ratios of the standard length without ventrorostral length:

(2) head length without ventrorostral length is 5.2-6.4 in

Sturisoma, 4.4-5.4 in *A.m.*, and 5.0-7.0 in *Farlowella*;

(3) predorsal length without ventrorostral length is 3.1-3.7 in *Sturisoma*, 2.4 in *A.m.*, and 2.3-3.1 in *Farlowella*;

(4) postdorsal length is 1.5-1.7 in *Sturisoma*, 1.9 in *A.m.*, and 1.6-1.9 in *Farlowella*;

(5) postanal length is 1.6-2.0 in *Sturisoma*, 1.9-2.0 in *A.m.*, and 1.7-1.9 in *Farlowella*;

(6) preventral length, measured from the anterior margin around the anal opening, without ventrorostral length was not measured in *Sturisoma*, is 2.8-3.1 in *A.m.*, and 2.8-3.7 in *Farlowella*;

(7) the area between the posterior point of the supraoccipital process and the origin of the dorsal fin was not measured in *Sturisoma*, is 4.4-5.3 in *A.m.*, and 4.2-7.5 in *Farlowella*;

(8) dorsal fin spine length is 3.4-5.1 in *Sturisoma*, 6.1-6.9 in *A.m.*, and 4.9-8.6 in *Farlowella*;

(9) length of the first branched dorsal fin ray is 3.5-5.2 in *Sturisoma*, 7.4 (N=1) in *A.m.*, and 5.4-8.6 in *Farlowella*;

(10) anal fin spine length is 3.8-6.2 in *Sturisoma*, 6.4-7.2 in *A.m.*, and 5.1-9.0 in *Farlowella*;

(11) pectoral fin spine length is 2.8-7.0 in *Sturisoma*, 6.6-6.9 in *A.m.*, and 6.0-12.8 in *Farlowella*;

(12) pelvic fin spine length is 4.5-7.4 in *Sturisoma*, 8.5-10.7 in *A.m.*, and 8.7-20.0 in *Farlowella*;

(13) length of the upper unbranched caudal fin ray (inclusive of the filament, if – still – present) is 1.6-3.5 in *Sturisoma*, 4.3-6.1 in *A.m.*, and 2.3-10.7 in Farlowella;

(14) the length of the lower unbranched caudal fin ray is 2.0-3.6 in *Sturisoma*, 6.2-7.9 in *A.m.*, and 2.1-10.1 in *Farlowella*.

Next, data are expressed as ratios of the head length minus ventrorostral length:

(15) snout length without ventrorostral length is 1.7-2.2 in *Sturisoma*, 1.7-1.8 in *A.m.*, and in *Farlowella* as in *Sturi-*

soma;

(16) width of the snout tip was not measured in Sturisoma, is 6.4-8.4 in A.m., and 4.8-15.6 in Farlowella;

(17) postorbital part of the head, measured to the tip of the supraoccipital process was not measured in Sturisoma, is 2.5-2.8 in A.m., and 2.1-2.7 in Farlowella;

(18) ventrorostral length is 2.1-7.3 in Sturisoma, 4.1-5.4 in A.m., and 0.6-14.9 (this latter figure means actually absent, viz., in some Farlowella curtirostra) in Farlowella;

(19) median length of the lower lip is 5.7-13.4 in Sturisoma, 4.4-5.2 in A.m., 6.8-11.2 in Farlowella;

(20) thoracic length is 0.9-1.3 in Sturisoma, 1.4-1.6 in A.m., and 1.0-1.5 in Farlowella;

(21) abdominal length is 1.0-1.7 in Sturisoma, 1.1-1.6 in A.m., and 1.1-1.5 in Farlowella;

(22) maximum orbital diameter is 4.7-7.0 in Sturisoma, 5.8-6.2 in A.m., and 6.0-10.3 in Farlowella;

(23) interorbital width is 2.3-2.7 in Sturisoma, 2.7-3.1 in A.m., and 2.5-4.1 in Farlowella;

(24) cleithral width is 1.1-1.5 in Sturisoma, 1.4-1.7 in A.m., and 1.6-2.8 in Farlowella;

(25) supracleithral width is 1.4-1.9 in Sturisoma, 1.5-1.9 in A.m., and 1.8-2.8 in Farlowella;

(26) head width is 1.1-1.6 in Sturisoma, 1.4-1.6 in A.m., and 1.6-2.7 in Farlowella;

(27) head depth is 1.8-2.7 in Sturisoma, 2.3-3.2 in A.m., and 2.4-4.3 in Farlowella;

(28) body depth at dorsal fin origin is 1.2-2.3 in Sturisoma, 2.1-3.0 in A.m., and 2.2-4.0 in Farlowella;

(29) body width at dorsal fin origin is 1.1-1.7 in Sturisoma, 1.7-2.5 in A.m., and 1.9-4.2 in Farlowella;

(30) body width at anal fin origin is 1.3-2.0 in Sturisoma, 1.7-2.6 in A.m., and 1.9-3.7 in Farlowella;

(31) depth of the caudal peduncle is 9.2-15.4 in Sturisoma, 11.7-13.4 in A.m., and 10.0-23.5 in Farlowella;

(32) width of the caudal peduncle is 4.5-8.6 in Sturisoma,

6.6-8.9 in *A.m.*, and 6.6-13.5 in *Farlowella*;

(33) length of the maxillary (= rictal) barbel is 4.4-10.7 in *Sturisoma*, 6.6-8.1 in *A.m.*, not measured in *Farlowella*, in which it slightly or not extends the lips;

The ranges of meristic characters are:

(34) lateral body scutes 34-38 in *Sturisoma*, 35-36 in *A.m.*, and 33-38 in *Farlowella*;

(35) coalescing lateral body scutes 14-21 in *Sturisoma*, 23-25 in *A.m.*, and 10-20 in *Farlowella*;

(36) thoracic scutes 6-9 in *Sturisoma*, 6 in *A.m.*, and 5-8 in *Farlowella*;

(37) predorsal scutes 4 or less in *Sturisoma* (but see description on p. 43), 9 in *A.m.*, and 7-10 in *Farlowella*; and finally,

(38) maximum number of teeth in each jaw section about 50 in *Sturisoma*, around 100 in *A.m.*, and about 20 in *Farlowella*.

The number of fin rays of all Loricariinae are shown on p. 54 (table VI,i). For *Farlowella* the following details, obtained from 129 specimens, are:

Three specimens have 6, one has 4 branched dorsal fin rays, the last one split to its base;

a single specimen was found with 3 branched anal fin rays, the last one split to its base;

six specimens have 5 branched pectoral fin rays on one side only and 6 on the other side, whereas one specimen has 5 branched pectoral fin rays on both sides;

four specimens have 4 branched pelvic fin rays on one side only, forty-one have the same number on both sides, all other specimens have 5 branched pelvic fin rays on both sides;

five specimens with a mutilated caudal fin were encountered, one with 4, two with 7, one with 8, and 1 specimen with 9 branched rays, while fifty-three specimens have 10 branched caudal fin rays, sixty-two have 11, seven have 12, and finally, two of our *Farlowella* have the unusual number of 13 of such rays.

As shown in table VI,i (p. 54), the number of (caudal) fin rays in the tribes Harttiini versus Loricariini are a reliable character to distinguish between these tribes, whereas *Lamontichthys* at once can be recognized by its high number of pectoral fin rays. As far as *Farlowella* is concerned, I am not even convinced as yet that the number of fin rays within the various species is invariable, thus may be not useful to distinguish between species.

There are 3 characters, listed above, which *A.m.* set clearly apart from both *Sturisoma* and *Farlowella*: the distinctly longer lower lip (character no. 19), the more numerous coalescing scutes (character no. 35), and the supernumerous teeth (character no. 38). It should be added here, that the range of standard lengths is not taken into account (smaller specimens of each genus are relatively less distinct from each other), but of *Sturisoma* the smallest specimen available has a standard length of 90.9 mm, the smallest *A.m.* at hand is 57.4 mm, and the smallest *Farlowella* is 38.1 mm in standard length.

The mouth of *A.m.* is very broad, the jaws being long in a transverse line, and the entire mouth agrees very much with the mouth of a *Chaetostoma*. This latter genus is known to be well-adapted to the torrential waters originating from high up in the Andes. Actually, *A.m.* was collected together with *Chaetostoma* (unidentified spp.).

The colour pattern of *A.m.* is that of a typical bottom-dweller. The ventral side is pale yellowish white, dorsum of head and body quite dark, uneven brown, and on the dorsum of the caudal peduncle posterior to the dorsal fin are some vaguely defined, rather broad transverse, darker brown stripes. Dorsum of pectoral fins, and the dorsal fin are spotted.

The caudal fin base posterior to the small caudal scutelets is almost black, and this colour extends to the end of the outer branched caudal fin rays on both lobes. This colour pattern of the caudal fin agrees with the same in various Sturisoma and several Farlowella spp., and in addition, is found in other genera of the Harttiini (e.g., Pterosturisoma, Lamontichthys, and Sturisomatichthys).

Secondary sexual dimorphism of A.m. is unknown.

ACESTRIDIINI

Acestridium Haseman, 1911

The Acestridiini are distinguished from all other Loricariinae by having: a) the origin of the dorsal fin somewhat over the origin of the anal fin (anal fin origin is opposite to about the middle dorsal rays); b) 6 branched dorsal fin rays, the last one split to its base; c) cleithrum and coracoid ventrally exposed, together forming a relatively large plate; d) the branchiostegal membrane and its rays extending far onto the lower surface of the head, along the anterior lateral sides of the cleithrum; e) lower lip medianly long, not entirely free from the ventral skin of the head like in other Loricariids, but attached to this area by a pair of membranaceous flaps of skin, arranged into an axial position at either side from the middle, at this latter point folded with a median depression forming a pocket-like structure.

The tribe Acestridiini consists of a single genus, Acestridium; only one species is recognized: A. discus Haseman, 1911. Hitherto, Acestridium was known from three tributaries of the Rio Negro around Manaus (Hassur, 1970: 157-158) only. A new locality record is: Colombia, Inírida/Orinoco drainage, lagoon about 1 km upriver from Puerto Inírida.

Acestridium is a genus of very small fishes. Haseman (1911: 309) recorded the still largest known specimen (holotype of Acestridium discus), 72 mm all over. From his drawing on pl. 50 a standard length of (about) 66.5 mm can be inferred.

Superficially, Acestridium is most reminiscent of some Farlowella.

I have measured and counted in detail only a single specimen (from Colombia, locality mentioned above), with a standard length of 54.4 mm, for a comparison with the Farlowellini. Thirty-eight (numbered) characters of this tribe are given above (pp. 60-63); these same characters are here given in the same order for the specimen of Acestridium, to facilitate a direct comparison:

(1) standard length 54.4 mm (total length as well as axial length of this specimen 58.8 mm); followed by measurements expressed as ratios of standard length (characters 2-14) or of head length (characters 15-32), which are:

(2) head length 4.6;

(3) predorsal length 2.6;

(4) postdorsal length 1.8;

(5) postanal length 1.8;

(6) preventral length 3.0;

(7) distance between supraoccipital tip and origin of the dorsal fin 5.9;

(8) dorsal fin spine length 7.8;

(9) length of the first branched dorsal fin ray ignored;

(10) anal fin spine length 8.4;

(11) pectoral fin spine length 10.6;

(12) pelvic fin spine length 15.2;

(13) upper caudal fin spine length 12.5;

(14) lower caudal fin spine length 11.6;

(15) snout length 2.1;

(16) snout width at tip 9.5 (viz., 1.1 mm, including the roundish expansion), or 13.1 (0.8 mm, measured just beyond the expanded tip, where the snout is narrowest in transverse section);

(17) postorbital head length 2.3;

(18) ventrorostral length 1.1;

(19) length of the lower lip 5.8;

(20) thoracic length 1.9;
(21) abdominal length 1.9;
(22) maximum orbital diameter 7.5;
(23) interorbital width 3.6;
(24) cleithral width 2.2;
(25) supracleithral width 2.2;
(26) head width 2.2;
(27) head depth 3.8;
(28) body depth at dorsal fin origin 4.4;
(29) body width at dorsal fin origin 3.9;
(30) body width at anal fin origin 3.9;
(31) depth caudal peduncle 21.0 (only 0.5 mm);
(32) width caudal peduncle 15.0 (only 0.7 mm);
(33) maxillary barbel invisible.

Meristic data are:

(34) lateral body scutes 27;

(35) coalescing body scutes (hard to distinguish from the parallel lateral body scutes as present along the sides of the caudal peduncle) 10;

(36) thoracic scutes 4;

(37) predorsal scutes 6;

(38) maximum number of teeth in each jaw section, up to 13 in the premaxilla as well as in the dentary.

The fin ray counts are already given on p. 54; C I,10,I.

In these morphometric and meristic characters, Acestridium is shown to differ from both genera of the Farlowellini in its relatively shorter upper and lower unbranched caudal fin rays; its lower lip length (intermediate between Farlowella and A.m.: the former has it 6.8-11.2 times in head length, Acestridium 5.8, and A.m. 4.4-5.2 times); its relatively shorter thoracic and abdominal distances; its more depressed body at the origin of the dorsal fin; its narrower body at the origin of the anal fin, and its distinctly narrower caudal peduncle; further in its reduced number of lateral body scutes (Haseman noted a range of 25-27), its lower number of thoracic as well as of the predorsal scutes, and finally, in its low number of teeth. In addition, Acestridium differs from Farlowella (but not from A.m.) in its distinctly longer head, from both genera again by attaining a much smaller adult size.

Some variability of Acestridium is worth mentioning. Like in Farlowella, the thoracic scutes often meet on the middle of the abdomen. In 10 specimens from around Puerto Inírida (ZMA 115.390), 4 have no abdominal scutelets at all, the thoracic scutes meeting on the middle of the abdomen without interruption. One specimen has 1 rather large abdominal scutelet just anterior to the large preanal plate in front of the anal opening (this preanal plate is present in all Acestridium). Another specimen has 1 quite small, completely isolated abdominal scutelet; the 7th specimen has 3 of such isolated scutelets, widely separated from one another, but in a median line; the 8th specimen has an uninterrupted row of 5 small median abdominal scutelets, the 9th fish has a row of 6, whereas the last specimen has a row of 8 small scutelets between the thoracic scutes.

The thoracic scutes are also subject to some variability in shape and number. The more regular number is 4: five specimens have 4 thoracic scutes on both sides, another three specimens have 4 on one side, coupled with 3 or 5 on the other side; a single specimen has 3 scutes on both sides, and another one has 5 on one side, 6 on the other side.

Acestridium has a well-developed mail of scutes covering almost the entire fish, leaving naked areas on the body only around the fin bases, allowing the fins to move. The rounded, somewhat expanded tip of the snout has a horizontal, narrow naked margin, and anterior to the exposed cleithrum there is a considerably wide and long unossified area, reaching to the origin of the lower lip, extending deeply inside the inner wall of the externally ossified head margin, then running forward along the sides of the (very narrow) upper lip through a median acute Λ-shaped notch in the base of the ventrorostral extension. This notch is ignored in the measurement.

The upper lip anteriorly unites fluently with the just described naked mouth part, laterally it is free from it with a very narrow margin, and posteriorly the upper lip unites fluently with the oval (much longer than broad) lower lip. The papillae on the outer surface of the upper and lower lip are feeble and ill-defined. Buccal cavity as in Harttiina, Farlowellini and as in most of the Loricariidae.

The premaxilla and dentary are well-developed although rather short in a transverse line, with gently curving outer margins. The teeth are reminiscent in shape most particularly of Ixinandria: they are not filiform, rather short and thick, provided with a dark brown crown consisting of a large inner lobe with a sharply oblique distal margin, somewhat beyond the tip being supplemented by a small, acute outer lobe.

Eyes are in lateral position. No orbital notch is present.

Especially the scutes surrounding the long caudal peduncle form conspicuous rings, with laterally almost straight vertical edges; in transverse section, the caudal peduncle is somewhat squarish.

The scutes on the dorsum and sides of the anterior half of the fish are not clearly discernible, on account of the strongly developed odontodes overlying the scute margins. Margin of the head around the mouth is formed by rather large, somewhat irregular scutelets externally.

The odontodes are sharp to the touch, present on all dermal ossifications and fin rays (particularly the unbranched ones, on most branched rays the odontodes are very weak). On the expanded snout tip the odontodes are remarkably large and thick, with an acute tip slightly curving towards the tail. On the pelvic fin 'spine' (which is comparatively thick) there are many elongate, fragile odontodes with an acute, brownish-yellow tip in a quite loose arrangement, all pointing to the median axis of the belly when the fin is not spread.

Series of well-developed odontodes are present on head and snout, dorsum and sides of the body and last but not least on the caudal peduncle, including the scutelets on the caudal fin base, arranged generally into remarkable longitudinal though weakly undulating lines. The odontodes on the abdomen, from the anterior margin of the cleithrum to just in front of the anal opening are smaller and less numerous than the other odontodes.

Except for the unbranched pelvic fin rays (or 'spines'), the unbranched fin rays are exceptionally fragile, never provided with a filamentous extension. The fins are distally rounded.

The fin rays of 16 specimens were counted. Only a paratype of Acestridium discus (FMNH 54340, snout broken, about 54.5 mm in standard length; holotype and another paratype were not re-examined) has 12 instead of the usual 10 branched caudal fin rays (see p. 54).

On the sides of the snout is a longitudinal, brownish stripe in front of the eyes; just beyond the eyes this stripe continues, extending to the base of the caudal fin. At a vertical from the pectoral fin origin, this stripe is a little broader than elsewhere. Thin lines of dark brown pigment are present between the strigilate series of odontodes.

Caudal fin with rather weak, thin and ill-defined vertical lines, dorsal, anal, pelvic and pectoral fins all with dark brown, widely distributed pigmentation.

Secondary sexual dimorphism is unknown in Acestridium.

Discussion.- Primarily because of its extremely produced rostrum, very elongate head and body, and long and slender caudal peduncle, *Acestridium* is superficially most reminiscent of *Farlowella*.

In this work an attempt is made to arrange all the taxa into an approximative phylogenetic order, but it should be emphasized here that the Acestridiini are placed after the Farlowellini at pure random - the tribe might as well have been placed after the Loricariini or still elsewhere - simply because I am at a loss where to put *Acestridium* with some confidence. Intuitively, I think that it might represent a very highly specialized offshoot from some early form near to the present Loricariini.

The combination of characters present in *Acestridium* is perplexing, and unique among the entire family Loricariidae. For example, in its shape of body and head, and also in some details of its colour pattern (not, however, in maximum size), *Acestridium* indeed approaches *Farlowella* most, but that is about where the similarities end. *Farlowella* and *Acestridium* both carry a certain mimetic resemblance to tiny twigs or leafstalks. The soft mouth structure and the shape of the lips of *Acestridium* are unique among the Loricariidae. Its expanded snout tip with the conspicuous retrorse odontodes strikingly reminds of the otherwise singularly shaped rostrum of *Hemiodontichthys*. The tooth shape and number of teeth of *Acestridium* are not unlike those of *Ixinandria*. The exposed cleithrum and coracoid, together with the peculiar odontodes on the unbranched pelvic fin ray ('spine') are characters otherwise occurring typically only in various members of the subfamily Hypoptopomatinae. *Acestridium* does not at all appear to bear any close relationships to *Farlowella*, *Hemiodontichthys*, *Ixinandria*, nor I guess to the Hypoptopomatinae.

All these distinct features of *Acestridium* no doubt are functional to its small adult size and adaptations to its habitat, about which only too little is yet known. Nothing is known about living *Acestridium*.

LORICARIINI

The Loricariini are characterized by having: a) the origin of the dorsal fin about opposite to the origin of the pelvic fins; b) 6 branched dorsal fin rays, the last one split to its base; c) 10 branched caudal fin rays; d) no more, and usually considerably less than 18 teeth in each premaxilla in adults (against at least 27 in the adults of the Harttiini); and e) a great differentiation in dentitions and lip shapes and structures.

The characteristic dentition present in almost all Hypostominae, Ancistrinae, Hypoptopomatinae, all Harttiina and in the Farlowellini, viz., very numerous, slender, filiform teeth with a strongly curved and bilobate crown, never occurs in the Loricariini. In spite of the great diversity in lip structures and shapes in the Loricariini, none is very similar to those present in any other Loricariid group.

The outer (naked) surface of the upper lip is devoid of dermal ossifications.

The orbital rim, with very few exceptions, is provided with a more or less conspicuous posterior notch.

The fin rays are usually dichotomously branched. Often the upper unbranched caudal fin ray extends as a very fragile, extremely long filament; a similarly prolonged lower unbranched caudal fin ray is very rarely encountered: only in some of the Rineloricariina.

Within the Loricariini, several different and most salient types of secondary sexual dimorphism have evolved. These include (a) excessive growth of odontodes in certain areas of the head, on dorsum of the body in front of the dorsal fin origin, and/or on dorsum of the pectoral fin, (b) change in the shape of certain minute odontodes – for example, those on the spines of the pelvic and anal fins – (c) change in the shape of the teeth, and (d) the development of a very long and broad lower lip, serving as a protective cover of the eggs. All these changes occur in the male of the several representatives of the Loricariini. The dimorphism indicated under (a) is restricted to the more primitive genera, that indicated under (d) is found only in the more specialized subtribes. In addition, secondary sexual dimorphism is unknown in various species and may prove not to exist at all in various instances.

The Loricariini no doubt are the sistergroup of the Harttini. The more generalized (primitive) representatives of both tribes do not appear to be very distantly related to each other, although the probably most primitive genus of the Loricariini (Ixinandria) is somewhat more advanced than the probably most primitive genus of the Harttiini (Harttiella, see for a comparison of these two genera on p. 77). There appears to be more variability among the Loricariini than among any of the remaining tribes of the subfamily Loricariinae, or even among the other subfamilies of the Loricariidae.

As a result of the present study, I propose to further subdivide the Loricariini into 8 subtribes, which are (treated below in the following order): the Rineloricariina, Ricolina (new), Loricariina, Planiloricariina, Reganellina, Pseudoloricariina (new), Loricariichthyina, and the Hemiodontichthyina. I think that this subdivision expresses the apparent dynamic evolution of the Loricariini best.

One rather general statement – but certainly not applicable to all of its members – is that various species of Loricariini reach a larger size than most other Loricariinae, many reaching over 300 mm in standard length (e.g., some Rineloricariina, Loricariina, Pseudoloricariina, and Loricariichthyina).

RINELORICARIINA

The Rineloricariina embrace the relatively most primitive members of the Loricariini. Their lips are relatively simple, distantly still reminiscent of the generalized Loricariid lips, more so than in the representatives of the remaining subtribes.

The secondary sexual dimorphism displayed by the various Rineloricariina (and not by other subtribes of Loricariini) primarily is obvious in the development of prolonged odontodes, a character also indicating a relatively more close relationship with the Harttiini.

Four genera of Rineloricariina are recognized. Rineloricaria is the largest genus in terms of the number of species, but probably will have to be split into at least 2 genera; for the second genus the name Hemiloricaria is available and may well prove to be definable.

The Rineloricariina include species with a relatively long head (3.6-5.9 in standard length), and long predorsal- (2.5-4.0 in standard length), postdorsal- (1.5-2.2 in standard length) and postanal (1.6-2.8 in standard length) areas, not unlike the dimensions of a majority of the Harttiini (head length 3.6-6.4, predorsal length 2.6-3.8, postdorsal length 1.5-2.2, and postanal length 1.7-2.9).

Perhaps the number of lateral and coalescing lateral body scutes (28-33 and 13-22, respectively) are also indicative for a rather close relationship with the Harttiini (which have 27-38 and 14-25, respectively).

In the tribe Loricariini there is especially a trend towards less premaxillary (but also less dentary-) teeth in the successively more specialized forms; the Rineloricariina contains representatives with the highest number of premaxillary teeth as compared to the other Loricariini. As will be indicated below, the same ancestor that gave rise to the Rineloricariina has at some time probably also given rise to other subtribes of Loricariini, e.g., the Ricolina, the Loricariina, and the Pseudoloricariina.

Further possible evidence to support a hypothesis that the Rineloricariina shares its ancestor with the Harttiini is put forward in the following discussion of Ixinandria.

Ixinandria Isbrücker & Nijssen, 1979

Ixinandria was recently established, including 2 nominal species, *I. steinbachi* and *I. montebelloi*, together known from only 4 specimens originating from northern Argentina and from (nearby) southern Bolivia, respectively. Both are very close to each other, and may prove to represent only a single species when additional material is available.

Ixinandria is more than to any other genus closely related to *Rineloricaria*. The two genera differ in various characters, each of which scarcely seems to support a generic distinction when considered separately. All these differences combined, however, clearly indicate that *Ixinandria* is a well-defined genus.

It has a small posterior orbital notch. The tip of the snout is naked. Caudal fin truncate, without filamentous extension of the outer unbranched rays. The lower lip is moderately long and broad, the posterior margin is somewhat irregular because of the presence of minute, flap-like extensions; the anterior margin of the narrow upper lip is smooth. The ventral surface of both the upper and the lower lips is covered with relatively few and large, round, low papillae, slightly larger towards the buccal cavity and quite conspicuous along the margins of the maxillary barbel, which itself extends somewhat beyond the sides of the lower lip. The premaxillary teeth are arranged into a curved line, notched at the symphysis; the dentary is somewhat shorter than the premaxilla and somewhat more robust. The teeth are arranged into a weakly curved line. They have a rather short peduncle, and two well-developed lobes, the inner lobe larger than the outer, both lobes have sharp, oblique edges.

Secondary sexual dimorphism. - Nuptial males of *Ixinandria* (see figs. 1-3 of a male, and fig. 4 of a female, in Isbrücker, 1979a) develop most conspicuously elongate and broadening odontodes along the lateral margin of snout and head, commencing about the height of the anterior margin of the upper lip and reaching to the opercular area. The outline of the head when viewed from above or below becomes almost circular in males, and is much more stout triangular in females.

Similar though much shorter odontodes develop on the sides and dorsum of the pectoral fin spine and on the dorsum of the pectoral fin rays. The odontodes on the dorsum of body anterior to the origin of the dorsal fin spine, and on the dorsum of the head are somewhat more conspicuous in males than in females.

The 4 known specimens of *Ixinandria* were compared to 110 specimens available of the various *Rineloricaria* species. They differ as follows:

1) Adult size. *Ixinandria* reaches a maximum size of 87.2 mm in standard length. This largest specimen, and the next to largest one (72.3 mm) are nuptial males. *Rineloricaria* contains 41 described species, including small and large forms (e.g., *Rineloricaria rupestre* is mature at 78.9 mm, *R. stewarti* at about 80 mm [cf. Boeseman, 1976: 156, key, pp. 167-169, pls. 6-7]; whereas *R. latirostris* ♂♂ reach a standard length of 228 mm); *Ixinandria* is in many details much more reminiscent of the larger rather than of the smaller *Rineloricaria* spp.

2) The abdomen of *Ixinandria* is completely naked, whereas in *Rineloricaria* it is at least partly (posteriorly) or completely covered with small to relatively large scutelets.

3) The predorsal scutes are irregular, more numerous and relatively smaller in *Ixinandria* than in *Rineloricaria*. In the former genus these scutes are not unlike those of some of the more primitive genera of the Hypostominae. It is perhaps noteworthy that the irregularity of predorsal scutes is stronger in the two mature males than in the two specimens of indetermined sex (either immature males, or – more likely – females) of *Ixinandria* at hand.

Ixinandria has a predorsal length of 2.5 in standard length, Rineloricaria has a ratio of 2.6-4.0. The head length of Ixinandria is 3.6-3.8 in standard length, 3.8-5.9 in Rineloricaria. Postdorsal length in standard length is 1.9-22 in Ixinandria, 1.5-1.8 in Rineloricaria, postanal length in standard length is 2.5-2.8 in Ixinandria, 1.6-2.4 in Rineloricaria; pectoral fin spine length is 4.6-5.3 in standard length in Ixinandria, 5.2-7.8 in Rineloricaria; maximum orbital diameter 5.7-9.6 in head length in Ixinandria, 3.7-6.9 in Rineloricaria; cleithral width, supracleithral width, and head width are 1.0-1.2, 1.4-1.6, and 1.1-1.2, respectively in the head length of Ixinandria, whereas in Rineloricaria the figures are 1.2-1.5, 1.6-2.2, and 1.2-1.8, respectively; depth of the caudal peduncle is 8.3-10.3 in head length in Ixinandria, 10.8-20.8 in Rineloricaria. Ixinandria has 19-22 coalescing lateral body scutes, Rineloricaria has 13-19.

One of the most distinctive features of Ixinandria is the relatively high number of premaxillary teeth: up to 18 against up to 13 in Rineloricaria (up to 12 in Dasyloricaria, up to 6 in Spatuloricaria). In fact, Ixinandria has the highest number of premaxillary teeth of all Loricariini: it has the highest number of strong, solid teeth, followed by Ricola, which has up to 15. Only some Loricariichthyina have slightly more (up to 17) premaxillary teeth, but the size and shape of these are markedly different from all other Loricariini.

Compared to the other Rineloricariina, Ixinandria has also the most numerous mandibulary teeth: up to 15 against up to 12 in Rineloricaria, up to 13 in Dasyloricaria, and up to 5 in Spatuloricaria.

Comparison with Harttiella. -
Ixinandria from Argentina/Bolivia and Harttiella from Surinam resemble each other in several characters. Partly this resemblance may be due to adaptations to their respective environments, but more likely one can visualize by comparison of these

two genera how an early Harttiine turned into an early Rineloricariine. The most important characters by which to distinguish Harttiella (and almost the entire tribe Harttiini) from Ixinandria (and almost all Loricariini) are: reduction of the number of branched caudal fin rays, from 12 in Harttiella to 10 in Ixinandria; development of a posterior orbital notch in Ixinandria, absent in Harttiella; and reduction of the number plus a change in the shape of the teeth in Ixinandria, together with a slight modification of the lips.

Harttiella is the smallest member of the Harttiini, Ixinandria is one of the smallest members of the Loricariini. Both have a completely naked abdomen, a naked tip of the snout, they both lack caudal filaments and possess a truncate caudal fin. Both Harttiella and Ixinandria possess a strikingly similar way of odontode development in mature males, although minor differences can be observed.

