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# The Auchenipteridae: Putative monophyly and systematics, with a classification of the neotropical Doradoid catfishes (Ostariophysi: Siluriformes)

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City University of New York, 1988

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PUTATIVE MONOPHYLY AND SYSTEMATICS,
WITH
A CLASSIFICATION OF THE NEOTROPICAL DORADOID CATFISHES
(OSTARIOPHYSI: SILURIFORMES)

BY

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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# ABSTRACT

THE AUCHENIPTERIDAE:

PUTATIVE MONOPHYLY AND SYSTEMATICS,

WITH

A CLASSIFICATION OF THE NEOTROPICAL DORADOID CATFISHES

(OSTARIOPHYSI: SILURIFORMES)

BY

CARL J. FERRARIS, JR.

Advisor: Dr. Gareth Nelson

The neotropical catfish family Auchenipteridae is redefined as a strictly monophyletic group based on a series of characters of the skeletal system and soft anatomy. The Auchenipteridae includes all species previously placed in the Ageneiosidae. The genus Werthemeria is removed to the Doradidae, and the family Centromochlidae is reinstated to include approximately 30 species previously placed in the Auchenipteridae.

The Auchenipteridae comprise the only catfish group known to practice internal fertilization. The family is hypothesized to be the sister group of the Centromochlidae, with the Doradidae the nearest relative of that combined lineage.

Within the Auchenipteridae, two subfamilies are recognized: the Auchenipterinae and the Trachycorystinae.

Three poorly known, monotypic, genera (*Asterophysus*, *Pseudotatia*, and *Tocantinsia*) are placed within the family *insertae sedis*. The genera *Trachycorystes*, *Trachelyopterichthys*, and *Liosomadoras* comprise the Trachycorystinae. The Auchenipterinae consist of the genera *Pseudauchenipterus* and *Auchenipterichthys* and the tribe Auchenipterini.

Within the Auchenipterini, *Trachelyichthys* is the sister group of a clade composed of the following three groups of genera: 1) *Ageneiosus* and *Tetranematichthys*, 2)*Trachelyopterus*, and 3) *Entomacorus*, *Epapterus*, and *Auchenipterus*.

The Centromochlidae include *Centromochlus*, *Glanidium*, *Gelanoglanis*, and *Tatia*, and two undescribed genera.

Sexually dimorphic characters of, primarily, the unpaired fins, maxillary barbel, and neurocranium provided much of the information used in this study. Adult male auchenipterids appear to acquire these characters each reproductive season and they have yet to be seen in several rare genera. Better resolution of the interrelationships of these fishes awaits the acquisition of additional material.

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# INTRODUCTION

A study of the relationships of catfishes currently placed in the family Auchenipteridae was undertaken with the following objectives:

1) to infer the interrelationships of the available species hitherto regarded as auchenipterids on the basis of shared, derived characters;

2) to determine the validity of the family Auchenipteridae and its genera using monophyly of each group as the sole criterion;

3) to infer the relationship of the group or groups of fishes currently called auchenipterids to other siluroid families; and

4) to provide a classification of auchenipterid catfishes consistent with the hypothesized phylogenetic relationships of the group.

As currently recognized (e. g. Nelson 1984), the siluroid family Auchenipteridae consists of about 20 genera and 65 species of neotropical freshwater fishes. Although no comprehensive treatment of the species has been published, current usage follows Mees (1974), with corrections and subsequent additions by Fernández-Yépez (1973), Greenfield and Glodek (1977), Böhlke (1980), Mago-Leccia (1984), Vari et al. (1984), and Ferraris and Fernandez (1987). In this Introduction, the term auchenipterids is used as an informal collective noun for the group in the sense of Mees, although later, as the argument advances, its meaning becomes substancially changed.

The status and limits of the Auchenipteridae have undergone considerable shifting since the group was first created by Eigenmann and Eigenmann (1890) as the subfamily Auchenipterinae. In recent years, auchenipterid species have been split up into as many as four separate families (P. Miranda Ribeiro 1968b) or they have been treated as a noncohesive part of the family Doradidae (e.g. Gosline 1945) or Pimelodidae (Eigenmann and Allen 1942).