Harttiella has the lowest number of teeth (35-40 in adults) of the subtribe Harttiina, whereas Ixinandria has the highest number of premaxillary teeth of the Loricariini.

Ixinandria has more (19-22) coalescing lateral body scutes than the average Rineloricaria (13-19), the number agreeing with those of Harttiella (about 20) and other Harttiini.

Ixinandria has more lateral body scutes (30-32) than Harttiella (27-28).

Harttiella has the deepest caudal peduncle (4.2-5.9 in head length) of all Harttiini, and Ixinandria has the deepest caudal peduncle (8.3-10.3) of all Loricariini. Harttiella also has the widest caudal peduncle (4.2 in head length) of all Harttiini. The width of the caudal peduncle of Ixinandria is 6.1-6.9, which is not particularly wide among the Loricariini.

The following dimensions of both Harttiella and Ixinandria may further be considered. Both have a rather large head, compared to the other genera of their respective groups, 3.6-3.8 in standard length in Ixinandria, 3.8-4.3 in Harttiella; this same trend is true for the predorsal length, which is 2.5 in standard length in *Ixinandria* and 2.6-2.7 in *Harttiella*; the postdorsal and postanal lengths are relatively short, 1.9-2.2 and 2.5-2.8 in standard length in *Ixinandria*, 2.0-2.2 and 2.7-2.9 in *Harttiella*.

An anal fin spine length of 5.2-6.6 in standard length as in *Ixinandria* is not unusual among the Rineloricariina, but a ratio range of 5.4-6.2 as in *Harttiella* is relatively long for a member of the Harttiina, the more so for a member of the *Harttia*-group of genera.

The maximum orbital diameter, expressed as a ratio of head length is 5.7-9.6 (including the orbital notch) in *Ixinandria*, whereas in *Harttiella* (which has no orbital notch) this ratio is 6.0-7.0.

Finally, there is some agreement in 4 dimensions, which are expressed as ratios of head length: head depth is 2.1-2.3 in *Ixinandria*, 2.0-2.2 in *Harttiella*; body depth at origin of dorsal fin is 2.2-2.7 in *Ixinandria*, 1.8-2.3 in *Harttiella*; body width at origin of dorsal fin is 1.3-1.6 in *Ixinandria*, 1.1-1.3 in *Harttiella*; and the body width at origin of anal fin is 2.0-2.1 in *Ixinandria*, 1.5-2.1 in *Harttiella*.

Rineloricaria Bleeker, 1862

Rineloricaria is at present the largest genus (41 described species) of the subfamily Loricariinae, consisting of all species of the Rineloricariina, except those referred to *Ixinandria*, *Dasyloricaria*, or *Spatuloricaria*. Very likely, *Rineloricaria* should be restricted to much less species. Together with *Rineloricaria*, Bleeker (1862) proposed *Hemiloricaria* as a new genus. *Hemiloricaria* has *H. caracasensis* as its type-species. Both the genus and the species were originally insufficiently diagnosed, and remained a mystery until Van der Stigchel (1946 & 1947: 176-178) redescribed in a composite description the single holotype of *Hemiloricaria caracasensis*, which he identified with *Loricaria lima*. The latter is the type-species of *Rineloricaria*. Van der Stigchel's identification is incorrect.

Boeseman (1972: 312-315, pl. 1) also redescribed - and illustrated for the first time - the holotype of Hemiloricaria caracasensis, which he considered as a species of the genus Loricaria.

I have examined rich material from all over tropical South America, which for the time being is referred to Rineloricaria. Type-specimens of most described species have been re-examined, and representatives of some species of which the original type-material cannot be located (usually being lost in such cases) were also available, in fact considerably more than the 110 specimens already measured and counted. Only Rineloricaria cacerensis, R. catamarcensis, R. cubataonis, R. henselii, R. hoehnei, R. kronei, and R. microlepidota were not yet available to me for study.

I am convinced that Rineloricaria lima plus a number of related species are generically distinct from Hemiloricaria caracasensis plus a number of related species (the first described of the latter is R. platyura). For the moment, however, pending further revision of all the species involved, I prefer to assign them all to Rineloricaria, because I am simply still unable to sufficiently indicate the distinguishing characters.

There is a very strongly developed secondary sexual dimorphism in many (but more probably in all) species and it is important to look for an opportunity to examine both mature males and females of each species, before Rineloricaria is satisfactorily to be split. It is also possible that there are more than two genera represented in Rineloricaria sensu lato.

Contrary to these statements, and with some hesitation, I am here dividing the genus Rineloricaria (on the basis of examined species only) into two groups, informally called

a) the Rineloricaria lima-group (or Rineloricaria sensu stricto), including also R. cadeae, R. felipponei, R. jaragu-

ensis, *R. latirostris*, *R. microlepidogaster*, *R. pareiacantha*, *R. thrissoceps*, and *R. uracantha*; almost certainly, *R. kronei* also belongs here; this group is restricted to S.E. Brazil, Uruguay, and possibly Argentina, with the exception of *R. uracantha* which dwells in Panama, and

b) the *Rineloricaria platyura*-group (or *Hemiloricaria* sensu lato), including also *R. altipinnis*, *R. beni*, *R. caracasensis*, *R. eigenmanni*, *R. fallax*, *R. formosa*, *R. hasemani*, *R. heteroptera*, *R. jubata*, *R. konopickyi*, *R. lanceolata*, *R. magdalenae*, *R. melini*, *R. morrowi*, *R. nigricauda*, *R. parva*, *R. phoxocephala*, *R. rupestre*, *R. sneiderni*, *R. steindachneri*, *R. stewarti*, *R. strigilata*, *R. teffeana*, and *R. wolfei*. These species occur in the various parts of the entire area of distribution of *Rineloricaria* sensu lato, some of them in S.E. Brazil and in Panama as well, like the species of the *R. lima*-group.

The dimensions and counts of 18 specimens of the *R. lima*-group are given first, followed by those summarized of 92 specimens of the *R. platyura*-group (which apparently is the more specialized compared to the *R. lima*-group) between parentheses:

1) standard length 60.8-228 mm (52.2-191 mm);
2) smallest mature male 83.7 mm (78.9 mm) in standard length;

Characters numbered 3 through 13 are expressed as ratios of standard length:

3) head length 3.8-4.8 (4.2-5.9);
4) predorsal length 2.6-3.3 (2.9-4.0);
5) postdorsal length 1.8-1.9 (1.5-1.8);
6) postanal length 1.9-2.4 (1.6-2.2);
7) dorsal spine length 4.5-6.8 (3.6-5.7);
8) length first dorsal fin ray 4.7-6.2 (3.8-5.9);
9) anal spine length 5.6-6.8 (4.3-6.6);
10) pectoral spine length 5.5-7.8 (5.2-7.2);
11) pelvic spine length 6.0-7.7 (5.2-7.7);
12) upper caudal 'spine' length 6.0-8.5 (1.2-9.9);
13) lower caudal 'spine' length 6.7-9.0 (2.0-8.8).

Characters numbered 14 through 29 are expressed as ratios

Plate XXXIII.

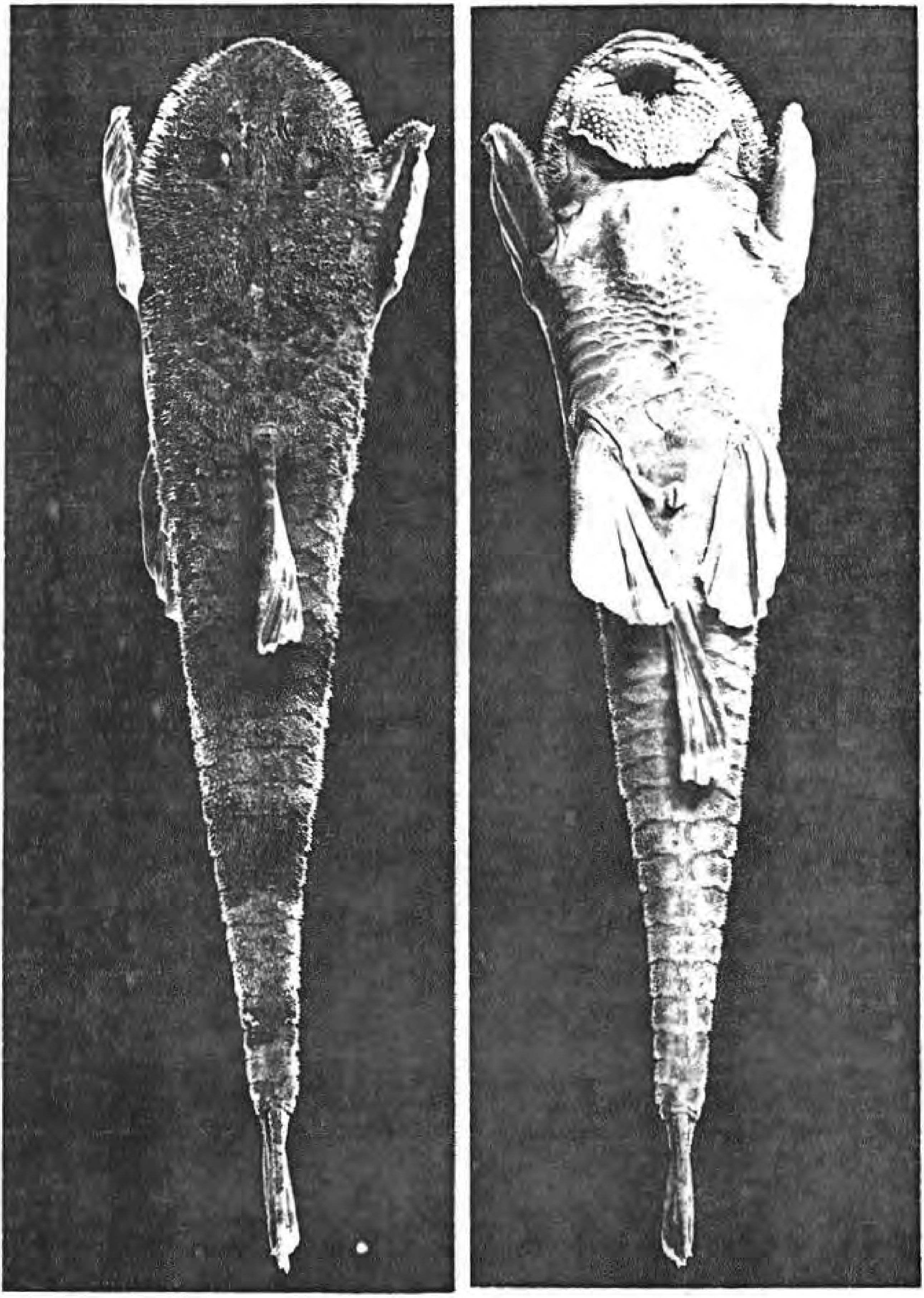


Fig. VI,46. - Rineloricaria jaraguensis (Steindachner, 1909), lectotype (photo L. A. van der Laan, ITZ, Amsterdam).

of head length:
14) snout length 1.9-2.4 (1.8-2.4);
15) length lower lip 4.7-9.7 (4.4-15.0);
16) thoracic length 1.1-1.6 (1.1-1.7);
17) abdominal length 1.1-1.6 (1.2-1.8);
18) maximum orbital length 3.8-6.1 (3.7-6.9);
19) interorbital width 3.9-5.1 (3.2-6.5);
20) cleithral width 1.2-1.4 (1.2-1.5);
21) supra-cleithral width 1.6-1.9 (1.7-2.2);
22) head width 1.2-1.4 (1.2-1.8);
23) head depth 2.0-2.8 (1.8-3.0);
24) body depth at dorsal fin origin 1.8-2.9 (1.6-2.9);
25) body width at dorsal fin origin 1.1-1.7 (1.2-20);
26) body width at anal fin origin 1.6-2.1 (1.4-2.5);
27) depth caudal peduncle 10.8-16.0 (11.0-20.8);
28) width caudal peduncle 6.0-9.0 (5.3-9.8);
29) length maxillary barbel 3.1-5.6 (2.3-6.1).

The counts are:
30) lateral body scutes 29-32 (28-33);
31) coalescing lateral body scutes 15-19 (13-17);
32) thoracic scutes 4-8 (5-11);
33) premaxillary teeth up to 12 (up to 13);
34) mandibulary teeth up to 10 (up to 12).

In several characters, the *R. lima*-group is somewhat intermediate between *Ixinandria* and the *R. platyura*-group.

The abdomen may be completely covered in adults (as in the *R. platyura*-group), but often it is incompletely covered (reduced to about the posterior half only, or with naked areas between the thoracic scutes and irregular abdominal median scutelets), or the abdominal cover consists of very small, roundish or irregular, isolated scutelets appearing at a relatively advanced age. The abdominal scutelets of the *R. platyura*-group are well-developed. We may here give an example (of *R. formosa*): it consists of (a) a posterior complex, consisting of a well-developed preanal plate, preceded by three comparatively large polygonal scutes. Anterior to these scutes are five to six smaller polygonal scutes in a curved transverse series, reaching the posterior thoracic scute. All these elements together may form an inflexible plate, although in some of the specimens the scutes in transverse series allow some movement. This posterior complex is preceded by:

(b) a flexible median complex, consisting of small polygonal scutes reaching the ventral edges of the thoracic scutes. There are three median series of 4 to 6 scutes in longitudinal rows; (c) an anterior inflexible complex of still smaller, polygonal scutelets in front of the median complex. This immovable plate is more or less rounded anteriorly and reaches to the height of a ventral extension of the dermal ossification of the head margin, at its broadest part.

It may be noted that this abdominal scute pattern is not restricted to the Loricariini, but also frequently is present in various Harttiini.

The snout tip of the members of the *R. lima*-group is provided with an ill-defined, roundish naked area; in the *R. platyura*-group there is a narrow, well-defined, often conspicuous horizontal naked line around the anterior part of the snout, margined below by an ossified area, covered with well-developed odontodes.

The lips in the *R. lima*-group may be very reminiscent of the lips of *Ixinandria*; sometimes (as in *R. lima*, and *R. jaraguensis*) the lower lip has a more or less deep median notch, while there is a tendency towards enlarged papillae on the surface of upper and lower lips, including gradually more conspicuous papillae along the anterior margin of the upper lip, and even (in *R. latirostris*) numerous – about 20 to 25 – short barblets along the posterior margin of the lower lip. A similar range of variability is present in the species of the *R. platyura*-group.

One of the most salient differences between the R. lima-group and the R. platyura-group is the apparent absence of filamentous extensions of the outer unbranched caudal fin rays in the former, and the presence of such filaments in the latter group. In the R. platyura-group a filament is usually producing from only the upper unbranched caudal fin ray, but not very rarely there is one on both the upper and the lower ray, like in Farlowella, Sturisoma, and a few other Harttiini.

The R. lima-group tends to have a more firm and truncate or subtruncate caudal fin, whereas it is relatively more fragile and much more forked in the R. platyura-group. Unfortunately, the caudal fin rays are often damaged in preserved specimens, thus it is not always possible to determine this character in still some species.

Secondary sexual dimorphism. - Generally, mature males of the R. lima-group on account of the development of enlarged odontodes, roughly remind of the male of Ixinandria. They occur along the sides of the head, on the body anterior to the dorsal fin origin, sometimes along the sides and dorsum of the caudal peduncle (as in R. jaraguensis), and on the dorsum of the pectoral fin.

The development of such enlarged odontodes in mature males shows specific differences in some details. The pectoral fin spine often is much shorter and thicker, and the head looks considerable thicker in mature males.

In some species of the R. platyura-group, the odontodes of nuptial males still develop in a similar way as in the R. lima-group; Rineloricaria caracasensis and R. magdalenae, for example, are quite reminiscent of R. lima in this respect, although not exactly similar.

However, several species of the R. platyura-group display most conspicuous variations in the pattern of odontodes involved with sexual maturity of the males.

In Rineloricaria jubata the male odontodes still are reminiscent of those in R. magdalenae, but the areas along the sides

Plate XXXIV.

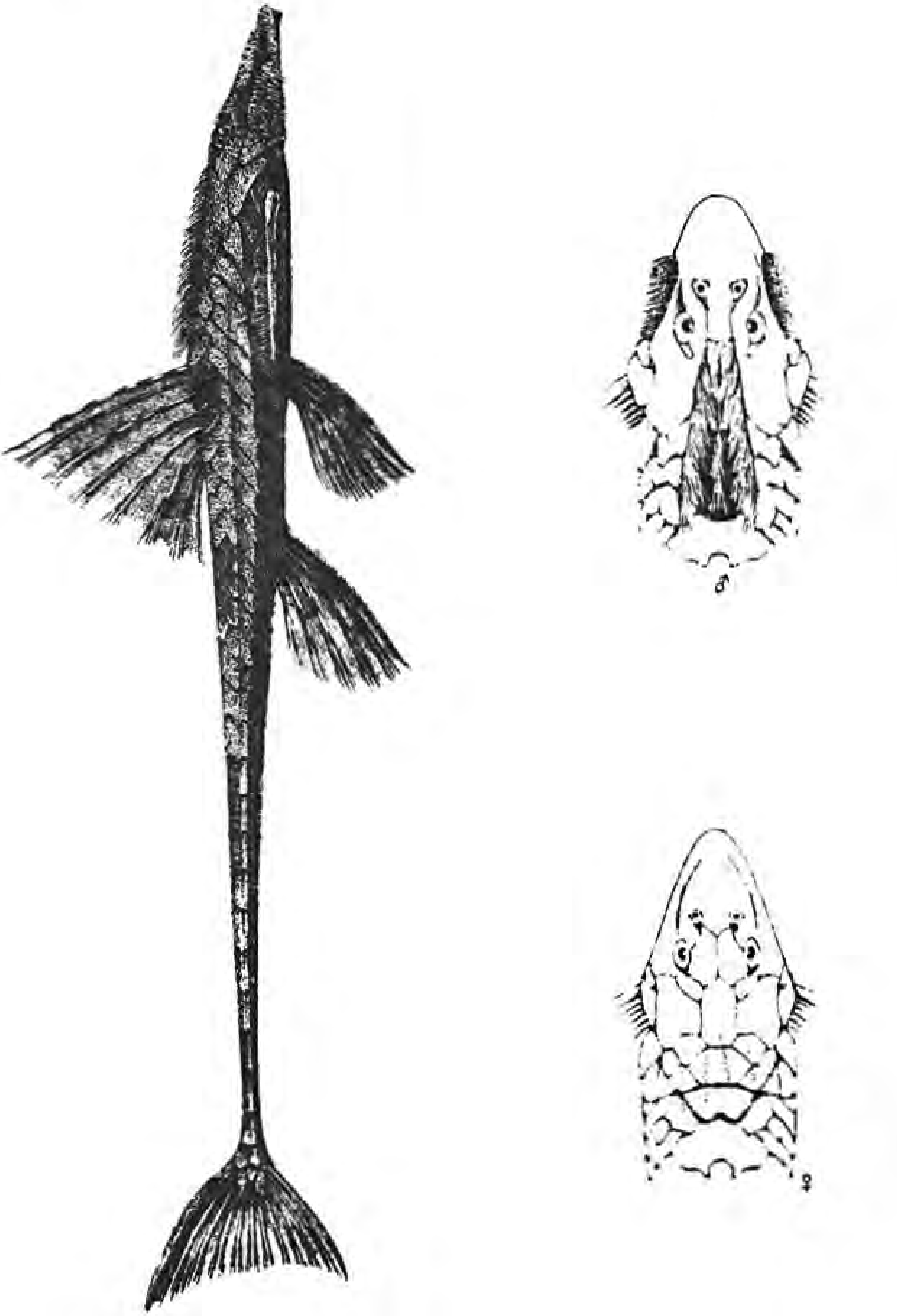


Fig. VI,47. - Rineloricaria jubata (Boulenger, 1902), syntype (after Regan, 1904, pl. 15 figs. 5-5a).

of the head and behind the interorbital area through the postdorsal scutes are sharper delimited, while the odontodes are somewhat longer than in R. magdalenae.

Rineloricaria heteroptera has a compact bunch of rather short odontodes along the sides of the head, which looks like some well-defined rough brush, whereas the odontodes on the predorsal region and on the dorsum of the pectoral fin cause a quite rugose appearance.

Rineloricaria fallax has a remarkable anteriorly coalescing series of relatively few and very long, erect odontodes arranged into two narrow rows on the predorsal area. The odontodes on the dorsum of the pectoral fin, and along the sides of the head are also most conspicuous.

Rineloricaria lanceolata, finally, has very long, quite thick and depressed odontodes in the interorbital/predorsal area, strongly curved odontodes on the pectoral fin, and very long, rather straight odontodes along the margin of the head, supplemented by short, thick, tooth-like odontodes around the opercular area.

In some species of Rineloricaria sensu lato, the males have somewhat shorter and broader tooth crowns, and blunter odontodes on the spine of pelvic and anal fins than the females. Such modifications are not observed in all the species of which both sexes were available for direct comparison.

Dasyloricaria Isbrücker & Nijssen, 1979

Dasyloricaria occurs in and about the Andean regions of Colombia, Venezuela, and Panama. It reaches a larger maximum size than recorded for Rineloricaria spp. – Meek & Hildebrand, 1916: 258 record a D. filamentosa latiura (probably one of the type-specimens of their D. tuyrensis) of 355 mm, probably axial length – but its morphometric characters are fully within the range of variability of Rineloricaria. Dasyloricaria differs gradually only in its higher number of coalescing lateral body scutes, 18-21 against 13-19 in Rineloricaria (19-22 in Ixinan-

dria, 18-22 in *Spatuloricaria*). *Dasyloricaria* has 31-32 lateral body scutes.

Dasyloricaria differs from *Rineloricaria* mainly in the shape and number of abdominal scutes anterior to the posterior thoracic scutes. Between the (long) thoracic scutes there is a double row of rather regular scutelets (in the movable part of the abdomen), often in a chevron-like arrangement, reaching to a series of irregular scutelets in a transverse series between about the origin of the pectoral fins.

There is a moderately large orbital notch. The tip of the snout is naked. The teeth are well-developed, rather generalized in shape and number for a Rineloricariina.

In the structure of the lips, *Dasyloricaria* is quite reminiscent of *Spatuloricaria*, and appears somewhat more specialized in this character than both *Ixinandria* and *Rineloricaria*. The upper lip has about 6 conspicuous barbels, 3 at either side (up to 3.1 mm long in a specimen of 220 mm in standard length); anterior margin of the upper lip is provided with conspicuous fringes, gradually decreasing in size posteriorly. The edge of the lower lip has about 18 conspicuous barbels and several smaller, papilla-like extensions.

Secondary sexual dimorphism. - *Dasyloricaria* apparently is rather closely related to *Rineloricaria*, sharing the development of enlarged odontodes along the margin of the head. These odontodes, however, are the least conspicuous among the Rineloricariina, giving a hairy rather than a spiny appearance of the head surface. Tooth crowns are more rounded in males.

In addition, *Dasyloricaria* (or at least *D*. *filamentosa*) has the lower lip in the females distinctly shorter than in the males, according to Steindachner (1878b: 48 [p. 30 of reprint]), who noted: "...(es dient bei diesen zum Schutze der Eier, welche das Mänchen ausbrütet), ..."

As far as is known, this is the only genus of Loricariids with bristle-like odontodes in the male, combined with nuptial lower lip enlargement. If egg protection by an enlarged lower lip has only once evolved in the Loricariidae, it is obviously most suggestive to trace here the relationships of at least the Pseudoloricariina, but also of the Loricariichthyina and even of the Hemiodontichthyina, three subtribes of Loricariini with a strongly developed secondary sexual dimorphism in the larger lower lip of mature males.

Spatuloricaria Schultz, 1944

Spatuloricaria occurs in the same area of distribution as Dasyloricaria, and in addition, it extends south east to some upper branches of the Amazon River; it has also been recorded from rather central Brazilian localities, e.g., the Rio Maranhão, a tributary of the Rio Tocantins (Dekeyser, Négrett & Rapp, 1976: 25-26), and from the Rio São Francisco (locality not further specified, unfortunately).

Together with Dasyloricaria, Spatuloricaria clearly has a Rineloricaria-like aspect. It may reach a standard length of up to 344 mm, and the upper (perhaps the lower as well) unbranched caudal fin ray may be extremely filamentous; Fowler (1945) recorded a total length, including caudal filament, of 520 mm, in the holotype of Euacanthagenys caquetae (= S. euacanthagenys).

The abdomen is naked or very incompletely covered with minute, almost always isolated scutelets, which appear at a rather late age and increase only a little during growth. The development of the thoracic scutes is also much weaker in Spatuloricaria than in the related genera: they may even be absent.

The lower lip is similar to that in Rineloricaria. The barbels along the anterior margin of the upper lip are strongly developed, up to 11.6 mm in a specimen of 310 mm in standard length (the holotype of S. lagoichthys), and the surface of these barbels may be conspicuously papillose. Often there

Plate XXXV.

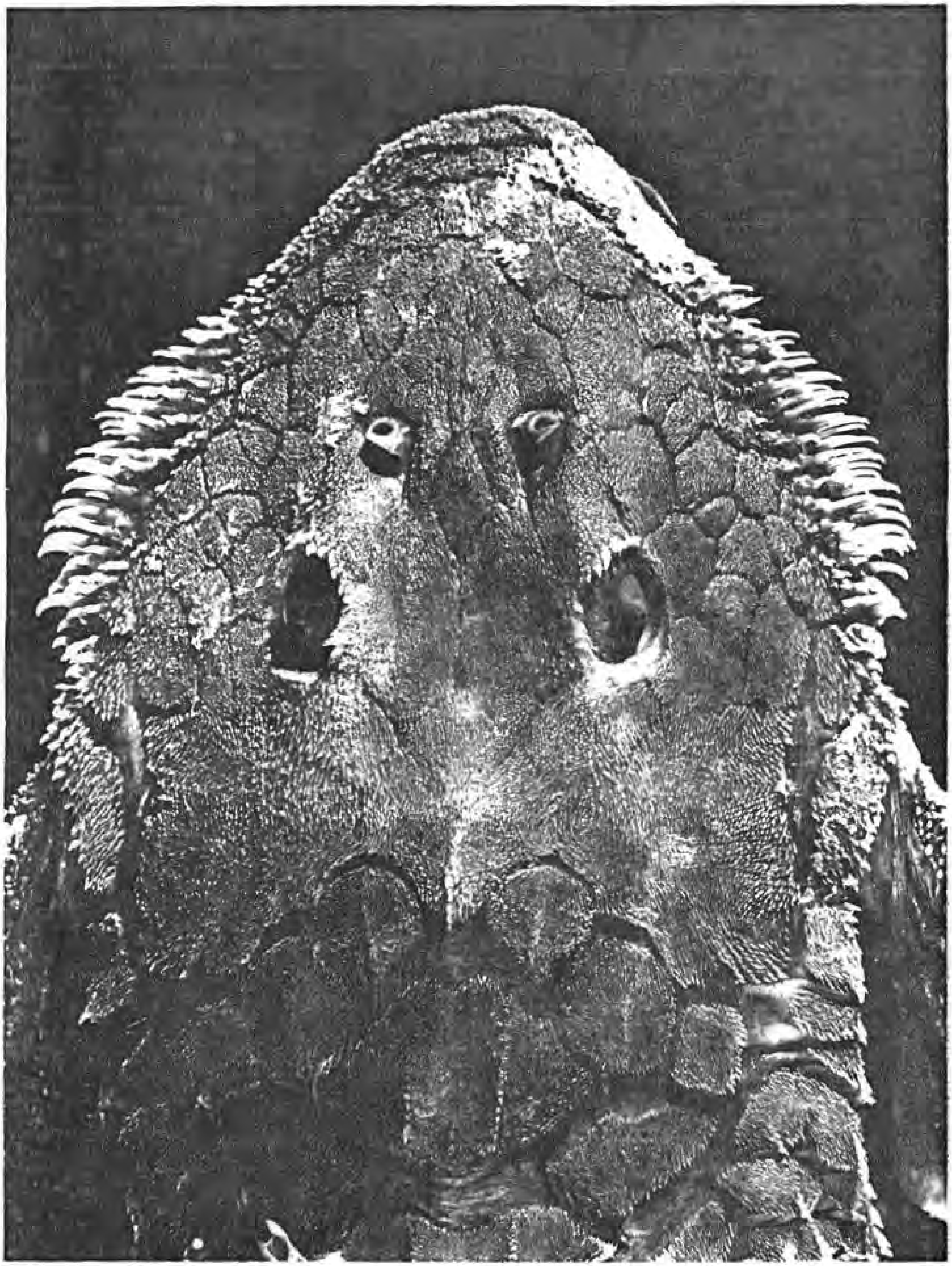


Fig. VI,48. - Spatuloricaria curvispina (Dahl, 1941), holotype (photo L. A. van der Laan, ITZ, Amsterdam).

is a conspicuous, papillose barbel in the buccal cavity at either side between the premaxilla and the dentary.

A further difference of Spatuloricaria with other Rineloricariina is the reduced number of teeth in both jaws: there are up to 6 premaxillary and up to 5 mandibulary teeth (contrasting to 12-18 premaxillary and 12-15 mandibulary teeth in the three other genera of this subtribe). This low number of premaxillary teeth is similar to that in some genera of the Loricariina (Paraloricaria, Crossoloricaria, and Rhadinoloricaria); however, the absence of filaments on the surface of the lower lip easily distinguishes Spatuloricaria from the members of the Loricariina.

Secondary sexual dimorphism. - Young specimens and females of Spatuloricaria are comparatively smooth in appearance, the odontodes on dermal ossifications and on the fins being regular in size, all with an acute tip. The teeth have a long, oblong crown with or without a very small, acute outer 'lobe' situated about the base of the crown. These specimens of Spatuloricaria frequently possess about 4 more or less dark transverse stripes posterior to the dorsal fin, although such stripes may be absent; the ground colour varies from greyish brown to pale yellow.

Males undergo marked change during maturity. Most conspicuous is the development of extremely strong odontodes, which initially gives a much coarser appearance of dorsum and sides of the head and body. These stronger odontodes are located about the tip of the snout, upper side of the orbital rim, sometimes along the outer sides of the nostrils, while the odontodes usually present on the middle of the dorsal, lateral, and coalescing body scutes become gradually more prominent.

As usual in Rineloricariina, males of Spatuloricaria have enlarged odontodes along the sides of the head and on the dorsum of the pectoral fin, those on the spine much more prominent than on the rays. The pectoral odontodes are relatively short, have a very broad base and an acute tip curving towards the head; they are most reminiscent of thorns.

The odontodes along the margin of the head may become most spectacular (cf. Isbrücker, 1979a, figs. 24-26): in the holotype of *Spatuloricaria euacanthagenys*, a male with a standard length of 330 mm, the longest marginal head odontode is 31.3 mm long. These long odontodes are almost erect, slightly curved backwards; towards the operculum the odontodes decrease somewhat in length and are thicker and more strongly curved. Some of such 'fully armed' males of *Spatuloricaria* (e.g., the respective holotype of *S. atratoensis* and of *S. euacanthagenys*), considering the damage were probably so frightening in appearance to their collectors that they were catched with an arrow.

The odontodes on the pelvic and anal fin spines have a blunt rather than an acute tip as in females.

The shape of the teeth also changes in the male: the peduncle becomes slenderer and looks longer, for the crown gradually turns into a cup-shape, with or without a smaller, rounded outer lobe (cf. Isbrücker, 1979a, figs. 27a-c).

In rather small males, probably at the stage of the onset of odontode development (e.g., the holotype of *S. evansii*, which is 174.3 mm in standard length), transverse stripes on the dorsum of the caudal peduncle may still be present. In larger males, 300 and more mm, a quite different, complicated colour pattern may be present. Whether these colour differences are specific, or an additional secondary sexually dimorphic phenomenon is not yet known. If it is not specifically but sexually different, some nominal species are likely to become synonymized (perhaps *S. lagoichthys* with *S. phelpsi*, and *S. euacanthagenys* with *S. caquetae*). The differences between most of the described *Spatuloricaria* species are not great. None has yet been studied from a good range including juveniles, females, and males.

The next 13 genera of Loricariini are distinguished from the Rineloricariina (and from the Harttiini and the Farlowellini) by the apparent absence of any prominent odontode development in the mature male. However, the absence of this sexual dimorphism needs confirmation in several of these 13 genera, for not all the included species are presently known from both sexes, rendering the conclusion still somewhat preliminary.

RICOLINA new subtribe

Type-genus: Ricola Isbrücker & Nijssen, 1978

Ricola consists of a single species, R. macrops, occurring in the Río de la Plata and higher up the Río Paraná, in Uruguay and Argentina. Ricola macrops can reach a standard length of 219 mm. It is characterized by three features:

(a) it is very strikingly similar in general appearance (shape of head and body, structure of the odontodes, arrangement of scutes and development of abdominal scutelets, and colour) to a member of the genus Loricaria, particularly of the Loricaria cataphracta-group;

(b) its dentition is strikingly reminiscent (shape and number, as well as relative size of the teeth) of a Rineloricaria, particularly of the Rineloricaria platyura-group;

(c) it is unique among all Loricariidae by the structure of its lips and barbels. These barbels are not only very numerous (like in Loricaria and related genera), but many of them are further subdividing into minute branches. Such a branching occurs with no other Loricariid.

The upper lip is very narrow; a series of about 5 barbels at either side along the posterior edge of this lip, increasing in length towards the maxillary barbel. Posterior to these series are 3 quite thick, deeply branched barbels present along the outer surface of the upper jaws. Outer side of the maxillary barbels with a series of long barbels (actually being a continuation of the series anterior to the upper jaws), each barbel being provided with numerous small barblets in a linear

Plate XXXVI.

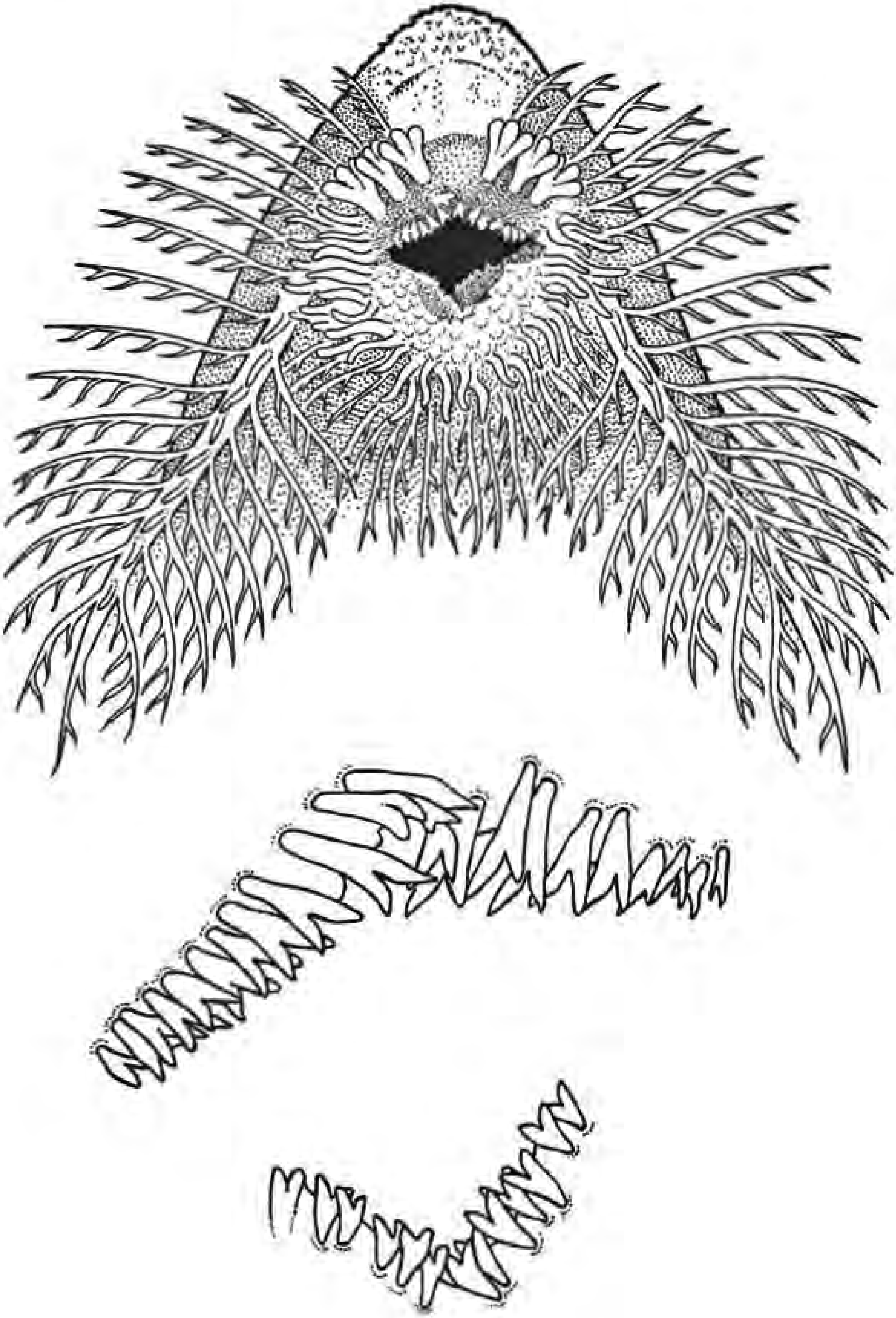


Fig. VI,49. - *Ricola macrops* (Regan, 1904), specimen in ZMA 114.327, sl 185.2 mm (drawing J. Zaagman, ITZ, Amsterdam).

series. Inner side of producing part of the maxillary barbels likewise with several long barbels with small barblets.

Lower lip narrow, the anterior half consisting of a thick, semicircular cushion-like structure. This structure bears irregular, very low papillae on the surface. The posterior part of the lower lip has numerous slender, simple papillae or subbarbels on its surface (like those in Loricaria spp.). Edge of the lower lip with numerous long barbels, each provided ventrally with shorter, slender subbarbels. A short, thick, triangular papilla between premaxilla and dentary. Three rather long papillae in the buccal cavity posterior to the premaxillae, one in the middle and one at either side.

Ricola has up to 15 teeth in each premaxilla and up to 14 teeth in each dentary. Those in the premaxilla are about twice as long than those in the dentary. They have a prominent inner lobe and a somewhat smaller outer lobe.

Ricola tends to have many, sometimes actually slightly more lateral body scutes (37-39) than the average Loricariina (32-38).

Secondary sexual dimorphism. - The pectoral fin spine is thicker in the male than in the female, just like the condition in males of Loricaria. Tooth lobes in mature males become somewhat broader and more rounded at the tip than in females and juveniles, which have acute tips. This type of change in tooth shape also occurs in males of representatives of various other subtribes of Loricariini (e.g., Rineloricariina, Loricariina, Pseudoloricariina, Loricariichthyina, and Hemiodontichthyina).

Discussion. - Considering the three characters of Ricola macrops just enumerated, I am now convinced that it can neither satisfactorily be included within the Rineloricariina, nor within the Loricariina. I propose a new subtribe for Ricola, because it is hard to imagine that this genus evolved from some early Loricaria-like ancestor which secondarily would have attained the very primitive dentition, compared to the Loricariina. On the other hand, one could judge Ricola as some highly specialized derivation of the Rineloricariina stock which retained its ancestral dentition and attained its unusual lip structures plus the generally Loricaria-like appearance independent from the Loricariina. Because of the remarkable combination of characters (general appearance of Loricaria, dentition of Rineloricaria, and unique barbel structure) I think it is justified not to unite the Rineloricariina with the Loricariina on account of Ricola.

LORICARIINA

With the exception of the Ricolina and the Planiloricariina, the Loricariina embrace all other genera of the Loricariinae having numerous long, fleshy filaments on the surface and/or along the outer edges of both the upper and the lower lips.

Loricariina have only up to 9 premaxillary and up to 11 mandibulary teeth (Ricolina have up to 15 and 14, respectively; Planiloricariina have no premaxillary teeth and 3 in each dentary). The number of lateral body scutes ranges in the Loricariina from 31 to 38; in the Ricolina there are 37-39 and in the Planiloricariina 40 lateral body scutes.

The Loricariina occur all over tropical South America. The largest member of the entire subfamily Loricariinae belongs here: Paraloricaria vetula, which reaches a standard length of 437 mm.

The subtribe Loricariina can be further subdivided into 2 distinct genus-groups, probably representing distinct phyletic lineages, which I here informally refer to as the Loricaria-group (also including Paraloricaria and Brochiloricaria), obviously being relatively somewhat less specialized (and into another direction) than the second group, which for convenience may be called the Pseudohemiodon-group (also including Crossoloricaria and Rhadinoloricaria).

The Loricaria-group still seems to be rather closely related (perhaps more so than the Pseudohemiodon-group) to the Rineloricariina. The ancestor of the Loricaria-group probably was a Rineloricariina which developed a tendency towards (a) fewer teeth; (b) slightly larger lips, especially the lower lip becoming longer; (c) more numerous and more prominent papillae which turned into filaments; (d) together with a tendency towards more numerous lateral body scutes, tending to coalesce more posterior than in the Rineloricariina stock; and finally, (e) a gradual loss of the once very conspicuous secondary sexual dimorphism in the odontode development in the males.

The Loricaria- and Pseudohemiodon-groups

The genera of the Loricaria-group have distinctly larger and less numerous premaxillary teeth, and the teeth in the dentary are likewise considerably more robust than those in the Pseudohemiodon-group genera. The teeth of the Pseudohemiodon-group are not only rather inconspicuous, but also either simple or bilobed, always more or less strongly spoon-shaped.

The filaments on the surface and along the posterior edge of the lower lip are considerably longer (sometimes bifid or trifid) and very smooth in the Loricaria-group. In the Pseudohemiodon-group the filaments may be almost entirely absent on the surface of the lower lip, sometimes being no more than small, elongate papillae. The long filaments on and along especially the lower lip are not smooth, but more or less strongly papillose; frequently these papillae are considerably elongate and can be described as short barblets.

The snout of the Loricaria-group genera is not produced, but in the Pseudohemiodon-group the snout is hardly or not at all produced in some species and up to quite considerably produced in others.

The following comparison of 166 specimens of Paraloricaria, Loricaria, and Brochiloricaria with 46 specimens of Crossolori-

caria, *Pseudohemiodon*, and *Rhadinoloricaria* was made. Characters numbered 1-4 are in mm, characters 5-15 are ratios of standard length, characters 16-33 ratios of head length, and characters 34-38 are counts. Those of the *Loricaria*-group genera are given first, followed by those of the *Pseudohemiodon*-group genera between parentheses:

1) standard length 29.1-437 (63-246.5);
2) axial length up to 482 (up to 273.9);
3) total length up to 764 (up to 444);
4) smallest mature male 103.8 (not known);
5) head length 3.7-5.2 (3.9-5.1);
6) predorsal length 2.9-3.7 (2.9-3.4);
7) postdorsal length 1.6-1.8 (1.6-2.1);
8) postanal length 1.8-2.2 (1.9-2.2);
9) dorsal spine length 3.4-6.5 (4.5-6.6);
10) length first dorsal fin ray 3.6-6.6 (5.1-7.3);
11) anal spine length 4.6-7.2 (6.0-13.2);
12) pectoral spine length 2.2-6.6 (5.0-6.6);
13) pelvic spine length 3.9-7.3 (6.0-8.7);
14) upper caudal fin spine 1.0-7.4 (0.4-6.9);
15) lower caudal fin spine 4.9-8.7 (6.1-9.9);
16) snout length 1.7-2.1 (1.7-2.1);
17) ventrorostral length --- (4.2-25.8);
18) length lower lip 3.7-9.4 (3.9-10.6);
19) thoracic length 1.1-1.8 (1.0-1.5);
20) abdominal length 1.2-2.0 (1.2-1.8)
21) maximum orbital diameter 4.2-9.2 (4.3-7.2);
22) interorbital width 4.3-6.4 (4.3-6.1);
23) cleithral width 1.0-1.5 (0.8-1.3);
24) supracleithral width 1.5-2.1 (1.3-1.9);
25) head width 1.0-1.5 (0.8-1.3);
26) head depth 1.9-3.1 (2.5-3.5);
27) body depth at dorsal fin origin 1.6-3.2 (2.2-3.5);
28) body width at dorsal fin origin 1.1-3.2 (1.1-2.0);
29) body width at anal fin origin 1.1-3.3 (1.2-2.5);
30) depth caudal peduncle 9.5-21.1 (9.7-18.3);

31) width caudal peduncle 3.6-9.9 (5.6-10.1);
32) length maxillary barbel 1.5-7.4 (1.1-2.4);
33) length longest barbel of lower lip 5.6-26.0 (4.5-12.1);
34) lateral body scutes 32-38 (31-34);
35) coalescing lateral body scutes 17-26 (13-21);
36) thoracic scutes 4-13 (5-11);
37) premaxillary teeth up to 6 (up to 9);
38) mandibulary teeth up to 11 (up to 11).

Paraloricaria Isbrücker, 1979

Paraloricaria is known from 3 species, all dwelling in the Rio Paraná system.

Paraloricaria resembles *Loricaria* in most characters, but differs particularly from that genus in its dentition. There are up to 6 teeth in the premaxilla and up to 8 in the dentary (in *Loricaria* the numbers of these teeth are 5 and 11, respectively). The premaxillary teeth of *Paraloricaria* are somewhat smaller than those in the dentary, whereas in *Loricaria* the premaxillary teeth are about twice as long as the mandibulary teeth (see Isbrücker, 1979a, fig. 22).

No freshly preserved specimen of *Paraloricaria* has been available to me; such are needed for a detailed description of the lip structure.

The holotype of *Paraloricaria vetula* is 437 mm in standard length. It has the abdomen completely covered with small, irregular scutelets, gradually decreasing in size and increasing in number anteriorly. Smaller specimens have a much more reduced abdominal cover, e.g., the holotype of *P. agastor* (153 mm in standard length) has an entirely naked abdomen (see Isbrücker, 1979a: 103, figs. 20-21, comparison of a *Paraloricaria* with a *Loricaria*).

Compared to *Loricaria*, *Paraloricaria* tends to have a deeper caudal peduncle (9.5-13.9 in head length, against 12.0-21.0 in *Loricaria*), the maxillary barbel tends to be longer (1.5-2.2 in head length, against 2.0-7.4 in *Loricaria*), whereas it may have slightly more lateral body scutes (36-38 against 32-37 in

Loricaria).

Secondary sexual dimorphism in Paraloricaria is unknown.

Loricaria Linnaeus, 1758

Loricaria consists of 11 species, which together occur in a wide range of localities in Surinam, French Guiana, Brazil (Estados Pará, Amazonas, Mato Grosso, Acre?, Roraima), Paraguay, Uruguay, Argentina, Bolivia, Peru, Ecuador, Venezuela, and Guyana (the distribution shown in fig. 17, chapter IX only includes examined material).

This genus was the main subject of an unpublished study (1978), which is presently being prepared for the press. Therefore, the present treatment is not too extensive.

Loricaria is unique among all Loricariidae in its dentition. There are up to 5, but usually 3 or 4, teeth in each section of the premaxilla, distinctly longer (about twice) than the teeth in the dentary. In juveniles and females, these teeth have a large, oblong crown with a more or less rounded tip. It is remarkable that very small specimens (e.g., one of only 29.1 mm in standard length) already have a completely developed number of teeth. The teeth are either simple, or clearly bilobate, but usually provided only with a considerably smaller outer lobe. In each section of the dentary there may be up to 11 (but usually much less) teeth. Generally, the crowns of the mandibulary teeth are provided with a much shorter, broader, and more rounded inner lobe and have a more conspicuous outer lobe than the premaxillary teeth.

The upper lip is short, provided with numerous slender, simple, bifurcate and rarely trifurcate, barbels, subbarbels and long papillae along the margin. These cirrhi are present all over the ventral surface of the lip, originating also from around the base of the teeth, whereas some are originating in the buccal cavity, as well as from the surface of the maxillary barbel.

Plate XXXVII.

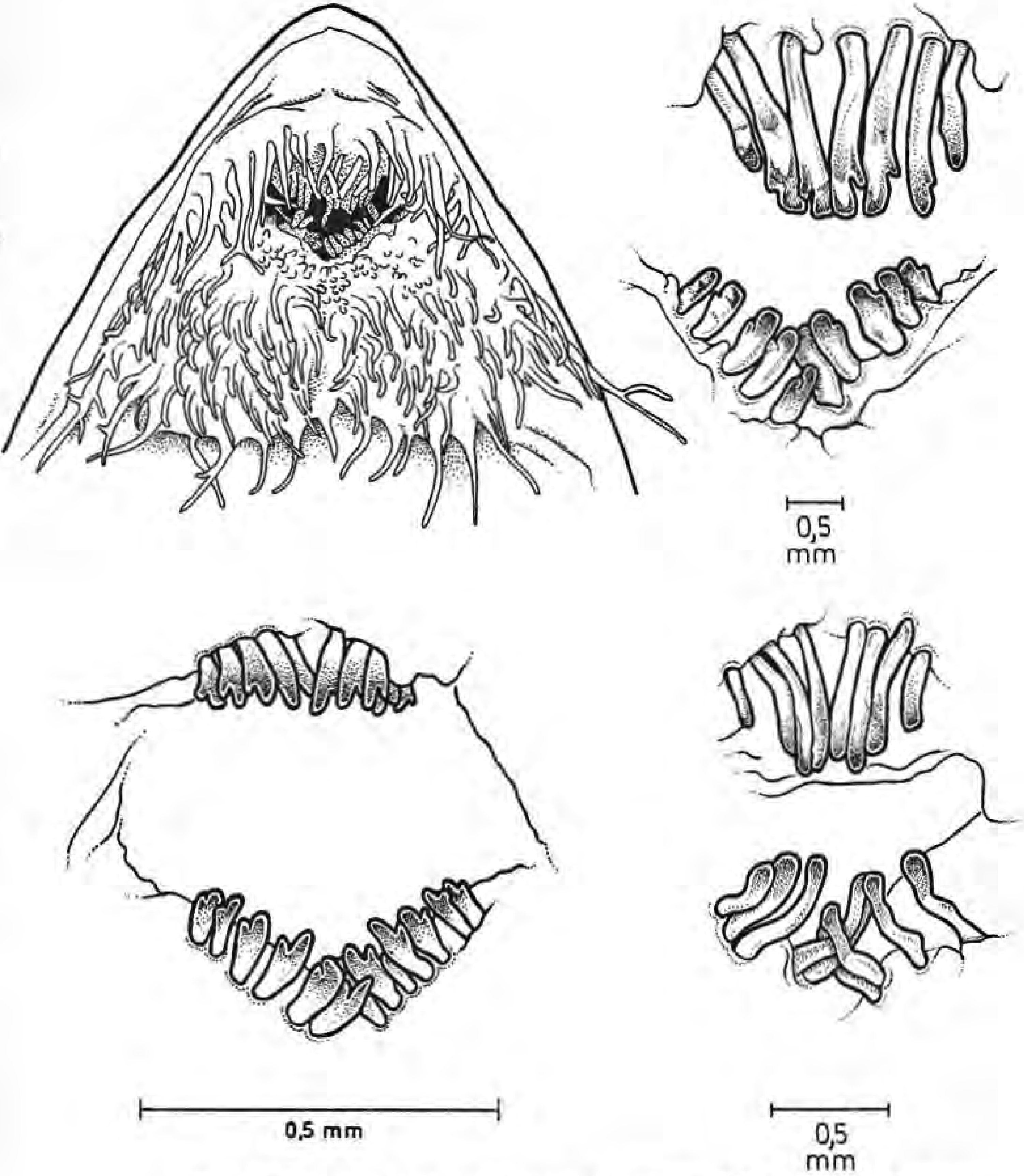


Fig. VI,50. - Loricaria cataphracta Linnaeus, 1758, neotype (top left), L. prolixa Isbrücker & Nijssen, 1978, dentition of a paratype, ZMA 113.537 (top right), Paraloricaria vetula (Valenciennes, 1840), dentition of a specimen in MNHN B.367 (bottom left), and Brochiloricaria macrodon (Kner, 1854), dentition of holotype (bottom right) (drawings J. Zaagman, ITZ, Amsterdam).

The lower lip is well-developed, usually having a more or less deep median notch. Just posterior to the dentary the surface of the lip is usually provided with a cushion bearing low papillae. Posterior to this, the lip is provided with many long, very slender filaments (elongated papillae) which continue along the posterior margin. None of these filaments is bifurcate.

A posterior orbital notch is usually present, mostly being quite inconspicuous and sometimes it is absent.

The pelvic fin spine is almost always longer than the adjacent branched ray. The upper unbranched caudal fin ray often extends as a fragile filament as long as or exceeding the standard length.

The abdomen may be naked, or is partially or entirely covered with relatively small scutelets, which develop with age. There are specific differences in the developmental speed of the abdominal scutelets: some species are fully covered at a distinctly earlier stage (smaller size) than others. In the relatively late development of these scutes, *Loricaria apeltogaster*, *L. prolixa*, and *L. lentiginosa* are quite reminiscent of the *Paraloricaria* spp. and of *Brochiloricaria macrodon*.

The morphometric and meristic variation within 155 specimens representing all species of *Loricaria* is summarized. Characters 1-4 are in mm, those numbered 5-15 are ratios of standard length, 16-32 are ratios of head length, and characters 33-37 are counts:
1) standard length 29.1-346;
2) axial length 31.7-377;
3) total length 35.0-515;
4) smallest mature male 103.8;
5) head length 3.7-5.2;
6) predorsal length 2.9-3.7;

7) postdorsal length 1.6-1.8;
8) postanal length 1.8-2.2;
9) dorsal spine length 3.4-6.5;
10) length first dorsal fin ray 3.6-6.6;
11) anal spine length 4.6-7.2;
12) pectoral spine length 2.2-6.6;
13) pelvic spine length 3.9-7.4;
14) length upper caudal 'spine' 1.0-7.4;
15) length lower caudal 'spine' 4.9-8.7;
16) snout length 1.7-2.1;
17) length lower lip 3.7-9.4;
18) thoracic length 1.1-1.8;
19) abdominal length 1.2-2.0;
20) maximum orbital diameter 4.2-9.2;
21) interorbital width 4.3-6.4;
22) cleithral width 1.0-1.5;
23) supracleithral width 1.5-2.1;
24) head width 1.0-1.5;
25) head depth 1.9-3.1;
26) body depth at dorsal fin origin 1.6-3.2;
27) body width at dorsal fin origin 1.1-3.2;
28) body width at anal fin origin 1.1-3.3;
29) depth caudal peduncle 12.0-21.1;
30) width caudal peduncle 3.6-9.9;
31) length maxillary barbel 2.0-7.4;
32) longest barbel along the lower lip 5.6-26.0;
33) lateral scutes 32-37;
34) coalescing lateral scutes 17-26;
35) thoracic scutes 4-12;
36) premaxillary teeth up to 5;
37) mandibulary teeth up to 11.

Secondary sexual dimorphism. - Mature males of *Loricaria* (of the *L. cataphracta*-group, which excludes *L. apeltogaster*, *L. prolixa*, and *L. lentiginosa*) have hypertrophied pectoral fin spines, blunter odontodes on the pelvic and anal fin spines, and shorter, more rounded tooth lobes than females. Rarely, males have unusual long and broad lips (e.g., a male of *L. clavipinna* in USNM 124930, from the Río Ampiyacu in Peru, 156.5 mm in standard length, has the lower lip shape rather suggestive of those Loricariidae which protect their eggs by the enlarged lower lip: *Dasyloricaria*, *Limatulichthys*, *Pseudoloricaria*, *Loricariichthys*, and *Hemiodontichthys*). A. de Miranda Ribeiro (1912: 10) reported a specimen of *L. cataphracta* from S. Manoel, Tapajoz, "...com uma placa de ovos sobre a lado abdominal." Males of *Loricaria apeltogaster*, *L. prolixa*, and of *L. lentiginosa* are unknown; maybe it is more appropriate to say that they have not yet been recognized as such.

Brochiloricaria Isbrücker & Nijssen, 1979

Brochiloricaria consists of 2 species, one (*B. macrodon*) occurring in the upper Rio Paraná drainage, the other (*B. chauliodon*) near the mouth of that stream. The genus is known from only 3 specimens, the largest being 282 mm in standard length.

Brochiloricaria shares all characters except for its dentition with *Loricaria*; in its morphometric characters it falls welll within the range of variation occurring in *Loricaria*. In the pattern and degree of development of abdominal scutelets, *B. chauliodon* very strongly resembles a species of the *Loricaria cataphracta*-group, whereas *B. macrodon* shares a reduced abdominal covering with the *Paraloricaria* spp. and with *L. apeltogaster*, *L. prolixa*, and *L. lentiginosa*.

Brochiloricaria and *Paraloricaria* have the same variation in number of lateral body scutes: 36-38. There are 21-25 coalescing lateral body scutes in *Brochiloricaria* (21-23 in *Paraloricaria*, 17-26 in *Loricaria*). *Brochiloricaria* has 8-13 thoracic scutes (6-11 in *Paraloricaria*, 4-12 in *Loricaria*). There are 3-5 teeth in the premaxilla of *Brochiloricaria*, and 4-6 teeth in the dentary.

Brochiloricaria has the most (extremely) elongate teeth of all Loricariidae: the mandibulary teeth are about twice the length of the mandibulary teeth of Loricaria, whereas the premaxillary teeth are still longer, compared to those in the dentary as well as compared to the premaxillary teeth of Loricaria.

Secondary sexual dimorphism is unknown in Brochiloricaria.

Discussion. - In my unpublished (1978) paper, both species of Brochiloricaria were ascribed to Loricaria, on account of their general similarity of appearance. Subsequently, Nijssen and I have come to the conclusion that the shared dental specialization of these two species, compared to the quite stabilized dental condition of Loricaria, indicate distinction at generic level, not unlike the distinction of Loricaria and Paraloricaria.

Brochiloricaria chauliodon was described in my 1978 paper (: II,47-48, fig. 29, figs. 36 first map, tables IIIb, XIe) as "Loricaria vieja", 'based' upon the single holotype. Subsequently, I came across a better preserved and larger specimen, which in the original description (Isbrücker, 1979a: 102) was designated as the holotype, instead of the specimen which initially was at hand. I also took the opportunity to withdraw the MS-name "vieja" (vernacular name, Spanish, meaning Old Woman) after I realized that already two species of Loricariinae (viz., Paraloricaria vetula and Loricariichthys anus) with which B. chauliodon might eventually prove to be sympatric have a specific name with exactly the same meaning as Vieja.

⁂

A comparison of Paraloricaria, Loricaria plus Brochiloricaria versus Crossoloricaria, Pseudohemiodon plus Rhadinoloricaria was already presented on pp. 93-95.

Crossoloricaria Isbrücker, 1979

Crossoloricaria contains 3 described and at least one undescribed species and dwells at both the Pacific and the Atlantic slopes of the Andes in Panama, Venezuela, Colombia, and Peru. The largest examined specimen is 246.5 mm in standard length.

The unique character of Crossoloricaria is a narrow strip of small, single scutelets arranged into a median series on the abdomen, which is otherwise naked except for the area between the base of the pectoral fins.

Crossoloricaria is evidently closely related to Pseudohemiodon. In this genus, the abdomen is completely covered with scutelets.

Crossoloricaria has the surface of the lower lip studded with supernumerous, very elongate papillae or very slender, rather short filaments, which are absent in Pseudohemiodon and any other genus of the Loricariidae. The lower lip sometimes is broader in Crossoloricaria (3.9-9.3 in head length) than in Pseudohemiodon (5.9-10.6).

Crossoloricaria is known to me from 21 specimens, 63-246.5 mm in standard length; Pseudohemiodon from 24 specimens, 66.3-220 mm in standard length. Both genera largely agree in most of the morphometric and meristic characters, but the following dimensions (all expressed as ratios of head length, which itself is contained 3.9-5.1 times in the standard length in Crossoloricaria and 4.0-5.1 in Pseudohemiodon) show gradual differences:

1) ventrorostral length is 12.3-25.8 in Crossoloricaria, 4.2-20.9 in Pseudohemiodon;

2) cleithral width, and (3) head width are both 1.1-1.3 in Crossoloricaria, 0.8-1.1 in Pseudohemiodon; and

4) supracleithral width is 1.7-1.9 in Crossoloricaria, 1.3-1.7 in Pseudohemiodon.

The colour pattern of Crossoloricaria spp. is quite well expressed in the specific name of its type-species: C. variega-

ta. No other genus of Loricariinae contains species with a similar colour pattern.

Secondary sexual dimorphism is unknown in *Crossoloricaria*.

Pseudohemiodon Bleeker, 1862

Pseudohemiodon, as defined by its type-species (*P*. *platycephalus*) appears to be well delimited, although I am still somewhat concerned about the fact that the holotype and still only described specimen of *Pseudohemiodon platycephalus* is lost.

Kner (1853a: 115, and 1854a: 75) established a new genus which he named *Hemiodon* (unfortunately preoccupied; substituted by *Reganella* Eigenmann, 1905), characterized by a very depressed body, teeth in the dentary only, premaxillae rudimental, toothless. Three species were included in 1854: next to *Hemiodon depressus* (now *Reganella depressa*) and *H*. *acipenserinus* (now *Hemiodontichthys acipenserinus*), Kner included *H*. *platycephalus*, providing a question mark between the generic and specific name, and stating (1854a: 90): "Diese Art theilt mit den beiden folgenden mehrere wesentliche Eigenschaften, namentlich die sehr plattgedrückte Form, die kurzen Flossen, und den Mangel sichtbarer Zähne in den Zwischenkiefern, es muss jedoch vorläufig fraglich bleiben, ob sie mit Recht dieser Gattung zugezählt wird, da das k. k. Museum hiervon nur ein ausgestopftes Exemplar besitzt, und dieses die Etiquette und Numer eines Individuums trägt, welches in Natterer's Notizen als *Lor*. *platycephala* bezeichnet, aber leider nur rhapsodisch beschrieben wird. Daselbst geschieht aber sieben beweglicher Zähne in der oberen Kinnlade Erwähnung. Ist nun dies der Fall, so wäre dieses Individuum allerdings der Gattung *Loricaria* einzureihen. Da aber die übrige Beschreibung unklar lässt, ob wirklich dieses Exemplar gemeint sei, so nehme ich wenigstens bei dem Mangel sichtbarer Zähne im Zwischenkiefer Anstand, dasselbe unbezweifelt für eine *Loricaria* zu erklären."

In spite of the absence of premaxillary teeth in *Planilori-*

Plate XXXVIII.

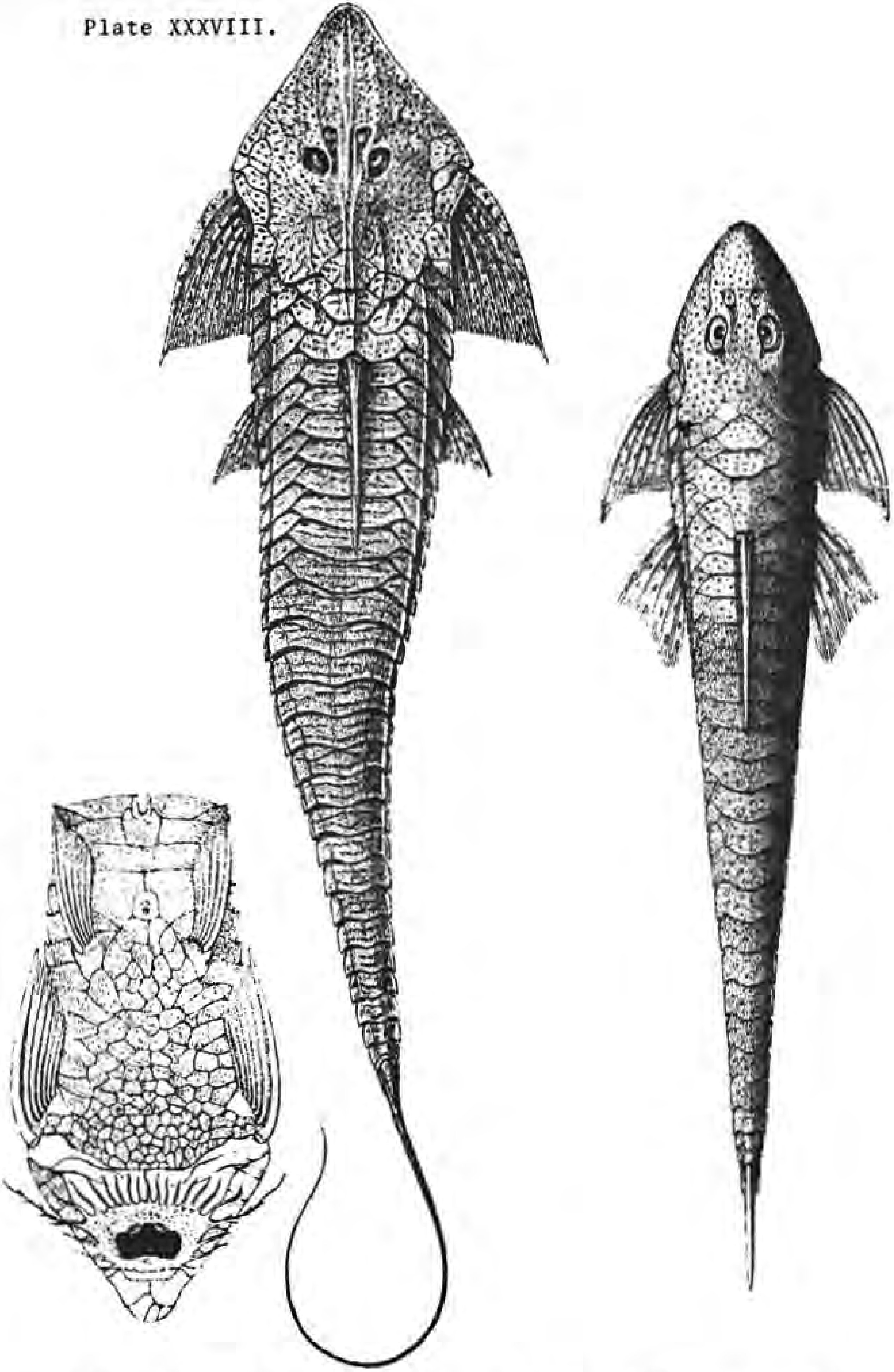


Fig. VI,51. - Pseudohemiodon laticeps (Regan, 1904), syntype (left & middle), and Limatulichthys punctatus (Regan, 1904), syntype (right) (after Regan, 1904, pl. 20 figs. 1-1a, and pl. 17 fig. 1, respectively).

caria, a genus which otherwise is superficially rather reminiscent of my concept of Pseudohemiodon (see below), I strongly doubt whether premaxillary teeth are actually absent in Pseudohemiodon platycephalus. On account of the very close resemblance of the 24 specimens I examined (belonging to at least 5 different species) to Kner's accurate description and illustrations of P. platycephalus, I have little doubt in accepting that they are all representative of the same genus, which may have up to 9 premaxillary teeth (and up to 11 mandibulary teeth; Kner counted 5 in his P. platycephalus).

The 7 species now assigned to Pseudohemiodon occur in tributaries of the Rio Paraná system and of the upper Amazon River. The largest known specimen is 220 mm in standard length.

Pseudohemiodon differs from the two other genera of the Pseudohemiodon-group of Loricariina by the following characters: it has a little to moderately strong ventrorostral extension, a relatively broad head, moderately long maxillary barbels, the abdomen covered completely. It can be readily distinguished from Crossoloricaria by the structure of the lower lip's surface. Contrary to the latter genus, Pseudohemiodon has well-defined although very short and apparently much less numerous papillae (which are not at all filamentous). Along the posterior edge of the lower lip there are many conspicuous barbels, each with a series of short papillae or fine, small filaments along the sides of the barbels.

Secondary sexual dimorphism is unknown in Pseudohemiodon. However, one of the species (P. apithanos) shows an unusual strong variability in colour pattern, part of which may prove to pertain to sexual dimorphism: the holotype of this species has chestnut brown streaks on the dorsum of body and head, lacking in the 6 paratypes; perhaps it is a male.

Rhadinoloricaria Isbrücker & Nijssen, 1974

Rhadinoloricaria is known only from the holotype of R. macromystax, 142 mm in standard length, collected in the Peruvian Amazon, and registered the 21st of May, 1869 in the collections of the British Museum (Natural History).

Rhadinoloricaria approaches Pseudohemiodon most, but differs from that genus in various characters. The most salient difference is in the shape of the snout, which is considerably produced. The (ossified) ventrorostral extension is 6.6 times in head length and falls within the range of variation of this character in Pseudohemiodon: 4.2-20.9. However, the naked area in front of the upper lip is in Rhadinoloricaria much longer than in Pseudohemiodon, while the head is more slender (1.3 in its own length in Rhadinoloricaria against 0.8-1.1 in Pseudohemiodon) and the sides of the head are tapering, those of the snout narrow and somewhat concave; in Pseudohemiodon the head profile seen from above is much shorter, triangular.

The lips of Rhadinoloricaria macromystax were described by Günther (1869: 426) as: "...the upper lip terminating laterally in a long barbel, extending beyond the axil of the pectoral fin; lower lip broad, with numerous barbels and smaller fringes". In the holotype the lips are now in a poor state of preservation.

The first dorsal fin ray is 7.3 times in standard length (5.3-6.8 in Pseudohemiodon), the anal fin spine 13.2 in standard length (6.0-8.3 in Pseudohemiodon). The cleithral width of Rhadinoloricaria is 1.2 in head length, 0.8-1.1 in Pseudohemiodon; supracleithral width is 1.9 in head length against 1.3-1.7 in Pseudohemiodon; head depth 3.5 in its own length against 2.5-3.3 in Pseudohemiodon; depth caudal peduncle 9.7 in head length against 12.3-17.3 in Pseudohemiodon. The already mentioned maxillary barbel of Rhadinoloricaria is 1.1 in head length, 1.4-2.4 in Pseudohemiodon.

Secondary sexual dimorphism of Rhadinoloricaria is unknown.

PLANILORICARIINA

Planiloricaria Isbrücker, 1971

Planiloricaria is known only from the single holotype of P. cryptodon, 214 mm in standard length, originating from the Río Ucayali near Pucallpa, Peru.

Superficially, it is reminiscent somewhat of a Pseudohemiodon with an extraordinary, disk-like head shape in dorsal and ventral view, and very much depressed in lateral view. It differs not only from that genus but also from all other species of the tribe Loricariini by:

a) its produced dorsal fin spine, 2.4 in standard length (3.4 or more times in standard length in all other Loricariini);

b) its small eyes, 13.1 in head length (9.6 or less times in head length in all other Loricariini);

c) its extremely long maxillary barbels, each with about 20 subsidiary barbels, 1.0 in standard length (maxillary barbel is 1.1 times in head length in Rhadinoloricaria and more in all other Loricariini);

d) its (24) extremely long, papillose barbels along the posterior edge of the lower lip, 2.6 times in head length (at least 4.5 in all other Loricariini);

e) its numerous lateral body scutes, 40 (against 27-39 in all other Loricariini); and

f) its reduced number of mandibulary teeth, 3 (against up to 11 and up to 34 in all other genera of Loricariini).

Planiloricaria has no premaxillary teeth; no orbital notch; no dorsal flap on the pupil; its lower lip is very narrow, 11.5 times in head length; numerous filaments and papillose extensions about the (rudimentary?) premaxillae; a smooth dorsum of head and snout, except for a feeble coalescing double ridge running anterior as well as posterior to the supraoccipital process;head and snout are devoid of prominent odontodes; a very long upper caudal filament; no produced pelvic fin spines; abdomen almost completely covered with minute scutelets.

Planiloricaria shares the absence of premaxillary teeth with Reganella and with Hemiodontichthys, but with both it does not seem to have any close degree of relationship. No doubt, many of the characters of Planiloricaria are adaptations to its environment, and the fact that only a single specimen is known yet indicates how little we know of the species. I consider it a highly specialized form which apparently evolved from an ancestor shared with the Loricariina.

Secondary sexual dimorphism is not observed in the holotype.

REGANELLINA

Reganella Eigenmann, 1905

Like the preceding, the Reganellina is also a monotypic subtribe, consisting of Reganella depressa only. This species was redescribed from 2 syntypes and the only 5 subsequently (after 1853) collected specimens, all from Amazonian localities, the largest specimen being approximately 170 mm in standard length (Isbrücker & Nijssen, 1974b); no additional specimens have come to our attention in the past 7 years.

The relationships of Reganella are obscure. The position of the dorsal, anal, and pelvic fins, the presence of a shallow posterior orbital notch, relative size, number and shape of the teeth (which are present only in the dentary, absent in the probably rudimentary premaxilla), shape and structure of body and caudal peduncle, and fin formulae are all characters which clearly indicate Reganella as a representative of the tribe Loricariini. The shape of the fins resembles those of the Pseudohemiodon-group of genera (Loricariina), and the dorsal head shape is reminiscent of Rhadinoloricaria most. Also the shape of the teeth is not unlike that of the Pseudohemiodon-group of genera, while it also resembles the shape of the teeth of Hemiodontichthys.

Reganella has a long, acute snout, slightly concave on the sides; the tip of the snout has a very narrow naked horizontal area and the tip is straight; odontodes on external ossifications are relatively weakly developed, though forming distinct ridges along the lateral body scutes; throat, breast and belly covered by small, irregular scutelets, decreasing in size anteriorly, almost reaching towards posterior edge of the lower lip; eye moderate; supraoccipital process with a broad tip.

Secondary sexual dimorphism is unknown in *Reganella*.

The pattern of abdominal scutelets is roughly similar in *Reganella* and in *Rhadinoloricaria*, and a comparison of these two genera (excluding the shared characters) gives the following data: *Reganella* has no premaxillary teeth, *Rhadinoloricaria* up to 6 in a single section; the former has up to 18 mandibulary teeth, the latter up to 7. The lips of *Reganella* are peculiar in shape, unique among all Loricariidae. Except for a relatively narrow naked connection bridging the anterior part of the upper lip with the posterior point of the ossified ventrorostral extension, the anterior and lateral sides of the lips are free from the ossified inner side of the mouth in *Reganella* (just like in Farlowellini and Acestridiini, for instance). In *Rhadinoloricaria* the lips are directly connected to the ossified inner side of the mouth, as in most Loricariidae. The maxillary barbel does not extend the lips in *Reganella*, whereas in *Rhadinoloricaria* the maxillary barbels are unusually long. The upper lip of *Reganella* anteriorly stretches in an almost linear transverse strip, it is rather narrow but has a conspicuous median, somewhat triangular extension pointing posterior towards the buccal cavity in *Reganella*, with a rather large fleshy lobe at either corner deeper inside this cavity; the upper lip of *Rhadinoloricaria* awaits description.

The lower lip is broad, with a median notch and about 4 flat fleshy expansions (irregularities) at both the right and the left half besides the notch in *Reganella*, and the entire ventral surface of upper and lower lips inclusive of the fleshy flaps are covered with numerous low, minute papillae. Rhadinoloricaria has many barbels along the posterior edge of the lower lip, absent in Reganella.

Reganella has the sides of the head convex to a point about a quarter on the ventrorostral extension, then it is concave anteriorly towards the tip (about half the length of this extension) and continues somewhat parallel, ending as a rounded apex.

In the following comparison, data of Reganella are given first, followed by those of Rhadinoloricaria. Characters numbered 1-4 are ratios of standard length, 5-15 are ratios of head length, and 16-18 are counts:

1) postanal length 2.2 and 2.1, respectively;
2) dorsal spine length 5.6-5.7 and 6.0;
3) length first dorsal fin ray 5.7 and 7.3;
4) anal spine length 5.5-7.5 and 13.2;
5) snout length 2.2 and 2.0;
6) ventrorostral length 1.6 and 6.6;
7) thoracic length 1.5 and 1.3;
8) maximum orbital diameter 3.7-4.4 and 5.4;
9) interorbital width 6.1-6.2 and 5.7;
10) supracleithral width 1.5-1.6 and 1.9;
11) head width 1.0-1.1 and 1.3;
12) head depth 3.1-3.4 and 3.5;
13) depth caudal peduncle 15.5-17.7 and 9.7;
14) width caudal peduncle 7.9-9.0 and 9.7;
15) length of maxillary barbel 3.9 and 1.1;
16) lateral body scutes 29-30 and 33;
17) coalescing lateral body scutes 14-15 and 17-18;
18) thoracic scutes 4-5 and 9-10.

The differences between Reganella and Rhadinoloricaria in short, are more numerous than their similarities.

A comparison of morphometric and meristic characters of Reganella (with its acute head shape and many other distinguishing characters) and Planiloricaria (having a rounded head; the comparison is made solely because both genera lack premaxillary teeth) is given, neglecting the few shared characters. Data of *Reganella* are followed by those of *Planiloricaria*; characters numbered 2-9 are ratios of standard length, 10-21 of head length, and 22-25 are counts:

1) standard length 111-113 mm and 214 mm;
2) predorsal length 2.8-3.0 and 3.5;
3) postdorsal length 1.8 and 1.6;
4) dorsal spine length 5.6-5.7 and 2.4;
5) length first dorsal fin ray 5.7 and 5.5;
6) pectoral fin spine length 5.8 and 5.0;
7) pelvic fin spine length 6.9-7.1 and 7.5;
8) upper unbranched caudal fin ray 5.0 and 0.6;
9) lower unbranched caudal fin ray 8.0 and 5.5;
10) snout length 2.2 and 1.8;
11) ventrorostral length 1.6 and not produced;
12) length of lower lip 6.2 and 11.5;
13) thoracic length 1.5 and 1.3;
14) abdominal length 1.1-1.4 and 1.6;
15) maximum orbital diameter 3.7-4.4 and 13.1;
16) interorbital width 6.1-6.2 and 5.2;
17) cleithral width 1.2 and 1.0;
18) depth caudal peduncle 15.5-17.7 and 12.7;
19) width caudal peduncle 7.9-9.0 and 7.0;
20) length maxillary barbel 3.9 and 1.0;
21) longest lower lip barbel absent and 2.6;
22) lateral body scutes 29-30 and 40;
23) coalescing lateral body scutes 14-15 and 19-20;
24) thoracic scutes 4-5 and 9;
25) mandibulary teeth up to 18 and up to 3.

Further differences between *Reganella* and *Planiloricaria* (see pp. 106-108 and 105-106) indicate that the lack of premaxillary teeth is due to convergent evolution rather than to relationships.

Reganella and *Hemiodontichthys* also share the absence of premaxillary teeth, obviously again not indicating a close relationship between these genera, as the following comparison may show. First, the morphometric and meristic characters of 3 specimens of Reganella depressa are given, followed by those differences as shown in 77 specimens of Hemiodontichthys acipenserinus. The figures given here differ from the figures given by Isbrücker & Nijssen (1974b), because in all Loricariinae with a produced rostrum the influence of the ventrorostral length is now excluded from all measurements in which it was previously involved. Characters numbered 2-4 are ratios of standard length, 5-10 are ratios of head length, and 11-13 are counts:

1) standard length 111-113 mm and 58.2-134 mm;
2) postanal length 2.2 and 1.8-2.1;
3) length pectoral fin spine 5.8 and 6.6-7.0;
4) pelvic fin spine length 6.9-7.1 and 7.9-10.4;
5) ventrorostral length 1.6 and 2.2-3.6;
6) abdominal length 1.1-1.4 and 1.5-1.7;
7) interorbital width 6.1-6.2 and 3.6-4.9;
8) head width 1.0-1.1 and 1.2-1.5;
9) head depth 3.1-3.4 and 2.4-3.2;
10) length maxillary barbel 3.9 and 2.3-3.0;
11) lateral body scutes 29-30 and 27-29;
12) coalescing lateral body scutes 14-15 and 11-14;
13) mandibulary teeth up to 18 and up to 16.

In Reganella the opercle does not reach the ventral margin of the head, in Hemiodontichthys it does. The interorbital area is anteriorly narrow in Reganella, broad in Hemiodontichthys. Reganella has a broader head than body, Hemiodontichthys has a broader body than head. The ventral margin of the ossified part of the head about the lips is broad and flattened in Reganella, it is narrow and rounded in Hemiodontichthys. Reganella has a narrow, weakly developed upper lip, free from the ventral head margin, whereas in Hemiodontichthys the upper lip is well-developed, fused with the ventral head margin through skin. The pectoral fin reaches the origin of the pelvic fin in Reganella, not in Hemiodontichthys. Reganella has a naked area around the anal papilla, in Hemiodontichthys this area is almost completely ossified. Reganella has numerous small, irregular scutelets anterior to the preanal scute, and these scutelets gradually decrease in size anteriorly, but in Hemiodontichthys the abdomen is covered with a few large scutes anterior to the preanal scute, not decreasing in size anteriorly. In Reganella the anterior ventral scutelets extend to the height of the gill openings and are connected with the ventral margin of the head, contrary to the condition in Hemiodontichthys.

Hemiodontichthys usually has the tip of the snout expanded and provided with distinctly large, recurved, tooth-like odontodes; odontodes which form distinct ridges along the longitudinal lateral body scutes, other odontodes (on dorsum of head and body, and on both the dorsal and ventral sides of the rostrum) are arranged into strongly undulate lines; eye with a large posterior orbital notch; it differs greatly from Reganella in all these characters.

PSEUDOLORICARIINA new subtribe

Type-genus: Pseudoloricaria Bleeker, 1862

The subtribe Pseudoloricariina as herein proposed is actually equivalent to the genus Pseudoloricaria sensu (for example) Isbrücker & Nijssen, 1976b. Then, Pseudoloricaria still was considered to contain 2 species, but since (Isbrücker & Nijssen, 1979) we established Limatulichthys as a genus to accommodate the second species.

While working on the present generic and higher classification within the subfamily Loricariinae, the still fairly close relationship between certain Rineloricariina and Pseudoloricaria plus Limatulichthys became more clearly perceptible than previously. In my opinion, Limatulichthys and Pseudoloricaria are descendants of some Rineloricaria (R. lima-group)/ Dasyloricaria lineage, which gradually lost the ability to develop masculine odontode enlargement, which ability became replaced by a strong tendency towards improvement of the masculine lower lip enlargement. It thus appears that the Pseudoloricariina are quite fairly intermediate between the Rineloricariina and the Loricariichthyina, which latter subtribe shows a much higher specialization, remaining with only a single genus (discussed after this subtribe).

As a definition of the Pseudoloricariina, our previous (1976b) diagnosis of Pseudoloricaria will do: Upper lip narrow, with many minute papillae extending anteriorly into a series of separate, short and broad barbel-like pointed flaps. The largest flaps are situated anterior to each of the premaxillae, decreasing in size posteriorly along the outer side of the maxillary barbel. The dorsum of these flaps bulging and smooth; the ventral side flat and covered with minute papillae. The largest flaps may be deeply notched and are often bifid or trifid, and have lumpy edges because of the presence of papillae. Teeth well-developed, reminiscent of the teeth often present in the Rineloricariina on account of the relative size, shape and number, up to 13 in the premaxilla and up to 15 in the dentary. Abdominal scutelets well-developed, those in Limatulichthys reminiscent very much of those present in Rineloricaria (particularly of the R. platyura-group), whereas those of Pseudoloricaria are (superficially at least) not unlike the abdominal scutelets of Loricaria (L. cataphracta-group). Posterior orbital notch moderate.

My reasons to elevate Pseudoloricaria plus Limatulichthys at subtribal rank is perhaps best demonstrated by the following table, allowing a comparison of Rineloricaria (sensu lato), Dasyloricaria, Limatulichthys, and finally, Pseudoloricaria. Measurements and counts of 45 specimens of Limatulichthys and of 32 specimens of Pseudoloricaria are involved in this comparison. As usual, characters numbered 3-13 are ratios of standard length, 14-30 are ratios of head length, and 31-35 are counts. Above each column, the initial letter of each genus is indicated.

	R.	*D.*	*L.*	*P.*
1) standard length (mm)	52.2-228	220-233.2	97.9-177.5	106.4-305
2) smallest mature male (mm)	78.9	-	105	198
3) head length	3.8-5.9	4.7-5.6	4.3-5.5	4.4-5.4
4) predorsal length	2.6-4.0	3.3-3.7	2.8-3.4	3.0-3.5
5) postdorsal length	1.5-1.8	1.6-1.7	1.7-1.9	1.6-1.8
6) postanal length	1.6-2.4	1.8-1.9	1.9-2.2	1.9-2.1
7) dorsal spine length	3.6-6.8	4.1-4.8	4.3-5.4	4.5-6.8
8) length first dorsal ray	3.8-6.2	4.3-5.1	4.5-5.4	4.8-7.7
9) anal spine length	4.3-6.8	5.4-6.3	5.3-7.0	5.6-6.9
10) pectoral spine length	5.2-7.8	5.9-6.7	5.5-6.6	4.2-5.9
11) pelvic spine length	5.2-7.7	5.4-6.8	5.8-7.9	5.3-7.6
12) length upper caudal fin spine	1.2-9.9	1.1-7.0	3.4-8.4	5.4-7.1
13) length lower caudal fin spine	2.0-9.0	6.1-8.7	7.4-9.5	7.0-7.8
14) snout length	1.8-2.4	1.8-1.9	1.9-2.2	1.7-2.1
15) length lower lip	4.4-15.0	5.1-5.9	2.2-8.1	1.8-4.3
16) thoracic length	1.1-1.7	1.3-1.6	1.2-1.8	1.4-1.8
17) abdominal length	1.1-1.8	1.3-1.4	1.2-1.4	1.2-1.4
18) maximum orbital diameter	3.7-6.9	4.5-4.6	3.6-4.4	3.9-4.9
19) interorbital width	3.2-6.5	4.8-5.1	5.7-9.1	7.4-10.8
20) cleithral width	1.2-1.5	1.2-1.3	1.2-1.4	1.3-1.4
21) supracleithral width	1.6-2.2	1.6-1.7	1.5-1.9	1.6-1.9
22) head width	1.2-1.8	1.2-1.3	1.2-1.4	1.3-1.4
23) head depth	1.8-3.0	2.4	2.4-3.2	2.6-2.9
24) body depth at dorsal fin origin	1.6-2.9	2.2	2.1-2.8	2.4-2.6
25) body width at dorsal fin origin	1.1-2.0	1.4-1.6	1.4-1.8	1.5-1.7
26) body width at anal fin origin	1.4-2.5	1.6-1.7	1.7-2.1	1.8
27) depth caudal peduncle	10.8-20.8	13.5-13.9	12.8-16.6	13.2-15.7
28) width caudal peduncle	5.3-9.8	6.2-6.5	7.0-9.2	6.0-8.4
29) length maxillary barbel	2.3-6.1	3.2-5.4	2.4-4.7	2.1-3.3
30) longest barbel along lower lip	16.8-23.2	27.8-41.9	-	-
31) lateral body scutes	28-33	31-32	30-32	33-37
32) coalescing lateral body scutes	13-19	18-21	18-22	22-27
33) thoracic scutes	4-11	8-9	4-7	5-10
34) premaxillary teeth	up to 13	up to 12	up to 13	up to 12
35) mandibulary teeth	up to 12	up to 13	up to 15	up to 13

Limatulichthys Isbrücker & Nijssen, 1979

Limatulichthys is known from a single species, *L. punctatus*, which dwells in the Rio Amazonas basin in Brazil, Peru, and Ecuador, in the Rio Parnaíba, Est. Piauí, Brazil, in the Essequibo River system in Guyana, and in the Río Meta system in Colombia. It reaches 177.5 mm in standard length.

Limatulichthys is distinguished from Pseudoloricaria most easily by its larger and fewer abdominal scutelets: 3-5 small scutes border the pre-anal scute anteriorly. It has 30-32 lateral- of which 18-22 are coalescing lateral body scutes, 4-7 thoracic scutes, and sometimes slightly more teeth (up to 13 in the premaxillary, up to 15 in the dentary). Tip of the snout with a narrow naked, horizontal area reaching to a vertical from halfway the eye. For additional (gradual) differences with Pseudoloricaria I refer to the table on p. 113.

The morphometric and meristic characters of Limatulichthys, its pattern of abdominal scutelets and its relatively shorter lower lip of mature males (compared to Pseudoloricaria) may indicate Limatulichthys as a less specialized genus than Pseudoloricaria.

Secondary sexual dimorphism. - Besides the enlarging lower lip in the males, the sexes differ in tooth shape: males have teeth with broader and rounder crowns than females, which have relatively more acute crowns.

Pseudoloricaria Bleeker, 1862

Pseudoloricaria also contains a single species, P. laeviuscula, which occurs in the middle and lower Amazon basin in Brazil only, reaching 305 mm in standard length.

Pseudoloricaria has smaller and more numerous abdominal scutelets: 9-15 border the pre-anal scute anteriorly. There are 33-37 lateral- and 22-27 coalescing lateral body scutes, 5-10 thoracic scutes, up to 12 teeth in the premaxilla and up to 13 teeth in the dentary. Tip of the snout with a narrow naked, horizontal area, reaching to about a vertical from the anterior point of the orbital rim.

Plate XXXIX.

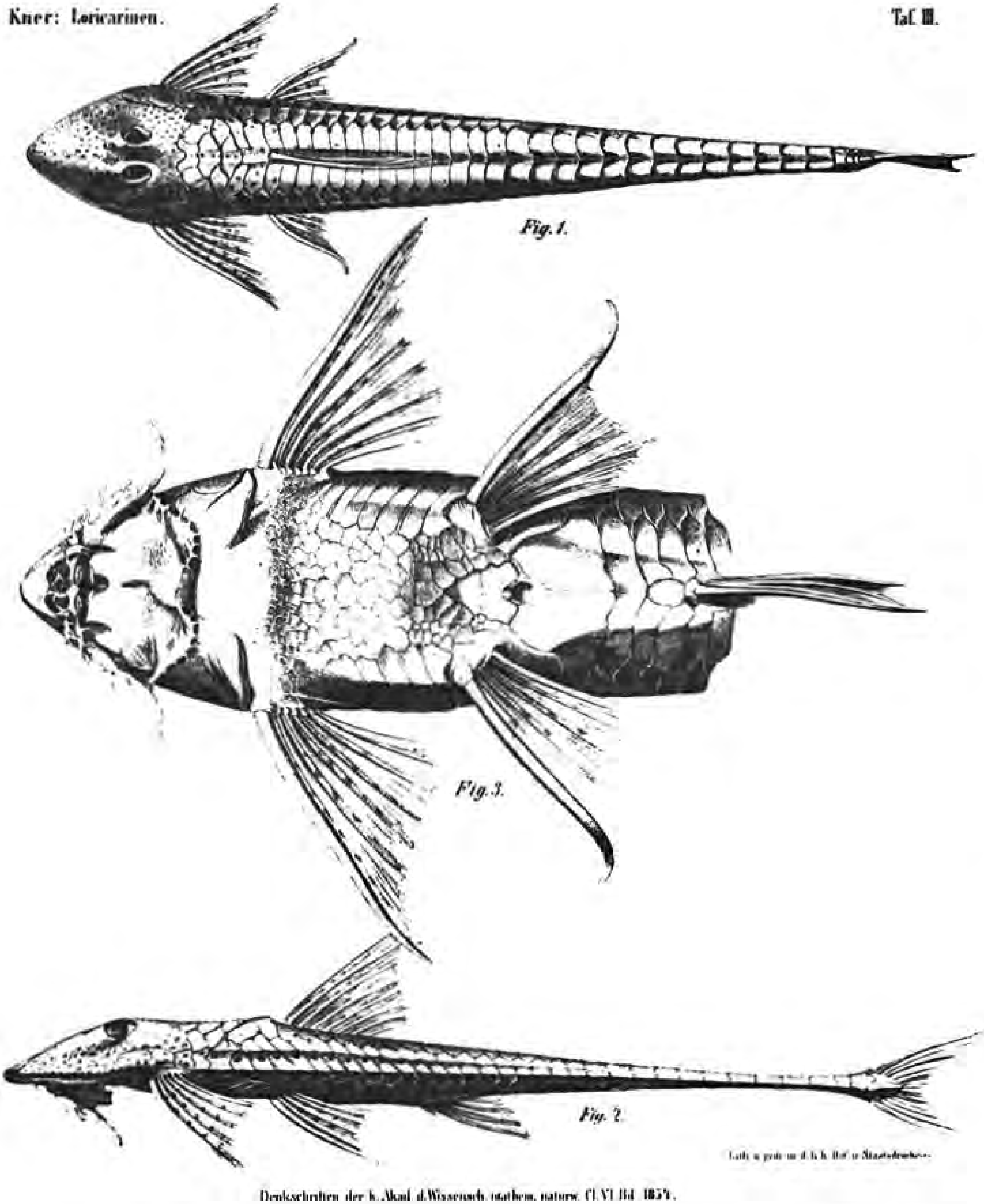


Fig. VI,52. - Pseudoloricaria laeviuscula (Valenciennes, 1840) (after Kner, 1854, pl. 3).

Plate XL.

Fig. VI,53. - Loricariichthys platymetopon Isbrücker & Nijssen, 1979, paratype, male, ZMA 110.929, sl 186 mm (photo L. A. van der Laan, ITZ, Amsterdam).

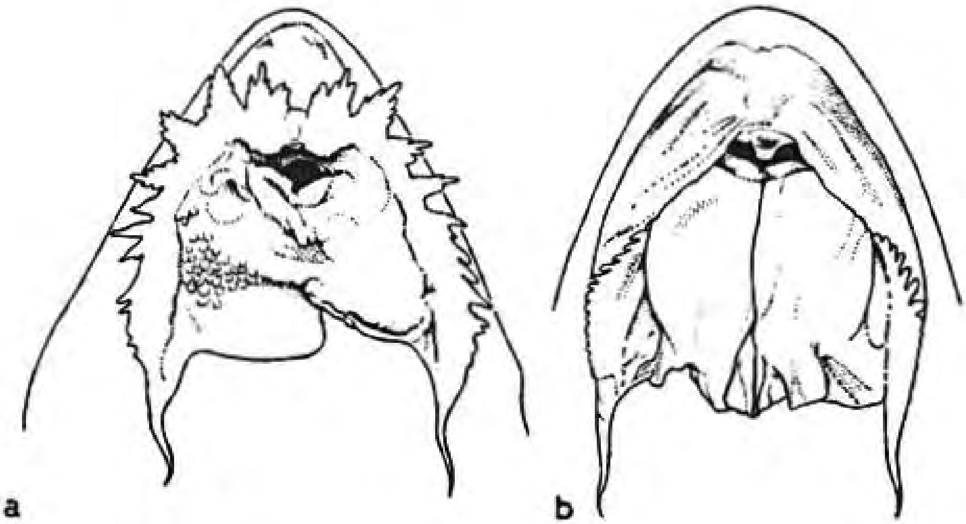


Fig. VI,54. - (a) Pseudoloricaria laeviuscula (Valenciennes, 1840), female, ZMA 112.740, sl 209 mm, upper lip spread out to show its characteristic flaps, and (b) Loricariichthys acutus (Valenciennes, 1840), female, BMNH 1925.10.28:300, sl 223 mm (drawing J. Zaagman, ITZ, Amsterdam).

Secondary sexual dimorphism. - Similar in all respects to that in Limatulichthys, but sometimes males have a longer lip than in that genus.

LORICARIICHTHYINA

Loricariichthys Bleeker, 1862

The genus Loricariichthys contains 16 described species, occurring in the Guianas (including the Orinoco River basin), the upper– and middle Amazon, the Rio Paraná system, and in southeastern Brazil. The largest standard length on record is 405.5 mm, the smallest mature male 156 mm.

Loricariichthys is the only genus of the subtribe Loricariichthyina, which is distinguished from the other subtribes in its specialized dentition and lip structure.

The following diagnosis is based largely upon that by Isbrücker & Nijssen (1976b: 109-110). Edges of right and left sides of upper lip separated from each other. A rather smooth-edged flap just anterior to the outer sides of the premaxillae, continuing as acute small flaps with principally the same structure (particularly in females) as the flaps in this same area of the lip of Pseudoloricaria and Limatulichthys. Small, acute barbel-like papillae are generally present posterior to these flaps. Teeth very reduced in size, in this respect and in shape they are diagnostic for the genus. There are up to 17 teeth in the premaxilla and up to 34 in the dentary. Abdomen completely covered with usually conspicuously large scutes, arranged into one to five median series. Orbital rim with a conspicuous, often very large posterior notch. Tip and sides of the snout with an often conspicuous, narrow naked horizontal line, the extent of which varies with the species.

Additional details are recorded for Loricariichthys in a comparison with Hemiodontichthys below.

Secondary sexual dimorphism. - Mature males of Loricariichthys have an extremely long and broadly expanded, thin lower

Plate XLI.

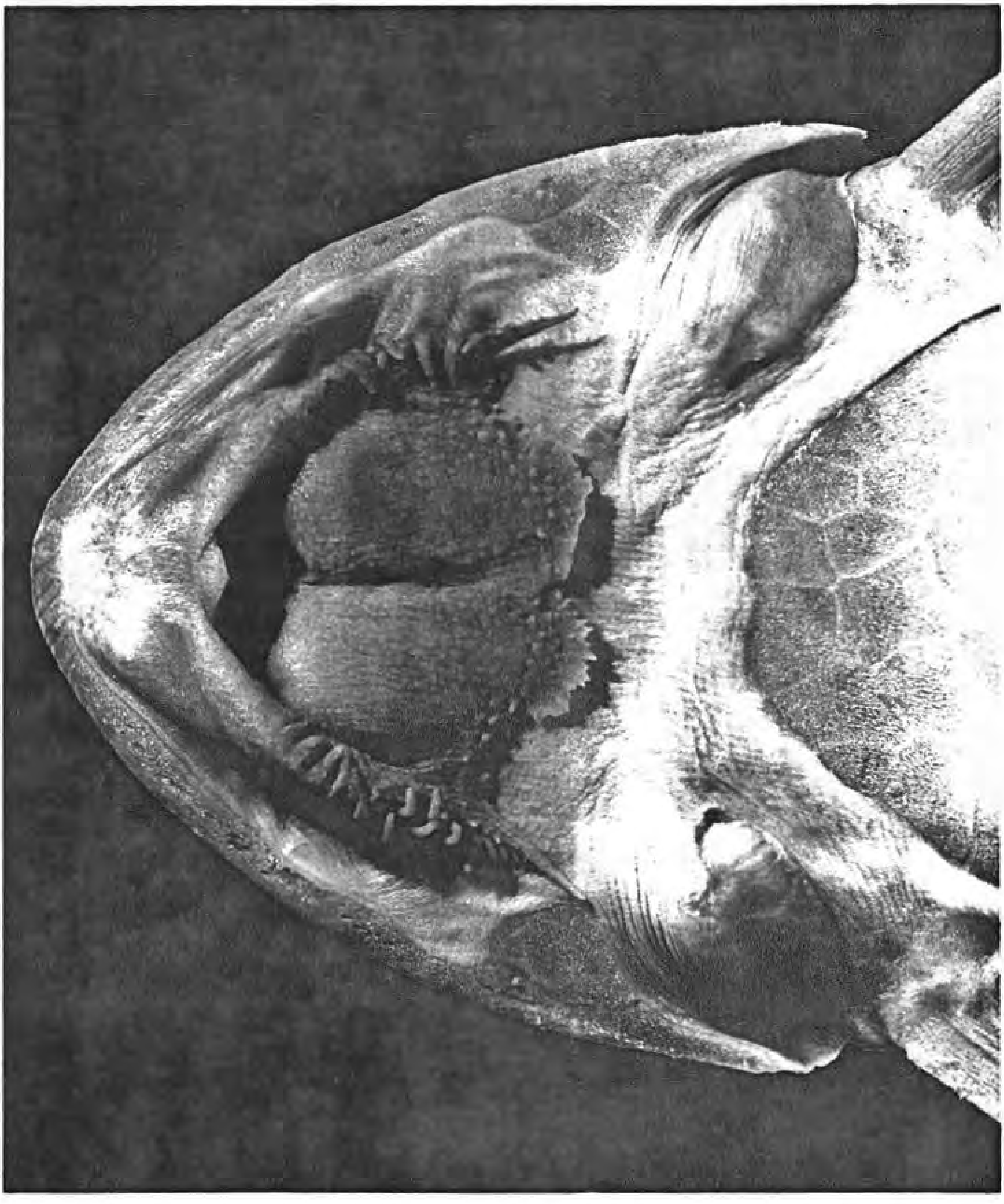


Fig. VI,55. - Loricariichthys platymetopon Isbrücker & Nijssen, 1979, paratype, female, USNM 181755, sl 276.5 mm (photo L. A. van der Laan, ITZ, Amsterdam).

lip, lacking the cushion-like thickening in the middle of each half lower lip in the females. Often the dorsal side of the lips are darker in males than in females (protective colour?). In addition, mature males have the crowns of the teeth with a broader, rounded apex; females and juveniles have teeth with an acute tip.

One hundred and twelve specimens of various Loricariichthys species were examined, and their morphometric and meristic data were compared to those of the Rineloricariina and of the Pseudoloricariina; Loricariichthys is apparently allied to at least the Pseudoloricariina. Apart from the characters mentioned, Loricariichthys has the same range in number of lateral body scutes as the Pseudoloricariina: 30-37, whereas the Rineloricariina have 28-33 lateral body scutes. Loricariichthys has 16-34 coalescing lateral body scutes, the Pseudoloricariina 18-27, the Rineloricariina 13-22. Loricariichthys shows almost the same variability in postdorsal length as the Rineloricariina: 1.6-2.2 in standard length against 1.5-2.2 in the latter. The snout length in Loricariichthys is 1.8-2.3 in head length, 1.7-2.2 in the Pseudoloricariina and 1.6-2.4 in the Rineloricariina. The lower lip of Loricariichthys varies from 1.3 to 7.3 in head length; in the Pseudoloricariina it is 1.8-8.1 and in the Rineloricariina 3.9-15.0. Thoracic length is 1.2-2.0 in head length in Loricariichthys, 1.2-1.8 in the Pseudoloricariina and 1.1-1.7 in the Rineloricariina. The abdominal length in head length is 1.4-2.0 in Loricariichthys, 1.2-1.4 in Pseudoloricariina, and 1.1-1.8 in the Rineloricariina. No further trends are apparent in the other data.

HEMIODONTICHTHYINA

Hemiodontichthys Bleeker, 1862

Hemiodontichthys contains only a single species, H. acipenserinus, which is distributed in a vast area, including the Amazon River, the Essequibo River, and the Rio Paraná system. The largest known specimen has a standard length of 134 mm, the

Plate XLII.

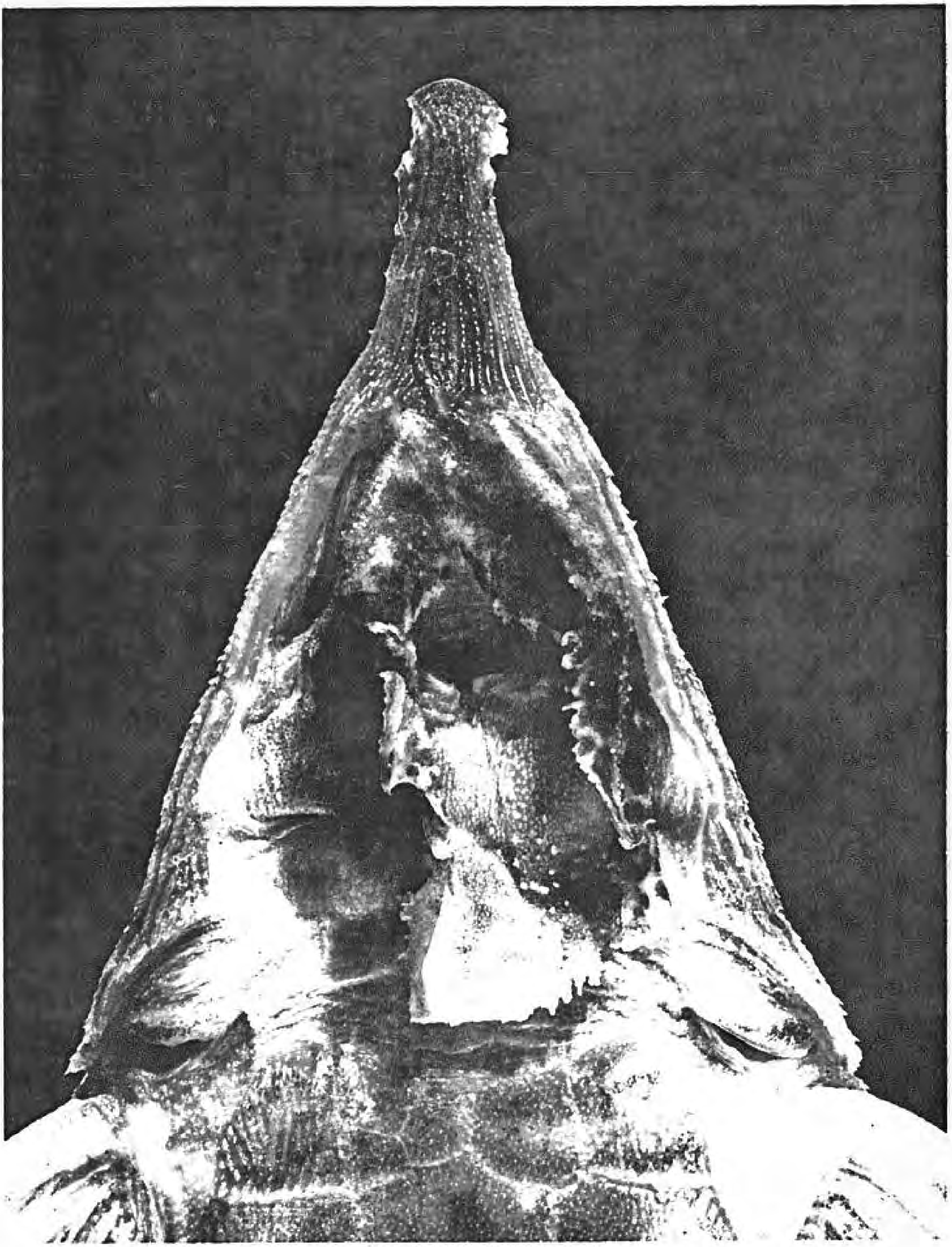


Fig. VI,56. - Hemiodontichthys acipenserinus (Kner, 1854), male in MCZ 46059, sl 130 mm (photo L. A. van der Laan, ITZ, Amsterdam).

smallest mature male is 75.1 mm.

Isbrücker & Nijssen (1974b) published a review of this unique species, which differs from all other Loricariini at subtribal level. Our diagnosis of Hemiodontichthys had the following effect: snout acute, long, usually with a terminal expansion provided with distinct, recurved, tooth-like odontodes; tip of the snout with a narrow naked horizontal area; small teeth in the dentary; premaxillae rudimentary, toothless; odontodes on dorsum of head and body, and on both sides of the rostrum, arranged into strongly undulate lines; odontodes are stronger and form distinct ridges along the lateral body scutes; breast and belly covered by large, mostly square-like scutes arranged into 3 transverse median rows (the outer rows are thoracic scutes, the middle row are abdominal scutes); anterior to these scutes two to several more, small, triangular or irregular scutelets may be present; eye moderate, orbit with a conspicuous posterior notch; supraoccipital process with a broad tip.

Secondary sexual dimorphism. - Remarkably similar in all respects to that in Loricariichthys (see pp. 115-116).

Subsequent to the publication of our study on Hemiodontichthys (in connection with a – still unfinished – revision of the almost always long-snouted and sometimes short-snouted species of Farlowella), we used to subtract the ventrorostral extension from all those measurements of which it is part. This revision of morphometric characters in 77 specimens of Hemiodontichthys resulted in the following ratios, useful for comparison (characters numbered 2-10 are ratios of standard length, characters 11-24 are ratios of head length, and characters 25-29 are the counts, added to provide a review of all available information):

1) standard length 58.2-134 mm;
2) head length 3.7-4.7;
3) predorsal length 2.8-3.1;

4) postdorsal length 1.7-1.9;
5) postanal length 1.8-2.1;
6) dorsal fin spine length 5.5-6.1;
7) length first dorsal fin ray 5.4-6.6;
8) anal fin spine length 6.6-7.7;
9) pectoral fin spine length 6.6-7.0;
10) pelvic fin spine length 7.9-10.4;
11) snout length 2.1-2.7;
12) ventrorostral length 2.2-3.6;
13) length lower lip 1.9-6.3;
14) thoracic length 1.3-1.6;
15) abdominal length 1.5-1.7;
16) maximum orbital diameter 3.7-4.6;
17) interorbital width 3.6-4.9;
18) cleithral width 1.1-1.5;
19) supracleithral width 1.4-1.9;
20) head width 1.2-1.5;
21) head depth 2.4-3.2;
–) body depth and width at origin of dorsal fin, and body width at origin of anal fin were not measured;
22) depth caudal peduncle 13.9-17.7;
23) width caudal peduncle 7.6-10.1;
24) length maxillary barbel 2.3-3.0;
25) lateral body scutes 27-29;
26) coalescing lateral body scutes 11-14;
27) thoracic scutes 4-5;
28) premaxillary teeth none;
29) mandibulary teeth up to 16.

Hemiodontichthys and Reganella are compared to each other on pp. 109-111.

As already noticed under 'Secondary sexual dimorphism', Hemiodontichthys is in this character strongly reminiscent of Loricariichthys, more than of any other genus. This is not where similarities end: both these genera have a larger posterior orbital notch than any other Loricariid, while some *Loricariichthys* species have median abdominal scutelets in all details strikingly similar to *Hemiodontichthys*. Even the lips of both genera (although actually slightly different) agree to a larger extent than one would expect, considering the great differences in general form. A large number of morphometric data of *Hemiodontichthys* fall or almost fall within the range of variability of (the more numerous species of) *Loricariichthys*: standard length, head length, predorsal–, postdorsal–, and postanal lengths, dorsal fin spine and its first ray lengths, pectoral fin spine length, lower lip length, thoracic– and abdominal lengths, maximum orbital diameter, interorbital width, cleithral width, supracleithral width, head width, head depth, depth caudal peduncle, and length of the maxillary barbel are all characters agreeing with *Loricariichthys*. Even the same number of thoracic scutes is found in both *Loricariichthys* (with a larger range of variability: 4-9) and *Hemiodontichthys*.

However, *Hemiodontichthys* also shows great differences with *Loricariichthys*: shape of head and snout; presence versus absence of a ventrorostral extension; odontode development; absence versus presence of premaxillary teeth; shape and maximum number of mandibulary teeth; the anal fin spine is 4.9-7.0 in standard length in *Loricariichthys*, 6.6-7.7 in *Hemiodontichthys*; pelvic fin spine length 5.4-9.4 in standard length in *Loricariichthys*, 7.9-10.4 in *Hemiodontichthys*, snout length 1.8-2.3 in head length in *Loricariichthys*, 2.1-2.7 in *Hemiodontichthys*, width of the caudal peduncle 4.8-9.7 in head length in *Loricariichthys*, 7.6-10.1 in *Hemiodontichthys*. In *Loricariichthys* there are 30-37 lateral body scutes (only 27-29 in *Hemiodontichthys*, see a further comparison below), 16-34 coalescing lateral body scutes (11-14, see below), up to 17 premaxillary teeth (none), up to 34 mandibulary teeth (16).

The teeth of *Hemiodontichthys* are reminiscent in quite some detail of those in the *Pseudohemiodon*-group of genera, not of

Loricariichthys at all. Still, to me the relationships of *Hemiodontichthys* appear to be more close to *Loricariichthys* than to any other genus.

If the tooth shape of *Hemiodontichthys* would be a convergency with the *Pseudohemiodon*-group of genera (and with *Reganella* and *Planiloricaria*, which also have similar teeth in the dentary), this presumed *Loricariichthys*/*Hemiodontichthys* relationship could more clearly be visualized, but there is no way of testing this hypothesis. Likely, both *Hemiodontichthys* and *Loricariichthys* have a shared ancestor. The lineage which gave rise to *Hemiodontichthys* likely split off from the lineage leading to *Loricariichthys* before the latter developed its peculiar dentition.

In fact, Isbrücker & Nijssen (1974a: 67-73) proposed an informal and provisional subdivision of the Loricariinae into 6 groups. It included the *Pseudohemiodon*-group, including *Pseudohemiodon* and *Rhadinoloricaria* (both of which are now assigned to the *Pseudohemiodon*-group within the Loricariina), and the genera *Hemiodontichthys*, *Reganella*, and *Planiloricaria* (each of which is now considered representative of a distinct subtribe). Our 1974 *Pseudohemiodon*-group was assembled on account of the shared tooth-characteristics: spoon-shaped, either simple or bilobed, in size about intermediate between those of *Loricaria*, *Rineloricaria*, *Spatuloricaria*, *Pseudoloricaria*, *Sturisoma*, *Harttia*, *Lamontichthys*, *Harttiella*, and *Farlowella* on the one hand, and those of *Loricariichthys* on the other hand. To this first group belong several genera established after 1974, mostly based upon species already known: *Cteniloricaria*, *Pterosturisoma*, *Sturisomatichthys*, *Metaloricaria*, *Ixinandria*, *Dasyloricaria*, *Ricola*, *Paraloricaria*, *Brochiloricaria*, and *Limatulichthys*.

Hemiodontichthys has rather few lateral body scutes (27-29); the Reganellina have 29-30, the Rineloricariina 28-33, all other

Loricariini 30 or more. In the Harttiini, only Harttiella has 27-28 lateral body scutes, and in the Acestridiini 25-27 are present; all other Loricariinae have 30-40.

The number of coalescing lateral body scutes in Hemiodontichthys is also quite low: out of 47 specimens (enabling 94 counts), 14 coalescing scutes are in 4 counts, 13 of such scutes in 34 counts, 12 scutes in 36 counts, 11 scutes in 18 counts and 8 and 7 scutes in only 1 count each. The coalescing scutes in Reganella are 14-15, in Pseudohemiodon 14-21, in Crossoloricaria 13-20, in Rineloricaria 13-19, in all other Loricariini there are 16 or more coalescing scutes. Of the Harttiini, the fewest coalescing scutes are in Lamontichthys (14-21), Sturisomatichthys (14-16), and in Sturisoma (14-21). Farlowella has 10-20, and Acestridium (about) 10 coalescing lateral body scutes.

Next to this agreement in a low number of these scutes in Acestridium and Hemiodontichthys, these two genera are most remarkably similar in some other details (see p. 71) otherwise absent in all remaining Loricariidae.

Hemiodontichthys and Loricaria have pharyngeal teeth which are most reminiscent of each other, and quite different from the pharyngeal teeth in Loricariichthys, for example. Most representatives of the Loricariidae are, however, awaiting an osteological examination.

VII DISCUSSION OF TAXONOMIC PROBLEMS

As stated in the introduction, my main efforts have been to complete a revision of the subfamily Loricariinae. The classification of the 28 genera of this subfamily into tribes and subtribes is based upon an extensive examination of almost all the primary type-specimens supplemented by either a few or numerous additional individuals representing practically each of the described species. Although the status of some forms – which are at least tentatively accepted at specific rank – is not yet always clear, I do not expect to find major changes in the classification of the known Loricariinae. Much work, however, remains to be done before all these Loricariinae can be quickly identified by reliable keys.

In contrast to the subfamily Loricariinae, however, numerous more serious taxonomic problems are still involved with the subfamilies Lithogeneinae, Neoplecostominae, Hypostominae, Ancistrinae and Hypoptopomatinae. The reason of these problems is twofold. First, there are many species well described and illustrated, but often some detail necessary to discriminate between closely related species is not or insufficiently stated. There are many descriptions which provide all information necessary for identification of the species. Still, some of the material on which these descriptions have been based proved to be quite different from what the description made me to expect: it is often hardly possible to interpret a description if not accompanied by illustrations. Second, a lot of original descriptions are incomplete now, rendering unreliable subsequent though excellent descriptions and illustrations of a taxon given the same name. The subsequent authors often did not confirm the identity of their material. These problems can be solved only when one succeeds to re-examine all of the material of such taxa, including type-specimens whenever possible. Most of the synonymy available in the literature is in my opinion too weakly established. However, it is likely that revision of each of especially the larger genera will result in some reduction in the number of valid species.

There are Loricariids of which the young is virtually only smaller than the adults and of which both parents do not show sexually dimorphic characters. Other young Loricariids differ from the adult in some characters, whereas striking secondary sexual dimorphism may occur in various characters in the different groups.

The classification recently (1980) proposed by me differs in several points from previous ones. It is the first reclassification since Gosline's (1945) catalogue which takes all taxa into account. Of the subfamilies presently recognized, the Lithogeneinae consists of 1 genus, just like the Neoplecostominae, the Hypostominae embrace 16 genera, the Ancistrinae 18, the Hypoptopomatinae 9, and the Loricariinae 28.

The Lithogeneinae comprises a single species, Lithogenes villosus. It was described from the still unique holotype, whose characters are incompletely known. Some of the recorded characters need confirmation. The subfamily is tentatively accepted, but I feel that Lithogenes might as well prove to represent a highly specialized genus of the Hypostominae, possibly with neotenic rather than with archaic characters as suggested by Gosline (1947). If my assumption would be correct, Lithogenes occupies a place within the Hypostominae comparable to the position of the Pseudacanthicini within the Ancistrinae.

The subfamily Neoplecostominae was established by Regan (1904) for the genus Neoplecostomus. He observed that it is far more nearly allied to Loricaria (sensu Regan) than to Hypostomus. Regan assigned only one species to Neoplecostomus, but I prefer to consider N. granosus and N. microps as distinct species until a revision has been accomplished. Gosline (1947) expanded the limits of the Neoplecostominae greatly, including several genera previously referred to the Hypostominae (= Plecostominae of many authors). However, the distinction between the Neoplecostominae and Hypostominae became so vague that it is hardly possible to recognize the group into which a given genus should be placed. Therefore, I prefer to preserve the Neoplecostominae in Regan's (1904) sense, although the systematic position proposed by Gosline appears to be an improvement. A detailed (also osteological) treatment of the Hypostomine genera has to be made before Neoplecostomus can be satisfactorily compared.

I have considered in vain a subdivision of the Hypostominae into tribes, one of them representing the more primitive and the other including the more specialized genera. On external characters alone, such a subdivision can not be made. Isorineloricaria, Hypostomus, Cochliodon, and Pterygoplichthys appear to be more closely related to each other than to the remaining genera of the Hypostominae. The latter three genera are considered as the most specialized of this subfamily. With the exception of these three genera and of Pseudancistrus, all genera now included in the Hypostominae had been assigned to the Neoplecostominae by Gosline (1947).

Pseudancistrus is still a genus which is rather difficult to classify, it possibly being a link to the Ancistrinae. Pseudancistrus also is reminiscent in several, possibly only superficial, characters of Hemipsilichthys. In addition, it is strikingly reminiscent of the Ancistrine genus Lasiancistrus. The actual relationship between these three genera is insufficiently known.

The Ancistrinae are distinguished from all other Loricariidae by the possession of a peculiar patch of actively movable spines, modified odontodes originating underneath the bare skin anterior to the operculum. In rest, these spines are retracted beneath the operculum. An internal median process of the operculum reaches the posterior, hemispherical inner face of the patch of spines. Alexander (1966: 141, fig. 18) described this structure in action: "When the operculum is adducted, the spines lie in a groove ventral to it, but when it is abducted the clump of spines swings laterally and anteriorly to project from the side of the head. When operculum and spines are adducted, the area of skin bearing the spines is concave and the spines are closely packed, but when they are abducted the skin flattens and the spines spread. The dilator operculi, which abducts the spines, is greatly enlarged and almost reaches the dorsal mid-line. A cavity has formed for it between the braincase and the dermal roof of the skull. No function of the spines is known. Their hooks curl anteriorly, so they seem unlikely to be used as anchors." From living Ancistrinae, it can easily be seen that this spiny apparatus is projected especially for protection and during close contact between specimens of the same species. Ancistrinae kept in tanks appear to maintain a territory.

Throughout the subfamily Ancistrinae there are grading stages in which this unique apparatus has evolved – often it is one of the easiest characters to discriminate between genera. It seems improbable that this structure has evolved more than once in the Loricariidae: among fishes it is unique. It is of interest to note that in many Trichomycteridae, one of the three families of Loricarioidea without dermal ossifications, odontodes are well developed in and largely restricted to the opercular area (see p. V,4). These odontodes of Trichomycteridae are not actively movable as in the Ancistrinae.

It is possible that a genus like Pseudancistrus evolved from an ancestor shared with Lasiancistrus and lost this spine structure subsequently. In that case Pseudancistrus is incorrectly placed among the Hypostominae. To me it seems that the Ancistrinae are monophyletic. In most of its characters it parallels the Hypostominae, and if not for the opercular spine structure both would be much more difficult to separate. The Ancistrinae are subdivided into three tribes. I imagine than an evaluation of the entire subfamily as very specialized representatives of the Hypostominae is also acceptable. This would then result in the recognition of the Hypostomini, Ancistrini, Acanthicini, and Pseudacanthicini within the Hypostominae. The considerable range of both the Hypostominae and the Ancistrinae in terms of number of genera and species as well as the still problematic interrelationships of the Hypostominae, induces me to recognize both groups at subfamily level.

Up to Regan's time, the genus Pterygoplichthys has been related with the present Ancistrinae. Large specimens of this genus often have prominent odontodes along the posterior margin of the operculum, originating from dermal ossifications rather than from the naked skin as in Ancistrinae. The odontodes of Pterygoplichthys are incapable of muscularly directed articulation. In spite of their strong resemblance to the spine structure of the Ancistrinae, they are only superficially similar. Similarly enlarged odontodes also occur along the opercular margin in various species of other genera within the subfamilies Hypostominae, Ancistrinae, and Loricariinae, and may better be compared to enlarged odontodes present on other parts of the body.

The subfamily Hypoptopomatinae, established in 1890 and never since questioned, consists of two tribes. One of these is the Otocinclini which contains 7 genera (two of which are being published by Britski), whereas the nominal tribe contains two valid genera. At present, none of the published genera, with the exception of Parotocinclus (which was revised by Garavello, 1977) appears to have been well delimited, rendering a correct classification of the numerous species impossible. Dr Britski recently informed me that the genus Pseudotocinclus shows some characters which are intermediate between those of the Hypoptopomatinae and the Hypostominae, thus confirming the suggestion expressed by Nichols (1919c), who established this genus.

Finally, Kner (1854a: 74) suggested that his "Hypostomidae" ("Hypostomiden" in a footnote to p. 74) might or might not belong to the same family as his "Loricata" including the subfamily (or group, in Kner's sense) Loricariinae. Subsequently Kner (1854b) positively united both groups in one family.

Regan (1911: 577) even went further, stating: "It seems to me that if the Argiidae [Astroblepidae] are to be separated off as a distinct family, the Plecostomidae [Hypostomidae] also should be recognized, as they differ quite as much from the Loricariidae."

Increasing knowledge about the mailed Loricariidae as currently understood might support Kner's and Regan's suggestion, although at present such a further separation would be a mere speculation. In perspect of the relationships recognized to exist between the families within the superfamily Loricarioidea (Trichomycteridae, Callichthyidae, Scoloplacidae, Astroblepidae and Loricariidae), recognition of a family Hypostomidae next to the Loricariidae seems unwarranted. However, for an expression of the relationships within the current Loricariidae a separation of both groups at full family level is not completely without its merits.

VIII STRUCTURE OF THE JAWS

Our knowledge of the morphology and osteology of the family Loricariidae is rather poor. Most publications presenting descriptions of Loricariids are accompanied only by illustrations showing part of the (or the complete) exoskeleton. Gregory (1933: 196-198) states for the Loricariid catfishes that in them: "...the Siluroid skull attains its highest specialization", and: "the underside of the skull also exhibits a high degree of specialization, ...". Indeed, the skull of a Loricariid fish is essentially that of a Siluroid, though very specialized. Actually almost every character of Loricariids is different from its counterpart in other Siluriformes, due to specialization.

A comparative osteology of the family Loricariidae is still in an immature stage. To a large extent, this is due because representatives of all the genera are not yet available in any museum collection, and identified material available for osteological studies is nowhere abundant. On the second hand, I can at present only piecemeal add to the knowledge of Loricariid osteology, it being a subject which will take long before I am sufficiently acquainted with. The available osteological contributions of various authors dealing with Loricariidae are briefly discussed in chapter X (Miscellaneous notes).

The present chapter deals with one of the many important characters by which the family Loricariidae is distinguished from other catfish families, viz., the structure of the mouth, especially the jaws. This structure is often also important to discriminate between the different genera. Apart from the literature mentioned in chapter X, I have examined the Loricariid skeletons in BMNH (prepared by Günther and Regan), radiographs of specimens in BMNH, USNM, and ZMA, dissected specimens, and alizarin preparations of various species.

- It is necessary to describe the jaw structure of some more generalized catfish genera before describing the differences found in several genera, representative for the specialized family Loricariidae. For this purpose, I have selected the genera Rhamdia, Diplomystes, and Astroblepus, each representative of a different family.

* Rhamdia quelen (Quoy & Gaimard, 1824), Pimelodidae. Rhamdia Bleeker, 1858, represents a genus of the more generalized type of catfish.

The ethmoid expands greatly anteriorly, bearing a firmly fused premaxilla, which has a band of minute teeth with acute tips. The palatine is long and slender, articulating with the very reduced maxilla, which supports the long maxillary barbel.

The lower jaw (mandibula) consists of an angulo-articular (like in Loricariids) and of a curved, thin and elongate dentary, which bears a strip of fine teeth as in the premaxilla.

Pharyngeal teeth are present in more or less triangular pads in the lower posterior part of the branchial apparatus, whereas in the upper part there are two separate, roundish pads of pharyngeal teeth.

* Diplomystes papillosus (Valenciennes, 1840), Diplomystidae. Diplomystes Bleeker, 1858 (= Diplomyste Dumeril, 1856) shows many characters which are considered to be very primitive for a Siluroid, e.g., a toothed maxilla. The specimen examined is that described and illustrated already by Regan (1911, fig. 2c) and again by Alexander (1966, fig. 4). Several characters found in Characoids are also basically present in Diplomystes. There appears to be little point in relating this catfish to a discussion of Loricariid phylogeny, each being so opposite to each other.

* Astroblepus heterodon (Regan, 1908), Astroblepidae.
Of all families of Siluriformes, the Astroblepidae seem to be most closely related with the Loricariidae, so close that it often has been referred to the Loricariids as a distinct subfamily.

The palatine is a short, rather broad bone with several gradual facets. The maxilla is long and thin, reaching beyond the outer margin of the premaxilla.

An anterior extension articulates with the distal tip of the supraethmoid, but it is otherwise similar to that in the Loricariidae.

The mandibula is of quite the same design as that found in the Loricariidae, although the teeth in the dentary are not restricted to a cup-shaped (bowl-shaped) structure as in that family, but also originate from towards the inner side (towards the anguloarticular) of the jaw on the surface of the dentary, more or less resembling the more generalized catfishes.

A most perplexing character, in my opinion, is the presence of two different shapes of teeth occurring in both the dentary and the premaxilla of a single specimen (fig. 1). There is an anterior strip of spathula-shaped teeth (presumably the functional teeth show up in a single row only in complete specimens, although in the specimen examined (a skeleton) several teeth are seen, which in the Loricariidae would be in the position of replacement teeth). Posterior to this row there appear to be two functional rows of bifid teeth in the premaxilla, one such row in the dentary: these have a shape very reminiscent of those frequently found in those Loricariidae with rather large, solid teeth.

Fig. 1. Astroblepus heterodon. Two premaxillary teeth of one specimen.

▪ Having given the jaw structure and pharyngeal dentition in three comparatively more generalized catfish genera, I would like to describe here the same characters of the highly specialized Loricaria cataphracta, after which these characters will be described of the nine genera in comparison, representative for the family Loricariidae.

* Loricaria cataphracta Linnaeus, 1758, Loricariinae (Loricariini, Loricariina).

The ethmoid is a long, triangular bone, its dorsal surface bearing a broad, medial ridge. Anteriorly, the tip is somewhat expanded. Anteroventrally, the bone is produced into a rounded lamellar extension. It is to this process that the ligaments supporting the premaxilla are attached.

The premaxilla consists of a rather small, thin cancellous bone with the shape of a half, straight peanutshell, or cup. The premaxillae are entirely separated from each other medially and are syndesmotically connected. There is a large cartilaginous pad of tissue at the ventral side of the ethmoid, with which the premaxillae articulate.

The maxilla is quite large, although in most other (naked) catfishes it is considerably smaller. The maxilla articulates with the anterior face of the elongate palatine. The rictal (= maxillary) barbel originates from the maxilla. The upper lip skin over the maxilla covers a layer of loosely formed fibrous tissue, without any muscle being present. the rictal barbel is for its greater part included in the skin of the lips and connected to the maxilla by a cartilaginous knob.

The lower jaw consists of two parts: the tooth bearing dentary and the anguloarticular on which it is firmly jointed. Posteriorly, the anguloarticular articulates with the quadrate. There is a large hole in both elements of the lower jaw, containing a muscle.

Loricaria cataphracta has well-developed pharyngeal teeth, which are much like those in certain Labrids and

Plate XLVI (for pls. XLIII-XLV, see chapter V).

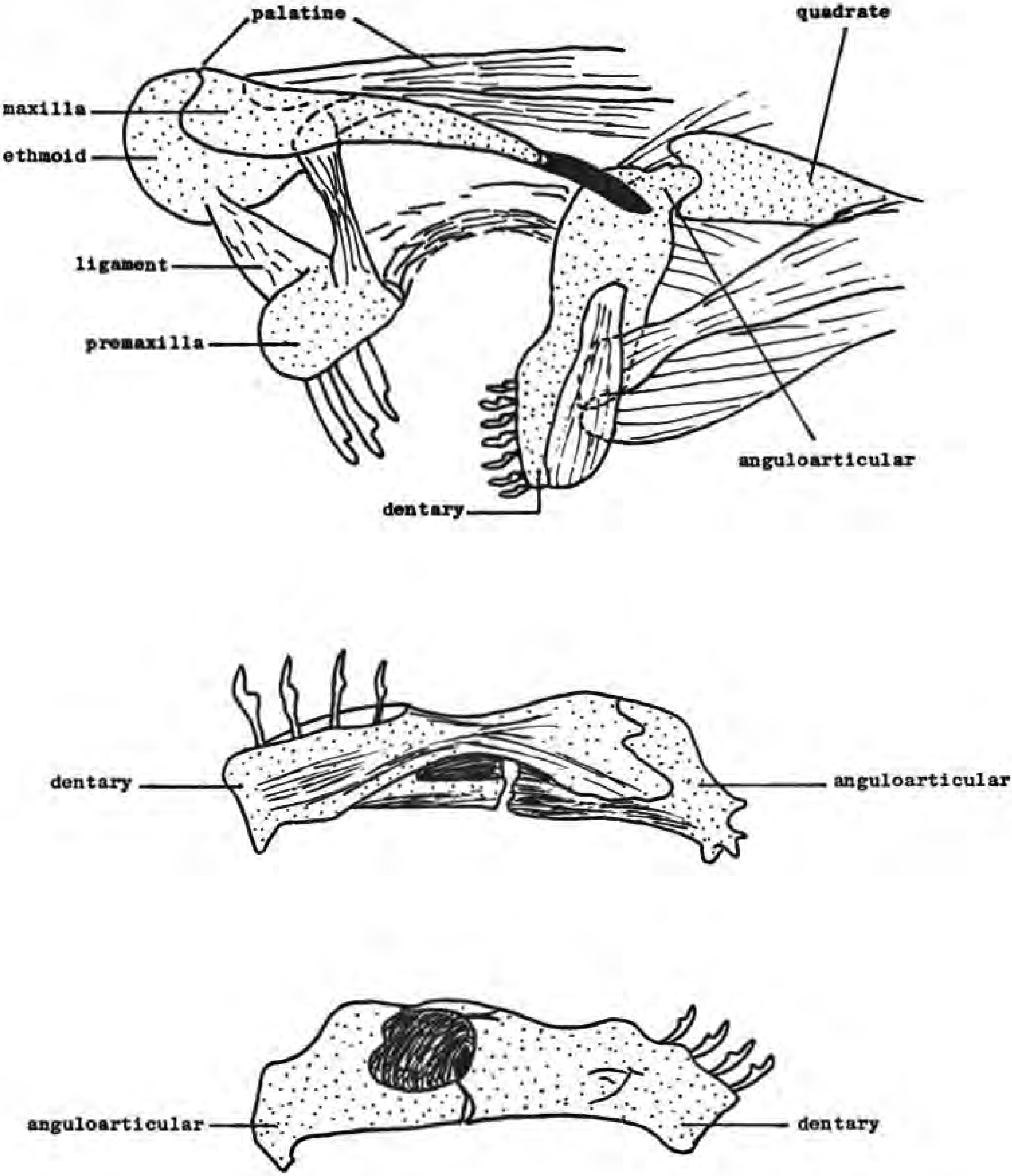


Fig. VIII,2. - Unfinished sketches of jaws of *Loricaria cataphracta*, made by Mr Howes while teaching me how to dissect.

Cichlids. They are situated close to the height of the origin of the pectoral fin spine, well back in the branchial apparatus.

The posterior series of the pharyngeal teeth are oval in shape, the narrow side of this oval being in a medial position, and the outer surface varies from smooth to somewhat course; the surface is flat and the teeth look to be grinding molariforms.

* *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979, Loricariinae (Loricariini, Loricariichthyina). This species has, compared to *Loricaria*, an elongate cup-shaped premaxilla, which is much reduced in size. The palatine is shorter and much broader than in *Loricaria* and articulates with a considerably better developed, long maxilla. Both elements of the lower jaw (dentary and anguloarticular) are more strongly developed than in *Loricaria*. The pharyngeal teeth are simple, acute (resembling the odontodes in shape) and much less conspicuous than in *Loricaria* (see also Angelescu & Gneri, 1949: 191, who illustrated the pharyngeals of *Paraloricaria vetula* (Valenciennes, 1840) and of *Loricariichthys anus* (Valenciennes, 1840), very reminiscent of those in *Loricaria cataphracta* and *Loricariichthys platymetopon*, respectively)

* *Hemiodontichthys acipenserinus* (Kner, 1854), Loricariinae (Loricariini, Hemiodontichthyina). This species has a well-developed 'rod'-like maxilla, like that of *Loricariichthys*.

The premaxillae are greatly reduced and never or barely ossified: both premaxillae are fused to a weak, cartilaginous structure which distally expands somewhat towards the sides. The lower jaw is much like that of *Loricariichthys*.

* *Sturisoma lyra* (Regan, 1904), Loricariinae (Harttiini, Harttiina). The ethmoid is conspicuous, elongated, and bends upwards from the rounded lamellar expansion.

The palatine and maxilla are greatly reduced in size when compared to *Loricaria* and *Loricariichthys*. However, the premaxilla is well-developed. It articulates with both the 'tip' of the ethmoid and the point where the maxilla articulates with the anterior face of the palatine.

Like the premaxilla, the dentary is well-developed. The anguloarticular part of the lower jaw is considerably smaller than the dentary.

Pharyngeal teeth are not found in the specimen examined, a skeleton.

* *Farlowella knerii* (Steindachner, 1883), Loricariinae (Farlowellini). The jaws of this species most closely resemble those of *Sturisoma lyra* just described.

* *Hypostomus verres* Valenciennes, 1840, Hypostominae. This species of *Hypostomus* has a considerably shorter ethmoid than found in the representatives of Loricariinae examined. The palatine and maxilla are also less developed. The premaxilla as well as the two elements of the lower jaw are well-developed.

* *Pterygoplichthys multiradiatus* (Hancock, 1828), Hypostominae, is very much like *Hypostomus verres* in its jaw structures.

* *Hypoptopoma joberti* (Vaillant, 1880), Hypoptopomatinae (Hypoptopomatini). The ethmoid is greatly produced, the roundish, ventrally expanding bony lamella with which the premaxilla articulates is situated well posterior from its tip. The premaxilla, palatine, and lower jaw are principally much like those in *Hypostomus verres*, although the bone is of an extremely cancellous structure. No maxilla is preserved in the skeleton studied.

* *Ancistrus stigmaticus* Eigenmann & Eigenmann, 1889, Ancis-

trinae (Ancistrini). The ethmoid is much like that of _Hypostomus_ (both have the tip expanded laterally) and so are the palatine and maxilla. The proximal part of the maxilla (articulating with the palatine) is more straight in _Ancistrus_ (against strongly curved in _Hypostomus_). The premaxilla is well-developed, forming a long, narrow oval cup. The anguloarticular is relatively short and small, whereas the dentary is remarkably well-developed.

* _Chaetostoma anomalum_ Regan, 1903, and _Chaetostoma breve_ Regan, 1904, Ancistrinae (Ancistrini). Ethmoid with the distal tip expanded laterally. Maxilla, very long and slender; premaxilla extremely well-developed, medianly more or less tightly connected with each other. Anguloarticular comparatively small, dentary well-developed, much like the premaxilla.

* _Pseudacanthicus serratus_ (Valenciennes, 1840), Ancistrinae (Pseudacanthini, Pseudacanthicina). The ethmoid is anteriorly slender and its distal tip curves downwards. The premaxillae are dorsally separate, but ventrally they are fused into a single, toothbearing cup. The maxilla is relatively short. The dentary is well-developed, larger than the anguloarticular. The left and right dentaries are anteriorly connected with each other by ligamentous tissue, whereas posteriorly they are free. The palatine is much like that in _Hypostomus_.

* _Neoplecostomus granosus_ (Valenciennes, 1840), Neoplecostominae. Very similar to _Hypostomus verres_. Dentary forms a cup-like structure with a triangular dorsal face (bearing the teeth). Palatine and maxilla like _Hypostomus_. Premaxilla somewhat more reduced in size than in _Hypostomus_.

IX ZOOGEOGRAPHY

The main pattern of distribution of fresh water fishes in South America is –according to Darlington (1957), modified by Géry (1969)–:

- Richness in main Rio Amazonas Basin.
- Less richness in adjacent river systems, north (Rio Orinoco, Guianas) and south (Rio Paraná) of Rio Amazonas.
- Isolation in Rio Magdalena and Rio Cauca.
- Moderate poverty in western drainages of Colombia, Ecuador, Peru and Bolivia.
- Progressive poverty southward, beginning in southeastern Brazil.
- Poverty and specialization of torrential fishes in the Andes and radiation in lakes.
- Antartic peripheral fauna in Patagonia.

The number of fish species in the different Faunas and presumed faunistic regions –after Fowler and Eigenmann, modified by Géry (1969)– are shown in fig. 1.

■ The richness of the Rio Amazonas can be explained by an acceleration of evolution in the Amazonian Basin after the Andean upheaval. The Amazonian Basin –formerly a marine environment (Harrington, 1962)– might have been repopulated from peripheral areas. This explains the similarities in the faunas in the peripheral areas as Géry (1969: 832) stated: "The Peruvian Amazon has more than 100 species in common with the remote Guianas, and this is also true for upper Rio Tocantins - Araguaia - Xingu in Brazil, upper Rio Meta in Colombia, etc., whereas the fauna is quite different in the centre."

The Ostariophysi originated in Gondwania. In early Cretaceous, Siluroids and Characoids diverged from the

Ostariophysi before the isolation of South America from Africa. After the isolation of South America in late Cretaceous, the Siluroids and Characoids (and from the latter the Gymnotoids) radiated.

- The Loricariids show a high degree of adaptive evolution. They are adapted to bottom life in cataracts and torrential streams. They show correlated characters, such as fusiform bodies, flattened breasts with often large pectoral fins, inferior mouth with a sucking disk, superior eyes, and several other adaptations.

The distribution of the various genera of Loricariidae is plotted on the maps in figs. 2-18. Except for the Loricariinae (of which distributional data are plotted from examined specimens), most distribution patterns shown, were achieved from those records in the literature permitting a sufficiently reliable generic identification (as compiled in my 1980 catalogue). Further studies very probably will show extension of the areas here illustrated to be inhabited by the various genera. Data on the distribution of some genera of Loricariidae is scarce; in several instances either the actual occurrence of a genus or the correctness of the identified genus still need verification, e.g., Rhinelepis (fig. 3), Neoplecostomus (fig. 2), Pseudancistrus (fig. 3), Hemipsilichthys (fig. 3), Cochliodon (fig. 4), Chaetostoma (fig. 8), and Pseudohemiodon (fig. 17).

- The pattern of peripheral distribution is recognizable in the Loricariidae. Hemiancistrus (fig. 6) and Pseudohemiodon (fig. 17) are good examples. To some extent, Pterygoplichthys (fig. 4), Lasiancistrus (fig. 5), Peckoltia (fig. 6), Chaetostoma (fig. 8), and Sturisoma (fig. 14) show a similar pattern of distribution. Of these genera most species occur in other drainages and/or in the upper courses of Amazonian tributaries —with only one or two species penetrating the main Amazon Basin.

- Members of the Loricariidae with plesiomorph characters —like *Lithogenes* (fig. 2), and *Neoplecostomus* (fig. 2)— do not occur in the Rio Amazonas. They are found in rivers on the Guianean Shield and on the (S.E.) Brazilian Shield. It should be noted that the occurrence of *Neoplecostomus granosus* in Cayenne must be verified. However, this pattern of distribution is found also for other genera with plesiomorph characters. For example, in *Delturus* (fig. 3), *Hemipsilichthys* (fig. 3), *Pseudancistrus* (fig. 3), *Corymbophanes* (fig. 3), *Megalancistrus* (fig. 6), *Harttia* (fig. 13), *Cteniloricaria* (fig. 13), and in *Paraloricaria* (fig. 16).

- Genera with apomorph characters are often found in the Amazonian Basin only. For example, *Parancistrus* (fig. 7), *Acestridium* (fig. 15), *Reganella* (fig. 17), *Pseudoloricaria* (fig. 18), and *Limatulichthys* (fig. 18).

- Many other genera with apomorph characters have a restricted area of distribution, contrasting to the genera just mentioned, occurring mainly outside the main Amazonian Basin: *Isorineloricaria* (fig. 4), *Cochliodon* (fig. 4), *Dolichancistrus* (fig. 5), *Panaque* (fig. 7), *Chaetostoma* (fig. 8), *Lithoxus* (fig. 10), *Pseudotocinclus* (fig. 11), *Lamontichthys* (fig. 13), *Pterosturisoma* (fig. 13), *Sturisomatichthys* (fig. 14), *Dasyloricaria* (fig. 16), *Spatuloricaria* (fig. 16), *Ricola* (fig. 16), and *Crossoloricaria* (fig. 17).

- Some genera with many species occur throughout tropical and temperate South America, viz.: *Hypostomus* (fig. 4), *Peckoltia* (fig. 6), *Ancistrus* (fig. 9), *Otocinclus* (fig. 11), *Hypoptopoma* (fig. 12), *Sturisoma* (fig. 14), *Farlowella* (fig. 15), *Rineloricaria* (fig. 16), *Loricaria* (fig. 17), and *Loricariichthys* (fig. 18).

Table IX,i.– Loricariidae. Distribution of the subfamilies Lithogeneinae, Neoplecostominae, and Hypostominae.

	Amazonas	Guianas	Orinoco	Magdalena	Andes	Paraná	E.-Brazil	Trans-Andes
Lithogeneinae								
Lithogenes	.	x	.	.	.	.	.	.
Neoplecostominae								
Neoplecostomus	.	(x)	.	.	.	x	.	.
Hypostominae								
(more primitive genera)								
Rhinelepis	x	.	.	.	.	?	.	.
Pseudorinelepis	x	.	.	.	.	.	.	.
Delturus	.	.	.	.	.	.	x	.
Pogonopoma	.	.	.	.	.	.	x	.
Pseudancistrus	.	x	.	.	.	.	?	.
Hemipsilichthys	?	.	.	.	.	x	.	.
Pareiorhaphis	.	.	.	.	.	.	x	.
Kronichthys	.	.	.	.	.	.	x	.
Corymbophanes	.	x	.	.	.	.	x	.
Upsilodus	.	.	.	.	.	.	x	.
Pareiorhina	.	.	.	.	.	.	x	.
Pogonopomoides	.	.	.	.	.	.	x	.
(more advanced genera)								
Isorineloricaria	.	.	.	.	.	.	.	x
Hypostomus	x	x	x	x	x	x	x	x
Cochliodon	(x)	.	x	x	.	?	.	.
Pterygoplichthys	x	x	.	.	.	x	.	.

Table IX,ii.– Loricariidae. Distribution of the subfamily Ancistrinae.

	Amazonas	Guianas	Orinoco	Magdalena	Andes	Paraná	E.-Brazil	Trans-Andes
Ancistrinae								
Ancistrini								
Lasiancistrus	x	x	x	x	.	.	x	x
Dolichancistrus	.	.	.	x	.	.	.	x
Cordylancistrus	.	.	x	.	.	.	.	.
Megalancistrus	.	.	.	.	.	x	x	.
Hemiancistrus	.	x	x	.	.	x	x	x
Peckoltia	x	.	.	.	.	(x)	(x)	.
Monistiancistrus	x	.	.	.	.	.	.	.
Parancistrus	x	.	.	.	.	.	.	.
Hypocolpterus	.	.	.	.	x	.	.	.
Panaque	(x)	.	x	x	.	.	.	x
Chaetostoma	.	.	x	x	x	.	.	x
Leptoancistrus	.	.	.	.	.	.	.	x
Lipopterichthys	.	.	.	.	x	.	.	.
Ancistrus	x	x	x	x	x	x	x	x
Acanthicini								
Acanthicus	x	.	.	.	.	.	.	.
Pseudacanthicini								
Pseudacanthicina								
Pseudacanthicus	x	x	.	.	.	.	.	.
Lithoxina								
Lithoxus	.	x	.	.	.	.	.	.
Exastilithoxus	.	x	.	.	.	.	.	.

Table IX,iii.– Loricariidae. Distribution of the subfamily Hypoptopomatinae.

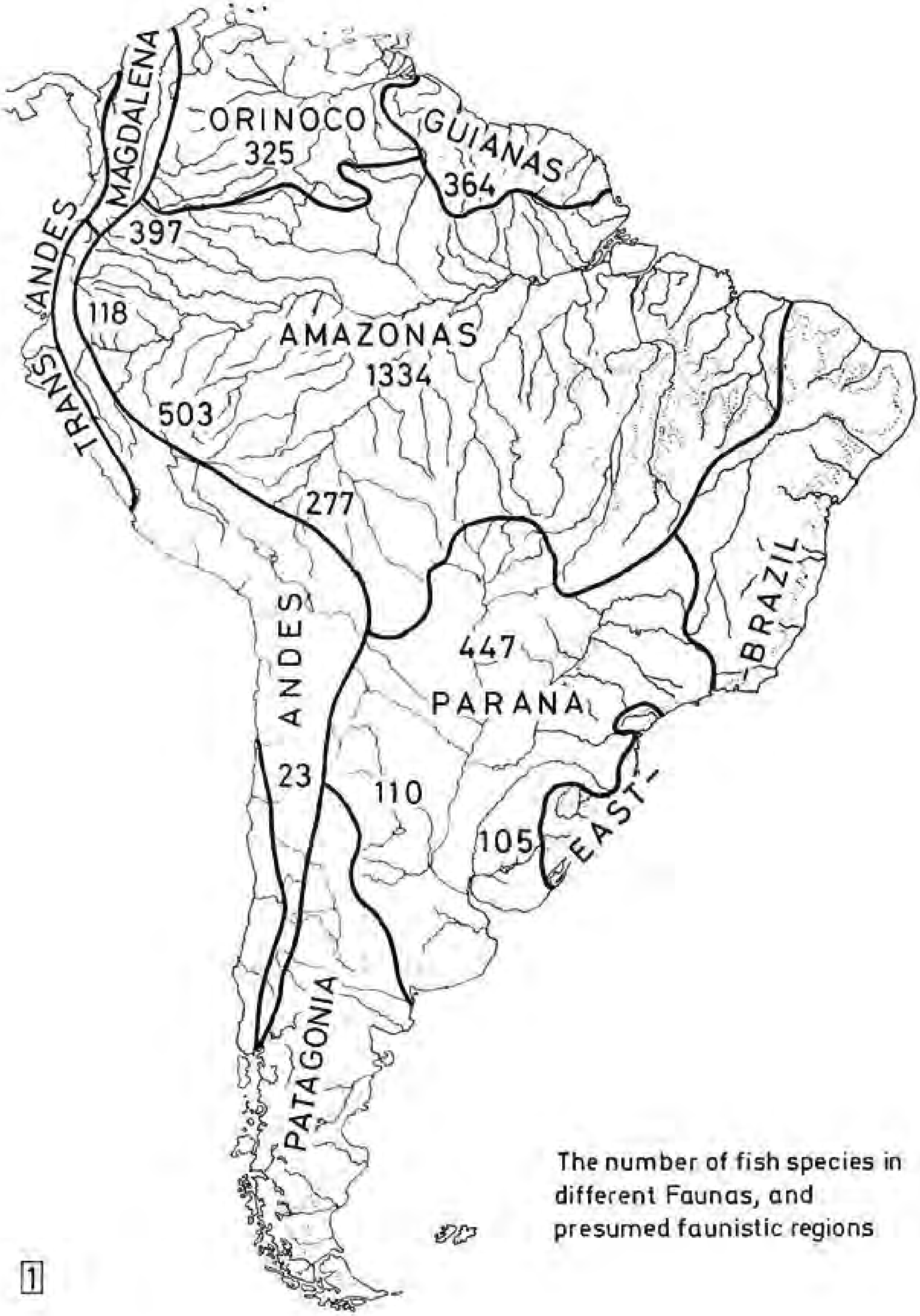
	Amazonas	Guianas	Orinoco	Magdalena	Andes	Paraná	E.-Brazil	Trans-Andes
Hypoptopomatinae								
Otocinclini								
Pseudotocinclus	.	.	.	.	.	x	.	.
Otocinclus	x	.	.	.	.	x	.	.
Parotocinclus	x	x	.	.	.	.	x	.
Otothyris	.	.	.	.	.	.	x	.
Hypoptopomatini								
Hypoptopoma	x	x	.	.	.	x	.	.

Table IX,iv.– Loricariidae. Distribution of the subfamily Loricariinae, tribes Harttiini, Farlowellini, and Acestridiini.

	Amazonas	Guianas	Orinoco	Magdalena	Andes	Paraná	E.-Brazil	Trans-Andes
Loricariinae								
Harttiini								
Harttiina								
Harttiella	.	x	.	.	.	.	.	.
Harttia	.	x	.	.	.	x	.	.
Cteniloricaria	.	x	.	.	.	.	.	.
Lamontichthys	(x)	.	.	.	x	.	.	.
Pterosturisoma	x	.	.	.	.	.	.	.
Sturisomatichthys	(x)	.	.	x	.	.	.	x
Sturisoma	x	x	x	x	x	x	.	x
Metaloricariina								
Metaloricaria	.	x	.	.	.	.	.	.
Farlowellini								
Farlowella	x	x	x	x	(x)	x	.	.
Acestridiini								
Acestridium	x	.	.	.	.	.	.	.

Table IX,v.– Loricariidae. Distribution of the subfamily Loricariinae, tribe Loricariini.

	Amazonas	Guianas	Orinoco	Magdalena	Andes	Paraná	E.-Brazil	Trans-Andes
Loricariinae								
Loricariini								
Rineloricariina								
Ixinandria	.	.	.	.	x	.	.	.
Rineloricaria	x	x	x	x	x	x	x	x
Dasyloricaria	.	.	.	x	.	.	.	x
Spatuloricaria	x	.	x	x	x	.	.	.
Ricolina								
Ricola	.	.	.	.	.	x	.	.
Loricariina								
Paraloricaria	.	.	.	.	.	x	.	.
Loricaria	x	x	x	.	.	x	.	.
Brochiloricaria	.	.	.	.	.	x	.	.
Crossoloricaria	.	.	x	x	.	.	.	x
Pseudohemiodon	x	.	x	.	.	x	.	.
Rhadinoloricaria	x	.	.	.	.	.	.	.
Planiloricariina								
Planiloricaria	(x)	.	.	.	x	.	.	.
Reganellina								
Reganella	x	.	.	.	.	.	.	.
Pseudoloricariina								
Limatulichthys	x	x	.	.	.	.	.	.
Pseudoloricaria	x	.	.	.	.	.	.	.
Loricariichthyina								
Loricariichthys	x	x	x	.	.	x	.	.
Hemiodontichthyina								
Hemiodontichthys	x	x	.	.	.	x	.	.



The number of fish species in different Faunas, and presumed faunistic regions


Lithogeneinae
Neoplecostominae
● Lithogenes
■ Neoplecostomus

2


Hypostominae
○ Rhinelepis
■ Pseudorinelepis
▲ Delturus
● Pseudancistrus
△ Hemipsilichthys
★ Corymbophanes
?

3


Hypostominae
○ Isorineloricaria
■ Hypostomus
▲ Cochliodon
● Pterygoplichthys
?

4

5


Ancistrinae
Ancistrini
○ Megalancistrus
■ Hemiancistrus
▲ Peckoltia
6

7


Ancistrinae
Ancistrini
?
O Chaetostoma
8

9


Ancistrinae
Acanthicini
Pseudacanthicini
○ Acanthicus
■ Pseudacanthicus
▲ Lithoxus
● Exastilithoxus

10


Hypoptopomatinae
Otocinclini
○ Pseudotocinclus
■ Otocinclus
▲ Parotocinclus

11


Hypoptopomatinae
Hypoptopomatini
O Hypoptopoma
12


Loricariinae
Harttiini
○ Harttiella
■ Harttia
▲ Ctenilorricaria
● Lamontichthys
△ Pterosturisoma

13

IX,22


Loricariinae
Harttiini
○ Sturisomatichthys
■ Sturisoma
▲ Metaloricaria
14


Loricariinae
Farlowellini
Acestridiini
○ Farlowella
■ Acestridium

15


Loricariinae
Loricariini
○ Rineloricaria
■ Ixinandria
▲ Dasyloricaria
● Spatuloricaria
△ Ricola
★ Paraloricaria

16


Loricariinae
Loricariini
?
○ Pseudohemiodon
■ Rhadinoloricaria
▲ Loricaria
● Brochiloricaria
△ Crossoloricaria
★ Planiloricaria
□ Reganella
17


Loricariinae
Loricariini
○ Loricariichthys
■ Pseudoloricaria
▲ Limatulichthys
● Hemiodontichthys

18

In addition to the publications referred to in my 1980 paper, various studies exist which deal with South American fresh water fishes including Loricariidae, or with general zoogeography of the area, e.g.: Eigenmann, 1905 (Panama), 1906 (South and middle America), 1907 (South America), 1920a (Colombia), 1920b (Cordillera of Bogotá), 1920c (Panama and Magdalena Basin), 1921a (west of the Maracaibo, Orinoco, Amazon, and Titicaca Basins), and 1921b (Pacific slope of Ecuador, Peru and Chili), A. de Miranda Ribeiro, 1937 (Brazil), Gosline, 1942 and 1944 (general, South America), Fernández Yépez, 1946, 1949, 1969a, 1969b, 1970, 1971 (Venezuela), Miles, 1947 (Magdalena Basin), Boeseman, 1960 (Trinidad), Lowe (McConnell), 1964 (Guyana), Miller, 1966 (central America), Mago Leccia, 1967, 1970 (Venezuela), Saul, 1975 (Amazonian Ecuador), Cala, 1977 (Colombia), Fink & Fink, 1979 (central Amazon), and Richter & Nijssen, 1980 (Surinam). The subjects of these publications (some of which contain referrences to additional works, which are not collected here) are not always strictly on zoogeography, also often containing ecological observations.

X MISCELLANEOUS NOTES

The various aspects of structure and life of the Loricariidae have been studied in more or less detail by several authors. Much information about external features is available in the numerous descriptive accounts, which I have attempted to summarize mainly in chapter VI of this work; references to these publications are provided in Isbrücker (1980). The present chapter mainly refers briefly to a variety of publications dealing with the aspects which are hardly or not yet discussed in previous chapters. These aspects may be grouped under three headings, not strictly defined: (1) structure, (2) ecology and behaviour, and (3) convergent adaptations of non-Loricariidae. Additional references to publications on those subjects are presented in many of the cited works, and no attempt has been made to collect all of them in this paper.

Structure of the Loricariidae

Regan (1924: 175-176) discussed the reversible evolution that took place in the Loricariidae. They evolved from naked Siluroids, which themselves evolved from scaled Ostariophysi. He stated: "The bony plates of the Loricariidae differ in histological structure from ganoid scales, but on their surface they bear conical denticles which are formed of dentine and enamel. Here we appear to have a genuine example of the redevelopment of an organ that has been lost...", and "...it seemed to me so curious that the skin of fishes, whose more remote ancestors had cycloid scales and whose more immediate ancestors were naked, should have retained, or regained, the power of forming denticles of the Selachian type over the whole surface of the body, that I gave Mr. C. T. Carter some material and suggested that he should examine it; the result is that he has described these denticles as formed of true dentine, capped with enamel (P.

Z.S. 1919, ii. p. 321)." Studies on the structure of the skin and odontodes of Loricariids and other fishes were e.g. published by Agassiz (1833: 74-76, figs. 30-32), Hertwig (1876), and Bhatti –who included an extensive bibliography– (1938). General (hardly or not including Loricariidae) publications on odontodes (also called dermal denticles, dermal teeth, integumentary teeth, denticulations, prickles, barbs, and spines) of interest for comparison are those by Miles & Poole (1967), Ørvig (1967, 1977), Poole (1967), and Nelson (1970). A thorough comparison of all families of Loricarioidea by Baskin (1978) demonstrated the importance of the odontodes.

Peyer (1922), on the basis of the structure of the fin spine and the presence of odontodes already separated the Loricariidae, Callichthyidae, and "...den Hauptteil der Trichomycteridae" from the Siluroidea, as the Loricarioidea.

Giltay (1936) gave an excellent account of the adaptive characters of the Loricariidae. Rössel (1968) more briefly discussed the adaptive characters of this family, now in comparison with other Siluriformes.

Hoedeman (1952: 1-2) proposed the Loricariicae as a new superfamily to include the Astroblepidae, Callichthyidae, and the Loricariidae. His conclusions were based largely upon Günther's (1864), Reissner's (1859), and Bridge & Haddon's (1893) osteological and anatomical studies of catfish groups.

Bertin & Arambourg (1958), Weitzman (in Greenwood et al., 1966), and Roberts (1973) provided interesting general comparisons between Loricariids and other Siluriformes.

Luengo (1965) recorded albinism in a specimen of _Rhinelepis aspera_.

Kner (1854a) quite in detail illustrated and described the internal skeleton of _Pseudoloricaria laeviuscula_, and Leege (1922) even more in detail the internal and external skeleton of _Hypostomus angipinnatus_ (the holotype, unfortu-

Plate XLVII.

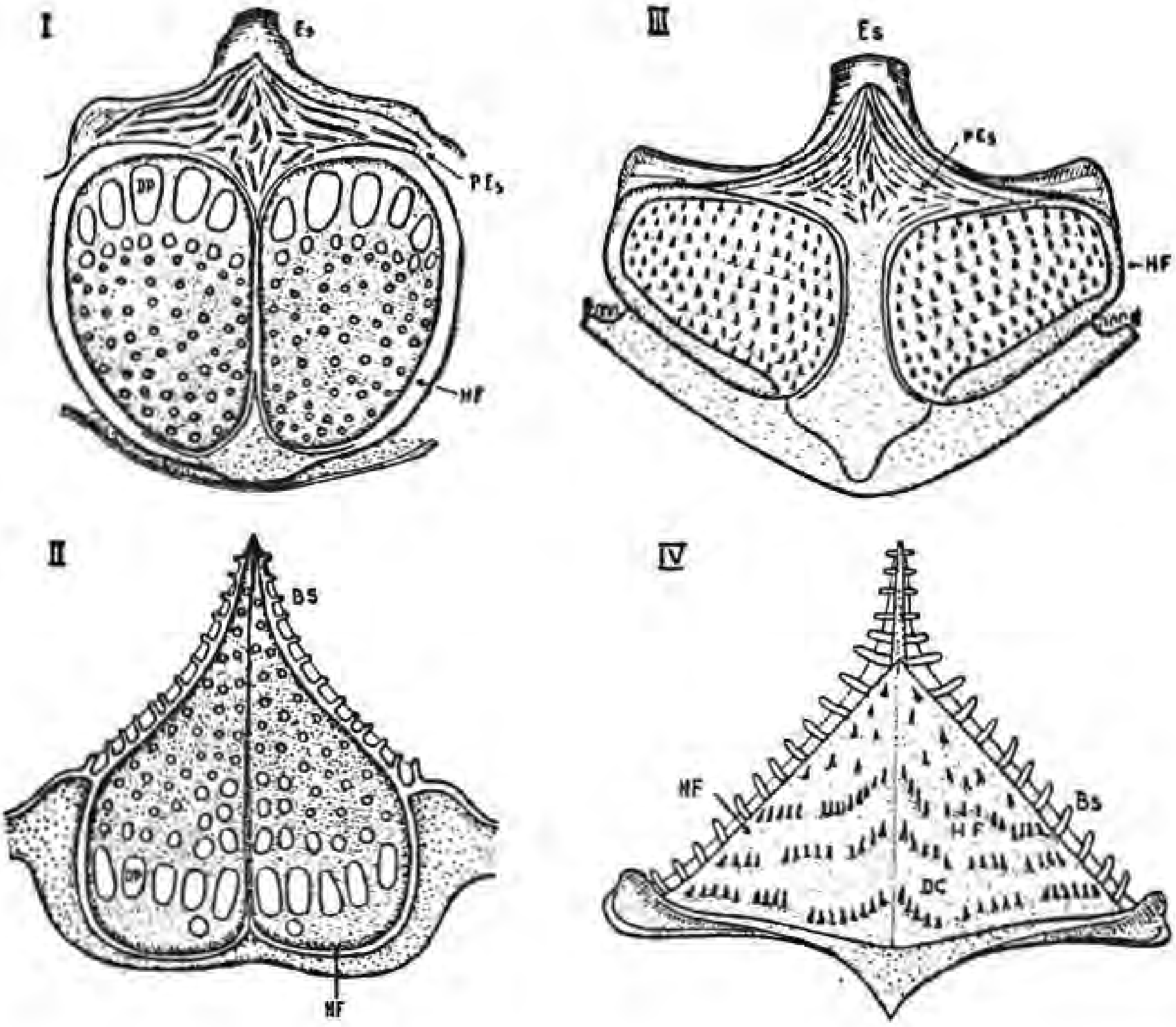


Fig. X,1. - Pharyngeal dentition of *Paraloricaria vetula* (Valenciennes, 1840): I, upper pharyngeal, II, lower pharyngeal, and of *Loricariichthys anus* (Valenciennes, 1840): III, upper pharyngeal, IV, lower pharyngeal (after Angelescu & Gneri, 1949, fig. 2).

nately). Descriptions (often with illustrations) of smaller osteological features were given by Reissner (1889, swimbladder and Weberian apparatus), Pollard (1895, oral cirri of Siluroids and the origin of the head in vertebrates), Starks (1926, ethmoid region of the skull), Gregory (1933, skull), Angelescu & Gneri (1949, pharyngeal dentition), Gomes (1955, pectoral girdle), Hoedeman (1961, caudal skeleton and hypural complex), Alexander (1964, Weberian apparatus), Alexander (1966, structure and function of several characters), Hoedeman (1967, pectoral and pelvic girdles), Chardon (1968, Weberian apparatus), Monod (1968, caudal skeleton), and Lundberg & Baskin (1969, caudal skeleton).

Pollard (1895: 417) stated about Loricariidae: "We are justified by the principles of geographical distribution in attributing to Loricarina an antiquity like that of Lepidosiren." Pollard cited Weyenbergh (1876): "...the fragility of these teeth [in the premaxillary and in the dentary] is enough to show that the fish cannot use much force with them, and this is not necessary, because these fish feed on more or less putrescent organic substances. I have met, for example, with many specimens round a dead horse, which was decaying in the river." Pollard (1895: 418) continued: "It is of no little importance to find that these archaic animals have a suctorial mouth. Possibly the symphysical teeth of Coccosteus may also have been used for hanging on."

Sawaya & de Petrini (1960) recorded the presence of a cloaca in Hypostomus plecostomus (though probably they had a species different from Hypostomus plecostomus from Surinam).

Angelescu & Gneri (1949: 259-261) found that Paraloricaria vetula feeds mostly on small mollusks, Loricariichthys anus mostly on Chironomid larvae, and Hypostomus mostly on mud, organic substances, diatomeae, and on filamentous algea. As shown by their illustrations, the pharyngeal dentition of Paraloricaria vetula (which is reminiscent of that in Lorica-

Plate XLVIII.

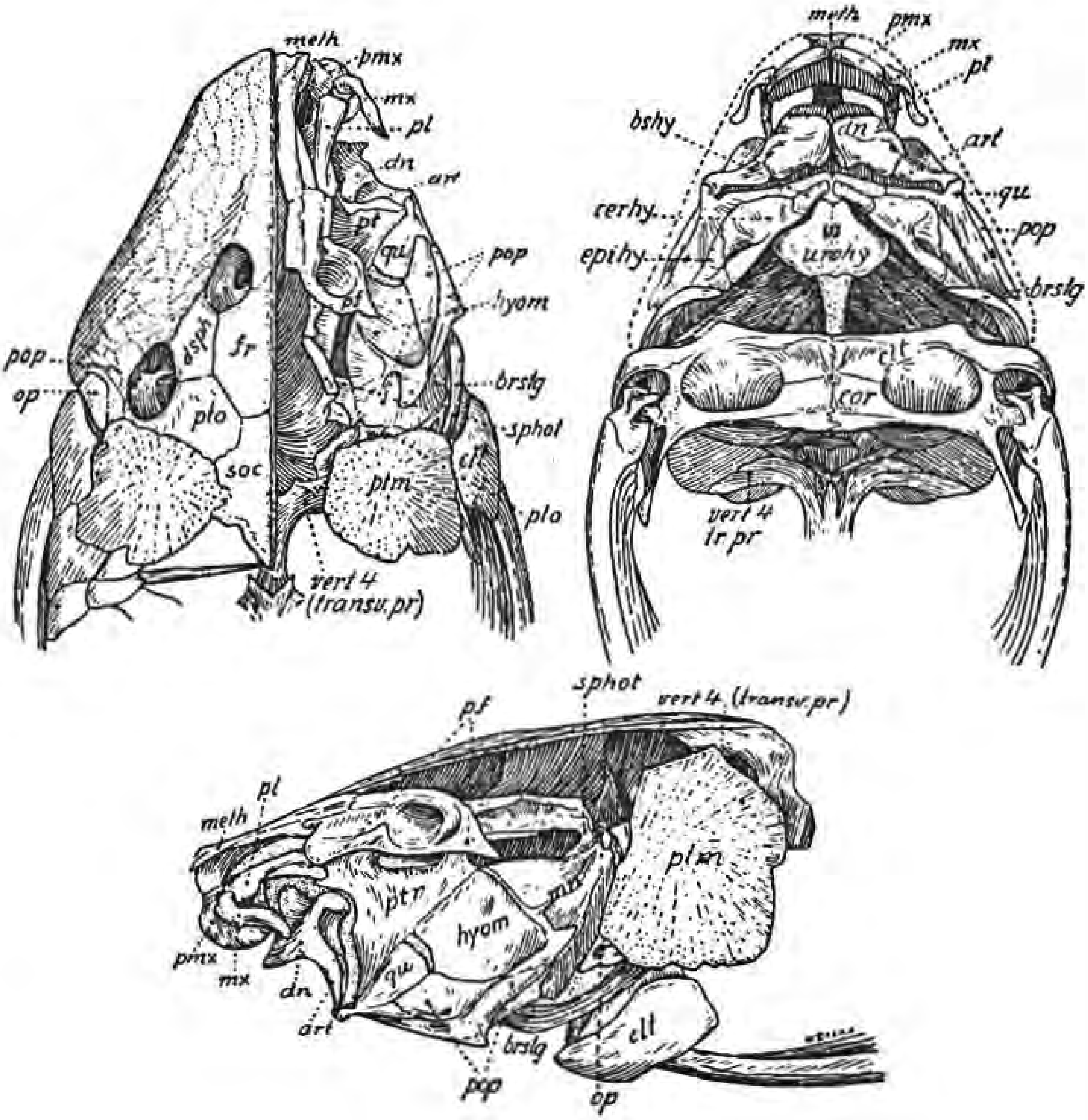


Fig. X,2. - **Hypostomus commersonii** (Valenciennes, 1840), skull (after Gregory, 1933, fig. 80).

Plate XLIX.

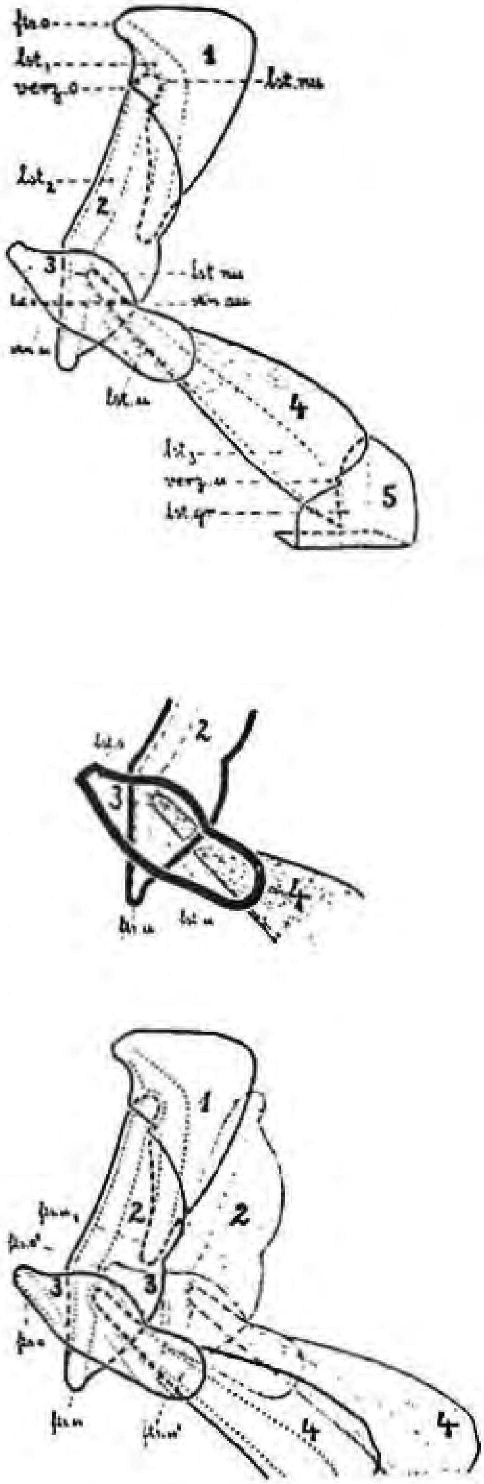


Fig. X,3. - Connection between the lateral body scutes in a vertical series in Hypostomus angipinnatus (Leege, 1922), holotype (after Leege, 1922, figs. 20-22).

ria and in Hemiodontichthys; pers. obs.) resembles that of the mollusk-feeding Labrids and Cichlids very much. The pharyngeal dentition of Loricariichthys spp. looks like that of other Cichlids, for example.

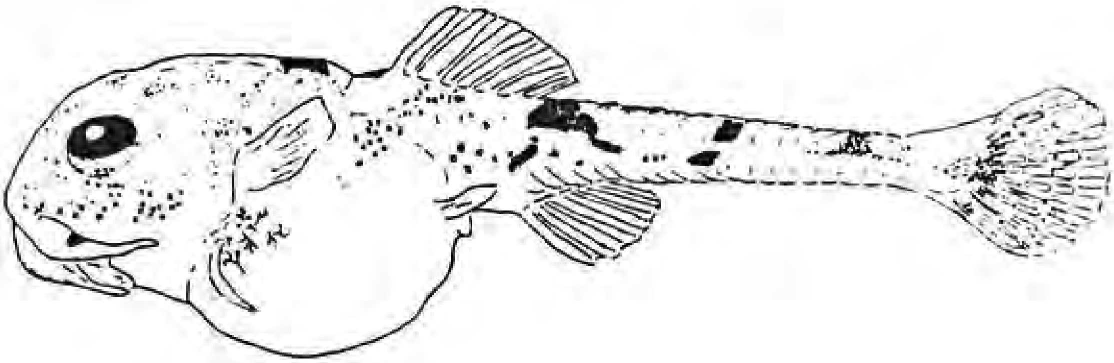
Ecology, behaviour and aquarium observations

There are numerous accounts dealing with ecology in the field, behaviour, bony contact organs, and observations on aquarium specimens (maintenance, breeding) of various Loricariidae. More classical accounts including or entirely dealing with ecology and other biological aspects of Loricariidae are those by Wagner (1865), Carter (1935), Mac Donagh (1938), and Menezes (1949). In alphabetical/chronological order reference may here be made to some recent publications, omitting those I already gave in my 1979b paper: Allison (1975a, 1975b, 1976a, 1976b, 1977, 1978a, 1978b, 1978c, 1980), Boakes (1976), Collette (1977), Foersch & Hanrieder (1980), Franke (in Sterba, 1978), Franke (1979), Gee (1976), Geisler (1969), de Gids (1977), Gradwell (1971), Hoedeman (1974), Howes (1976), Janssens (1979), Knöppel (1970), Lüling (1971, 1974, 1975, 1977, 1979), Mayland (1979), Roberts (1972), G. Sandford (1979), M. Sandford (1979), Sands (1980a, 1980b), Shannon (1980), and Turner (1980). The two publications by Sands are identical, dealing with the interesting colour pattern sharing of Otocinclus cf. flexilis and the sympatric Corydoras paleatus (Jenyns, 1842), and of an unidentified Otocinclus sp. and the sympatric Corydoras nattereri Steindachner, 1877.

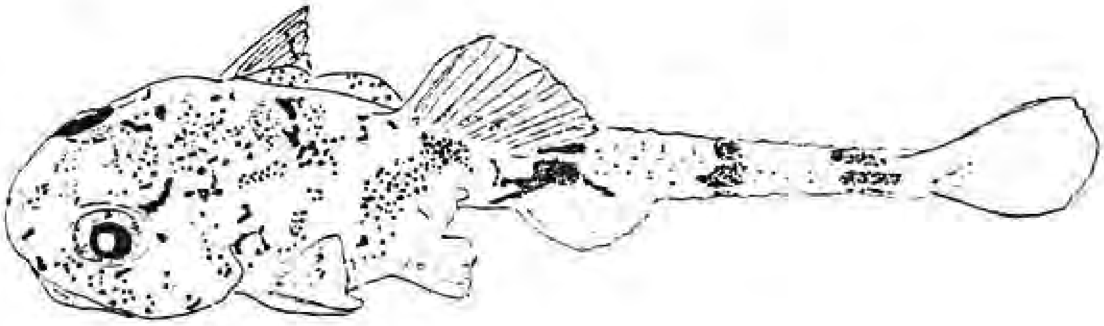
During the last few decades interest in various Loricariidae as aquarium fishes is increasing. Several species of Ancistrinae, Hypoptopomatinae and Loricariinae have been successfully bred in captivity.

López Rojas & Machado Allison (1975) gave an interesting

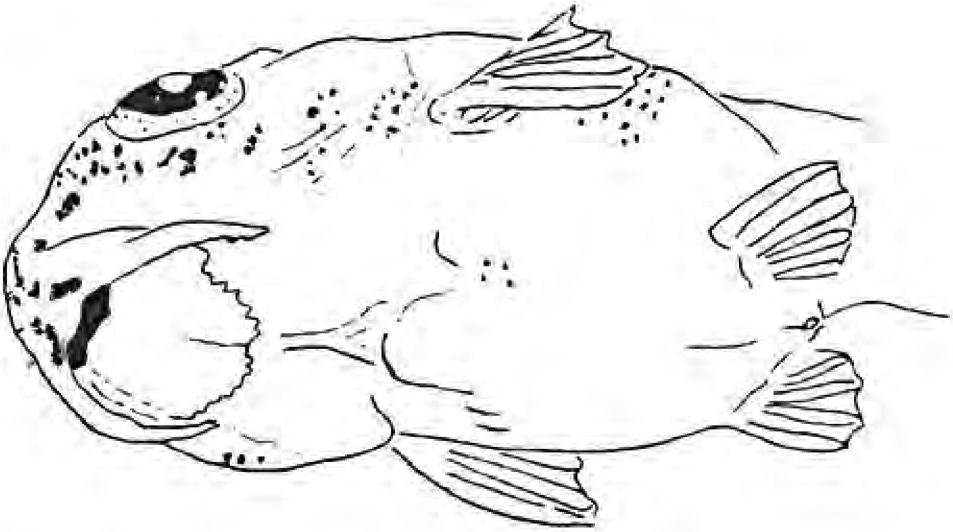
Plate L.



(a) larva, 12 hours.



(b) larva, 24 hours.



(c) detail of larva, 24 hours.

Fig. X,4. - Larvae of *Loricariichthys* cf. *platymetopon* Isbrücker & Nijssen, 1979 (after Machado Allison & López Rojas, 1975, figs. 8-10, resp.).

treatment of the development of Pseudohemiodon cf. apithanos (as Loricaria laticeps). Juveniles of 16 mm in standard length already have a produced upper caudal unbranched fin ray, and their colour pattern, especially of the fins, is largely the same as in adults.

Machado Allison & López Rojas (1975) also published a similar study on the development of Loricariichthys cf. platymetopon (as Loricariichthys typus). Juveniles of this species have no produced upper caudal unbranched fin ray.

Convergent adaptations

There is a perplexing superficial similarity between Loricariidae and the earliest known vertebrates, e.g., the agnathan family Cephalaspidae (Osteostraci) in various characters. Romer (1966: 17) wrote: "The cephalaspids were obviously, from their depressed shape and dorsally situated eyes, bottom-dwelling forms. Their small mouths and expanded gill chambers suggest that they were forms which made their living by straining food particles from the mud of the stream bottoms." Except for the gill chambers, this description fits well with some members of the Loricariinae. In addition to shared body shape and dermal ossifications, Loricariids tend to show an evolutionary convergence with certain Agnathes in their reduced strength of the jaws: three genera of the tribe Loricariini have very reduced premaxillae, lacking teeth.

Pollard (1895: 419) cited Huxley (1861), who wrote: "No one can overlook the curious points of resemblance between the Siluroids, Callichthys and Loricaria, on the one hand, and Cephalaspis, on the other, while in other respects, they may be still better understood by the help of the Chondrostean Ganoids." Finally, Pollard (1895: 420) stated: "Pander, Huxley, and Ray Lankester are therefore agreed that the dermal armature of Loricarina is like that of the oldest known vertebrate fossils."

Most similarities in structures of Loricariids and other fishes are convergent adaptations to their mode of life (bottom-dwelling) and habitat. Hora (1922a) published an excellent account of Indian hill-stream fishes (Siluroids and Cyprinids) and their adaptations, many of which are reminiscent of Loricariids. He found that the adhesive apparatus on the ventral surface of the pectoral fin spine of Glyptothorax sp. (Siluriformes, Sisoridae) is provided with spines, similar to the odontodes of Loricariidae (Hora, 1922a, fig. 19; see also Saxena & Chandy, 1966). To a lesser degree, tadpoles of frogs and toads living in mountain streams show also similar convergencies (especially in mouth structures) as fishes (Annandale & Hora, 1922).

Many African Amphiliidae (Siluriformes) also are adapted to torrential streams and are in various characters similar to Sisoridae and Loricariidae (Harry, 1953; Poll, 1957). The occurrence of odontodes or odontode-like structures is not recorded in Amphiliidae, but various genera have dermal ossifications somewhat like those in Loricariidae.

Hora (1922b) described and illustrated secondary sexual dimorphism of certain Cobitid (Cypriniformes) fishes (e.g., Nemacheilus and Diplophysa spp.) from high altitudes in central Asia. This dimorphism consists of the presence in males of minute hooked denticular tubercles on the sides of snout and head ventral to the eye, and on the dorsum of the pectoral fin, just like in several males of Loricariidae. A review of breeding tubercles and contact organs in various unrelated fishes was published by Wiley & Collette (1970).

The odontodes of Loricariidae are perhaps hard to compare with the integumentary teeth of sharks and rays, although in both they are equally numerous and sharp to the touch. Some Loricariinae have sexually dimorphic tooth shapes, those of the males gradually becoming stouter and broader distally.

Plate LI.

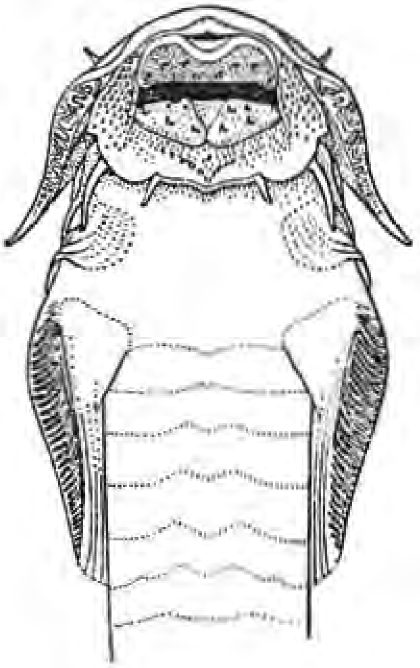


Fig. X,5. - Ventral aspect of *Glyptosternon* *labiatus* M'Clelland, 1842, showing its superficial similarity to some Loricariid (after Hora, 1922a, fig. 8, part).

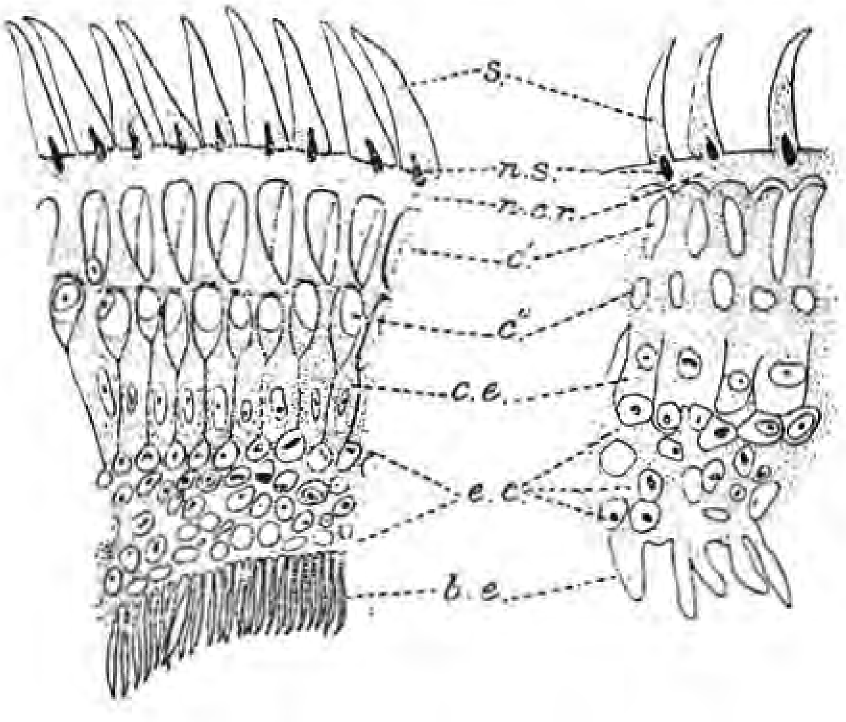


Fig. X,6. - Minute structure of the adhesive apparatus on the under surface of the pectoral fin spine of *Glyptothorax* sp., showing spines (s.) reminiscent of Loricariid odontodes (after Hora, 1922a, fig. 19, part).

Plate LII.

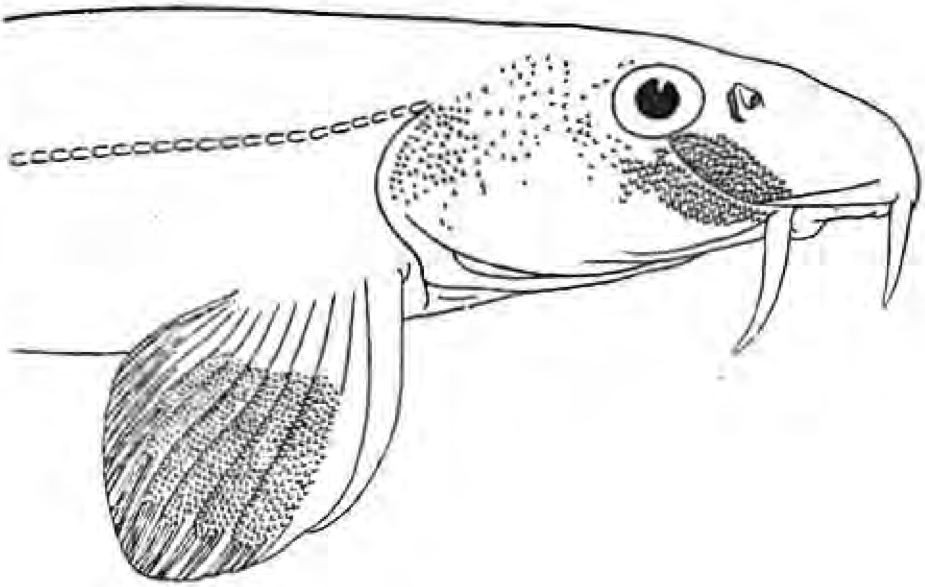


Fig. X,7. - Lateral view of head and upper surface of pectoral fin in a male specimen of Nemacheilus tibetanus Regan, 1905, showing secondary sexual dimorphism reminiscent of that in some Loricariidae (after Hora, 1922b, fig. 4).

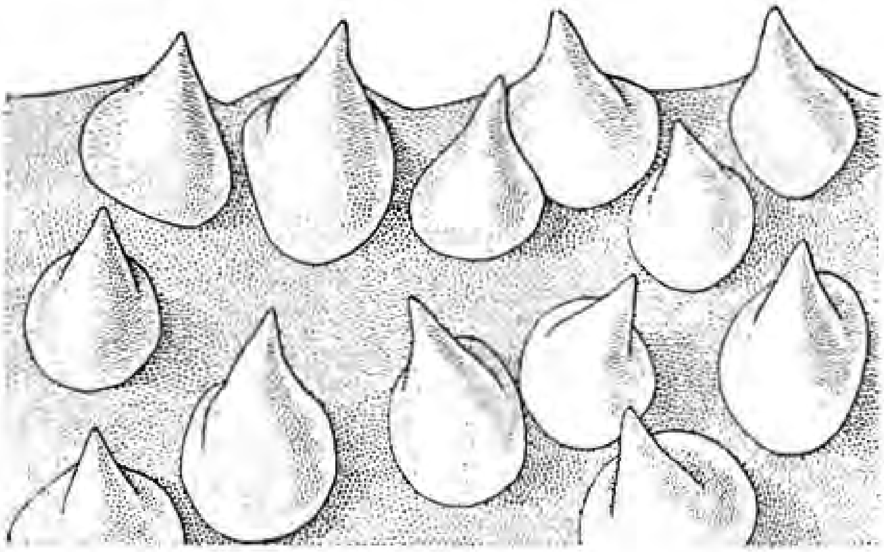


Fig. X,8. - Tubercles covering secondary sexual pads of male of Nemacheilus tibetanus Regan, 1905; highly magnified (after Hora, 1922b, fig. 5).

Various species of Rajidae also have sexually dimorphic teeth, those of the males being more acute than those of the females. McEachran (1977) found that both sexes of such sexually dimorphic rays have no different feeding habits and he suggested that the different tooth shapes is of more importance in reproductive behaviour: males hold the female during copulation using their jaws and alar spines. The function, if any, of different tooth shape in males and females of Loricariinae is entirely unknown.

Most Loricariidae, at least the more primitive members, maybe together with the Astroblepidae differ from most other catfishes – which are in general carnivorous, usually predators – in their herbivorous feeding habits (perhaps excepting the most specialized Loricariinae, which have well-developed pharyngeal dentitions). A small proportion of the catfishes bears dermal ossifications on the body, all others being naked. Catfishes usually are bottom-dwelling, nocturnal animals with barbels with sensory organs well-developed on the snout.

No fossil remains of a Loricariid are known. Therefore, little can be said about the possible age of the family. Because of their large distribution, it seems reasonable to assume that the family did evolve after the isolation of South America by continental drift. Catfishes related to the Loricariidae are not found outside South America.

The general distribution of the Loricariidae parallels that of several other South American groups of freshwater fishes, such as many other catfish families, Characoids, Gymnotoids, and Cichlids.

The ancestor of the Loricariidae (which reasonably certainly was ancestral also of the Astroblepidae) was a catfish that adapted to a life in torrential environments. These environments probably offered a great ecological potential to those among the catfishes (already well adapted to a bottom-dwelling life) which were able to turn from a mainly carnivorous to an increasingly more herbivorous diet. These factors must greatly have influenced the drastical reorganization of structures to become a Loricariid.

Alexander (1966: 142), in his interesting account of various catfishes, concluded: "The catfish appear to have evolved from an ancestor which closely resembled primitive Characinoidei, such as *Creatochanes* [now considered as a subgenus of *Bryconops*, see Knöppel, Junk & Gery, 1968] and *Brycon*, but probably lacked their specialized shearing teeth. The changes involved in the evolution of primitive catfish from such an ancestor would be numerous and profound. A very large proportion of them, however, have been shown to be corollaries of one of three basic changes: depression of the body in adaptation to a bottom-feeding habit, sensory modifications associated with nocturnal habits, and the acquisition of defensive fin spines." It is apparent that the changes in the evolution of Loricariids from other catfishes have again been numerous and profound.

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20-XI-1981

PROVISIONAL KEY TO GENERA OF LORICARIIDAE

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SOUTH AMERICAN FRESHWATER CATFISHES; MOUTH INFERIOR, WITH EXPANDED LIPS FORMING A SUCKING DEVICE; BODY WITH SCUTES, WHICH ARE PROVIDED WITH ODONTODES (SMALL TO MINUTE DERMAL DENTICLES, OR INTEGUMENTARY TEETH); FIN SPINES AND RAYS LIKEWISE PROVIDED WITH ODONTODES.

1a Pectoral fin with 7 or less branched rays; body completely covered with scutes dorsally and laterally . . . . 2.

1b Pectoral fin with 8 branched rays; body naked anteriorly . . . . *Lithogenes* Eigenmann, 1909.

2a Pectoral fin with 6, rarely with 5 branched rays . . . . 3.

2b Pectoral fin with 7 branched rays . . . . *Lamontichthys* P. de Miranda Ribeiro, 1939.

3a Abdomen naked or partly to completely covered with scutelets arranged into different patterns, none however, as in *Neoplecostomus* (see couplet 3b) . . . . 4.

3b Abdomen covered with a large, rather regular, nearly square or six-sided patch of small granular scutelets, bordered with a naked area at all sides . . . . *Neoplecostomus* Eigenmann & Eigenmann, 1888.

4a Caudal fin with 14 branched rays (Note: the number of caudal fin rays often was neglected in descriptions, so perhaps not all genera keyed out here do actually have 14 branched rays) . . . . 5.

4b Caudal fin with less than 14 branched rays . . . . 46.

5a Lower transverse portion of clavicles and coracoids not exposed . . . 12.

5b Lower transverse portion of clavicles and coracoids exposed . . . 6.

6a Caudal peduncle not depressed . . . . 7.

6b Caudal peduncle depressed . . . .

. . . . <u>Oxyropsis</u> Eigenmann & Eigenmann, 1889.

7a Anterior margin of snout with small, separate scutelets which are covered with fragile, spine-like odontodes; margin of the externally ossified ventral side of head with small scutelets anterior to 3 large scutelets . . . . 8.

7b Anterior margin of snout with large, firmly united scutelets which are covered with retrorse, tooth-like odontodes; margin of the externally ossified ventral side of head with a series of 6 scutelets . . . . 9.

8a Scapular bridge completely exposed; dorsum of head with 3 conspicuous keels '<u>Otocinclus</u>' (non Cope, 1871); Auct.; unnamed genus B, Britski MS.

8b Scapular bridge usually hardly exposed laterally, covered with skin medially; head without conspicuous keels . . . . '<u>Microlepidogaster</u>' (non Eigenmann & Eigenmann, 1889); Auct.; unnamed genus A, Britski MS.

9a Dorsal fin with a spine locking mechanism; dorsal and ventral side of orbital rim distant from the dorsal and ventral profile of head 10.

9b Dorsal fin without spine locking mechanism; head depressed; orbital rim usually reaching both the dorsal and the ventral profile of head <u>Hypoptopoma</u> Günther, 1868.

10a Adipose fin absent 11.

10b Adipose fin present <u>Parotocinclus</u> Eigenmann & Eigenmann, 1889.

11a Eye in lateral position, larger than the area which separates it from the ventral margin of head; scapular bridge completely exposed . . <u>Otocinclus</u> Cope, 1871.

11b Eye in dorsolateral position, smaller than the area which separates it from the ventral margin of head; scapular bridge usually exposed medially . . . . <u>Microlepidogaster</u> Eigenmann & Eigenmann, 1889.

12a Dorsal fin with different numbers of branched rays; interopercular area with or without evertible odontodes; mouth moderately to very wide; snout with or without a naked margin. However, none of these characters combined as in couplet 12b . 13.

12b Dorsal fin with 7 to 10 branched rays, the last one split to its base; interopercular area with evertible odontodes; mouth very wide; snout with a wide naked margin . . . . Chaetostoma Von Tschudi, 1845.

13a Dorsal fin with 6 or 7 branched rays, the last one split to its base . . 16.

13b Dorsal fin with more than 7 branched rays . . . . 14.

14a Interopercular area without evertible odontodes . . . . 15.

14b Interopercular area with well-developed evertible odontodes; dorsal fin with 10 branched rays (or with 9 rays, the last one split to its base?) . . . . Megalancistrus Isbrücker, 1980.

15a Caudal peduncle flattened ventrally, somewhat triangular in cross-section; caudal fin obliquely concave, the ventral (unbranched) ray the longest; dorsal fin with 9-10 branched rays (or 8-9, the last ray split to its base?) . . . . Delturus Eigenmann & Eigenmann, 1889.

15b Caudal peduncle somewhat compressed ovate in cross-section; caudal fin deeply forked; dorsal fin with 10-15 branched rays (or 9-14, the last ray split to its base?) . . . . Pterygoplichthys Gill, 1858.

16a Numerous (from about 20 to considerably more in each jaw segment) slender, filiform teeth present . . . . 21.

16b Considerably less than 20 teeth, which are broad and with a spoon- or cup-shaped crown . . . . 17.

17a About the same number of teeth in each jaw segment . . . . 18.

17b Premaxillae with much less teeth than there are in the dentaries; interopercular area with evertible odontodes . . . . 19.

18a Interopercular area without evertible odontodes . . . . Cochliodon Heckel, 1854.

18b Interopercular area with evertible odontodes, which during growth become increasingly conspicuous . . . . Panaque Eigenmann & Eigenmann, 1889.

19a Body without extremely conspicuous odontodes; ~~caudal peduncle~~ body and head depressed 20.

19b Body and head with extremely conspicuous odontodes; ~~caudal peduncle~~ body and head compressed Pseudacanticus Bleeker, 1862.

20a Margin of lower lip without conspicuous barbels . . . . Lithoxus Eigenmann, 1910.

20b Margin of lower lip with conspicuous barbels . . . . Exastilithoxus Isbrücker & Nijssen, 1979.

21a First scute of lower lateral series posterior to the temporal plate (which is of moderate size), with which the second scute of the lower lateral series is not in contact . . . . 22.

21b First two scutes of the lower lateral series below the (very large) temporal plate and in contact with it above . . . . Acanthicus Von Spix, 1829.

22a Anal fin present 24.

22b Anal fin absent 23.

23a Margin of snout granular . . . . Leptoancistrus Meek & Hildebrand, 1916.

23b Margin of snout naked Lipopterichthys Norman, 1935.

24a Supracleithral plate margined posteroventrally by the exposed cleithrum . . 35.

24b Supracleithral plate margined posteroventrally at least in part by a naked area or by a few to several small scutelets . . . . 25.

25a Twenty-two to 26 lateral body scutes . . . . 31.

25b Twenty-seven to 32 lateral body scutes . . . . 26.

26a Teeth either simple or with a small lateral lobe; lateral scutes meeting along middorsal line at least for part of the distance between dorsal fin and (if present) adipose fin . . . . . 27.

26b Teeth with 2 approximately equal lobes; lateral scutes not meeting along middorsal line between dorsal fin and adipose fin, leaving a naked middorsal band about as wide as the eye diameter *Upsilodus* A. de Miranda Ribeiro, 1924.

27a Abdomen naked or with small scutelets . . . . 28.

27b Abdomen completely covered . . . . *Pseudotocinclus* Nichols, 1919.

28a Head broad and depressed, its length contained 3.4 or fewer times in standard length . . . . 29.

28b Head short and comparatively narrow, its length contained about 3.7 times in standard length . . . . *Kronichthys* A. de Miranda Ribeiro, 1908.

29a Adipose fin present; caudal peduncle short, rounded or ovate in cross-section, its depth contained 3.2 or fewer times in its length . 30.

29b Adipose fin absent; caudal peduncle rather rectangular in cross-section, its depth contained 3.7 or more times in its length . *Pareiorhina* Gosline, 1947.

30a Abdomen completely naked; adults with very strong, straight, bristle-like odontodes along margin of head, becoming greatly elongate spines in adult males . . . . *Hemipsilichthys* Eigenmann & Eigenmann, 1889.

30b Abdomen with scattered, embedded scutelets; margin of head with minute, bristle-like odontodes . . . . *Pareiorhaphis* A. de Miranda Ribeiro, 1918.

31a Caudal peduncle rounded ventrally; abdomen in adults with scutelets at least along bases of lateral scutes; supracleithral plate bordered posteriorly by a few to numerous small scutelets; anal fin at least half as long as the pelvic fin . 32.

31b Caudal peduncle flattened ventrally, somewhat triangular in cross-section; abdomen completely naked; supracleithral plate bordered posteroventrally by a naked area; anal short, its longest ray about a third of the length of the pelvic fin . . . . . *Corymbophanes* Eigenmann, 1909.

32a Abdomen in adult largely naked, but with well-developed, transversely elongate scutelets at the ventral base of lateral body scutes; frontals forming part of the supraorbital rim 34.

32b Abdomen in adult almost completely covered with small scutelets; interorbital area very broad, the frontals not reaching the supraorbital rim . . . . 33.

33a Margin of head with well-developed odontodes . . . . *Pseudorinelepis* Bleeker, 1862.

33b Margin of head without well-developed odontodes . . . . *Rhinelepis* Von Spix, 1829.

34a Adipose fin present; margin of head with prominent odontodes; 22 lateral body scutes . . . . *Pogonopoma* Regan, 1904.

34b Adipose fin absent; no prominent odontodes along margin of head; 25-26 lateral body scutes . . . . *Pogonopomoides* Gosline, 1947.

35a Interopercular area with a patch of evertible odontodes . . . . 39.

35b Interopercular area without evertible odontodes . . . . 36.

36a Head and body without very prominent odontodes . . . . 38.

36b Head and/or body with very prominent, inevertible odontodes . . 37.

37a Prominent odontodes on head and body; head not depressed; caudal peduncle very long and slender . . . . *Isorineloricaria* Isbrücker, 1980.

37b Prominent odontodes confined to margin of head; head and body, including caudal peduncle, depressed . . . . .

. . . . *Pseudancistrus* Bleeker, 1862.

38a Adipose fin usually present . . . . *Hypostomus* Lacepède, 1803.

38b Adipose fin absent *Monistiancistrus* Fowler, 1940.

39a Snout granular to its margin; evertible interopercular odontodes needle-like . . . . 41.

39b Snout with a wide naked margin; evertible interopercular odontodes hook-like 40.

40a Anal fin about as long as dorsal fin; snout margin without barbels . . . *Hypocolpterus* Fowler, 1943.

40b Anal fin considerably shorter than dorsal fin; snout margin usually with numerous shorter or longer barbels, becoming forked tentacles in adult males . . . . *Ancistrus* Kner, 1854.

41a Membrane of dorsal fin not or hardly extending posterior to last branched ray 42.

41b Membrane of dorsal fin extending far beyond last branched ray, either to the 3 or 4 scutes behind this ray or to the spine of the adipose fin . . . . *Parancistrus* Bleeker, 1862.

42a Head and body robust, not depressed; margin of head and snout without bristle-like odontodes . . . . 45.

42b Head and body depressed; margin of head and snout usually with short, bristle-like odontodes . . . . 43.

43a Head not extremely wide; standard length at least about 80 mm, usually more 44.

43b Head extremely wide; standard length not exceeding about 65 mm . . . . *Cordylancistrus* Isbrücker, 1980.

44a Some of the interopercular odontodes extending much beyond the head in adult males; largest known total length 120 mm . . . . . *Dolichancistrus* Isbrücker, 1980.

44b None of the interopercular odontodes extend beyond the head in adults; total length up to about 200 mm . . .

. . . . Lasiancistrus Regan, 1904.

45a Posterior lateral body scutes moderately rugose; adult size probably always more than 150 mm in total length; several species without a conspicuous colour pattern .
. . . . Hemiancistrus Bleeker, 1862.

45b Posterior lateral body scutes distinctly rugose; adult size probably always less than 150 mm in total length; several species with a conspicuous colour pattern . .
. . . . Peckoltia A. de Miranda Ribeiro, 1912.

46a Scapular bridge covered by skin or by dermal ossifications
. . . . 48.

46b Scapular bridge exposed . . . .
. . . . 47.

47a Body robust; head with 3 pronounced keels; snout not produced . . Otothyris Myers, 1927.

47b Body cylindrical; head without keels; snout produced .
. . . . Acestridium Haseman, 1911.

48a Dorsal fin with 5 branched rays, the last one split to its base; dorsal fin about opposite to anal fin . . .
. . . . 49.

48b Dorsal fin with 6 branched rays, the last one split to its base; dorsal fin about opposite to pelvic fins . .
. . . . 50.

49a Premaxillae and dentaries each with a single row of teeth, which are not running parallel to each other; jaw segments relatively short, each containing about 20 teeth . . Farlowella Eigenmann & Eigenmann, 1889.

49b Premaxillae and dentaries each with a single row of teeth, running almost parallel to each other; jaw segments very long, each containing up to 125 teeth . . .
Aposturisoma
. . . . "A.m."; unnamed genus C, Isbrücker, Britski, Nijssen & Ortega, MS.

50a Caudal fin with either 10 or with 12 branched rays; body depressed or somewhat triangular in cross-section; snout produced or not 51.

50b Caudal fin with 11-12 branched rays; body somewhat triangular
in cross-section; snout not or hardly produced . . . .
. . . . *Sturisomatichthys* Isbrücker & Nijssen, 1979.

51a Caudal fin with 10 branched rays . . . .
. . . . 57.

51b Caudal fin with 12 branched rays . . . .
. . . . 52.

52a Each jaw segment with 40 or many more teeth . . . . .
. . . . 53.

52b Each jaw segment with 27 or less teeth . . . .
. . . . *Metaloricaria* Isbrücker, 1975.

53a Snout not produced 54.

53b Snout produced *Sturisoma* Swainson, 1838.

54a Head and body depressed . . . .
. . . . 55.

54b Head and body not depressed . . . .
. . . . *Pterosturisoma* Isbrücker & Nijssen, 1978.

55a Caudal peduncle strongly depressed . . . .
. . . . 56.

55b Caudal peduncle rather roundish in cross-section . . .
. . . . *Harttiella* Boeseman, 1971.

56a Abdomen naked or covered with numerous minute scutelets;
caudal fin not deeply forked; head and body relatively
broad . . . . *Harttia* Steindachner, 1876.

56b Abdomen covered with small scutelets; caudal fin deeply
forked; head and body relatively slender . . . .
. . . . *Cteniloricaria* Isbrücker & Nijssen, 1979.

57a Premaxillae with teeth . . . .
. . . . 60.

57b Premaxillae rudimentary, toothless . . . .
. . . . 58.

58a Snout considerably produced; head acute in dorsal and
ventral view; lower lip without long barbels . . . .
. . . . 59.

58b Snout hardly produced; head rounded in dorsal and ventral
view; lower lip with many long barbels . . . .

. . . . Planiloricaria Isbrücker, 1971.

59a Abdomen with numerous irregular scutelets, gradually decreasing in size anteriorly . . . .
. . . . Reganella Eigenmann, 1905.

59b Abdomen with few large scutes, not decreasing in size anteriorly . Hemiodontichthys Bleeker, 1862.

60a Abdomen naked or covered with small scutelets in different patterns 63.

60b Abdomen completely covered with relatively large scutes . . . 61.

61a Teeth well-developed, relatively large . . . .
. . . . 62.

61b Teeth minute Loricariichthys Bleeker, 1862.

62a Snout not acute; lower lip without long barbels . . .
. . . . Dasyloricaria Isbrücker & Nijssen, 1979.

62b Snout acute; lower lip with about 6 long barbels at either side, each barbel with elongate papillae along the ventral surface . . . Furcodontichthys Rapp Py-Daniel, 1981.

63a Margin of lower lip with long filamentous barbels . .
. . . . 64.

63b Margin of lower lip smooth, or fringed with papillae or short filamentous barblets . . . .
. . . . 70.

64a Premaxillae with 6 or more teeth in each segment . . .
. . . . 65.

64b Premaxillae with 5 or less teeth in each segment . . .
. . . . 66.

65a Premaxillae with up to 9 teeth in each segment; maxillary (= rictal) barbel with subbarbels which are not subdivided into minute branches 67.

65b Premaxillae with up to 15 teeth in each segment; maxillary barbels with subbarbels which are subdivided into minute branches . . Ricola Isbrücker & Nijssen, 1978.

66a Premaxillary teeth about twice the length of the mandibular teeth . . Loricaria Linnaeus, 1758.

66b Premaxillary teeth about one third longer than the mandibular teeth, which latter are about as long as the premaxillary teeth of *Loricaria* *Brochiloricaria* Isbrücker & Nijssen, 1979.

67a Abdomen naked or covered with scutelets in different patterns, not however, arranged into a single median strip . . . . 68.

67b Abdomen naked except for a single median strip of small, roundish scutelets *Crossoloricaria* Isbrücker, 1979.

68a A ventrorostral extension . . . . 69.

68b No ventrorostral extension . . . . *Paraloricaria* Isbrücker, 1979.

69a Sides of head and snout more or less triangular in dorsal and ventral view; cleithral width contained 0.8-1.1 times in head length; supracleithral width contained 1.3-1.7 times in head length; head depth contained 2.5-3.3 times in its length; maxillary barbel contained 1.4-2.4 times in head length; depth caudal peduncle contained 12.3-17.3 times in head length . *Pseudohemiodon* Bleeker, 1862.

69b Sides of head tapering, sides of snout narrow and somewhat concave in dorsal and ventral view; cleithral width 1.2, supracleithral width 1.9, head depth 3.5, maxillary barbel 1.1, and depth caudal peduncle 9.7 times in head length, respectively *Rhadinoloricaria* Isbrücker & Nijssen, 1974.

70a Margin of upper lip anteriorly with a series of separated, short, broad, barbel-like, pointed, bifid or trifid flaps; lower lip of adult males greatly enlarged; adult males without conspicuously developing odontodes . . . . 73.

70b Margin of upper lip without flaps as indicated in couplet 70a; adult males do not develop an enlarged lower lip; adult males with conspicuously developing odontodes . . . . 71.

71a Abdomen almost completely naked . . . . 72.

71b Abdomen covered either completely or only posteriorly with scutelets *Rineloricaria* Bleeker, 1862.

72a Predorsal length contained 2.5 times in standard length; up to 18 teeth in each of the premaxillae; up to 15 teeth in each of the dentaries; adult males with enlarged odontodes which are not extremely long . . . . <u>Ixinandria</u> Isbrücker & Nijssen, 1979.

72b Predorsal length contained 2.6-3.1 times in standard length; up to 6 teeth in each of the premaxillae; up to 5 teeth in each of the dentaries <u>Spatuloricaria</u> Schultz, 1944.

73a Lateral scutes 31-32; coalescing scutes 18-22; 3-5 small scutelets anteriorly bordering the pre-anal scute . . . . <u>Limatulichthys</u> Isbrücker & Nijssen, 1979.

73b Lateral scutes 34-36; coalescing scutes 23-27; 9-15 small scutelets anteriorly bordering the pre-anal scute . . . . <u>Pseudoloricaria</u> Bleeker, 1862.

Remarks.- This key is an addendum to my unpublished work: "A treatise of the Loricariidae Bonaparte, 1831, a family of South American mailed catfishes, with emphasis on the subfamily Loricariinae (Pisces, Siluriformes)", forming a part of my thesis (due 4-XII-1981).

I have made free use of information in the published keys to Loricariid genera by Regan (1904), Gosline (1947), and Isbrücker (1981), whereas Dr H. A. Britski (São Paulo) most generously permitted me to use his provisional -manuscript- key to genera of the subfamily Hypoptopomatinae. In addition to studying actual specimens of many genera of this family, I have included data from descriptions, the latest of which was by Rapp Py-Daniel (1981).

Users of this key are kindly requested to consider it as unavailable for their own publications until the unnamed genera mentioned, have become published.

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NOTE

Distribution of this provisional key is informal and is intended to have it tested and improved before actual publication. Therefore, a very limited number of copies has been made available. The author would appreciate your comments and criticism within a reasonable period.

Amsterdam, 20-XI-1981