Much of the recent debate regarding the status of auchenipterids revolves around the relationship of these fishes to the two families with which they have been most closely associated: the Ageneiosidae and the Doradidae. Jordan (1923) placed the genera of all three groups into one family, the Doradidae. Regan (1911) also included all three in the Doradidae, but he arranged the genera into unnamed groups that correspond to the current families. Eigenmann (1912) included each of the three families as a subfamily of his extensive Siluridae. Van der Stigchel (1947) and Fowler (1951) considered all three to be of family rank, as did Chardon (1968) who grouped them, together with the Mochokidae, into the superfamily Doradoidae (sic). Gosline (1945) placed the auchenipterids as the second subfamily of the Doradidae and gave the Ageneiosidae family rank. Fowler (1940), in contrast, included _Ageneiosus_ LaCépède in the family Auchenipteridae, separate from the Doradidae. A. Miranda Ribeiro (1911) regarded the Doradidae and the Ageneiosidae as family taxa, but split the auchenipterids into two families, the Auchenipteridae (containing only _Auchenipterus_ Valenciennes and _Epapterus_ Cope) and the Trachycorystidae. No indication was given of the relationship of these latter two families to each other. Miranda-Ribeiro also transferred the monotypic genus _Tetranematichthys_ Bleeker from the Auchenipteridae to the Ageneiosidae. P. Miranda Ribeiro (1968b) further divided the auchenipterids by removing a number of genera from the Trachycorystidae and creating two additional families: the Centromochlidae and the monotypic Asterophysidae. _Tetranematichthys_, however, was transferred out of the Ageneiosidae and into the Trachycorystidae. Eigenmann and Allen (1942) presented a novel scheme of relationships by including auchenipterids as a subfamily of the Pimelodidae while maintaining the families Doradidae and Ageneiosidae.

Classifications proposed prior to Eigenmann's recognition of the auchenipterid group provide yet another perspective on presumed relationships of these taxa. Bleeker (1862a, 1863) put most of the then-known auchenipterid genera into a separate sub-group of the subfamily Bagriformes. _Auchenipterus_, however, was kept apart as a monotypic subgroup of the same subfamily.

*Tetranematichthys* was also separated from the bulk of the auchenipterid genera and was placed, instead, into another bagriform subgroup consisting of ageneiosids, schilbeids, and pangasiids. Two monotypic auchenipterid genera, *Trachelyopterus* Valenciennes and *Trachelyopterichthys*, Bleeker were grouped in a subfamily with the cetopsids. Günther (1864) placed all ageneiosids, auchenipterids, and doradids, together with the cetopsids and the mochokids (except the genus *Mochokus*), into his Doradina.

When characters purporting to define the auchenipterids were given, they were most often external and invariably primitive, relative to the group from which they were being distinguished. Little osteological support has been provided for the definition and relationships of this family. Regan (1911) differentiated the genera of auchenipterids from the doradids and ageneiosids with the following characters: absence of lateral bony plates on body and absence of an encapsulated air bladder. Chardon (1968) presented a series of seven osteological characters with which to contrast the four families of his superfamily Doradoidae (Table 1). Of these characters, only in the last three is the derived state present in the Auchenipteridae and in each case it is common to the three families. Britski (1972) provided a detailed phylogeny of the auchenipterids in which the Auchenipteridae was distinguished from the Ageneiosidae and Doradidae by a series of comparative characters summarized in Table 2.

As in the analysis of Chardon, none of the characters presented is uniquely derived for auchenipterids and thus, they cannot provide any basis for an hypothesis of the monophyly of the group. The family Auchenipteridae has never been defined by the presence of uniquely derived characters, and this situation hav been reflected in the lack of agreement on the limits of the family.

Similarly, little information has been published on the interrelationships of the auchenipterid genera. P. Miranda Ribeiro (1968) argued that his restricted use of the family name Trachycorystidae reflected the natural grouping of species characterized by an elongated urogenital canal in adult males. Mees (1974) suggested affinities for a number of the genera he recognized, but his notions of affinity were based on general similarity in appearance, rather than the presence of shared derived characters. Both Miranda Ribeiro and Mees had very limited access to specimens of sexually dimorphic adults, and this allowed them to unite distantly related taxa on the basis of sexually dimorphic characters that are now known to be widely distributed among the auchenipterids.

Britski (1972) provided the first extensive comparative osteology of auchenipterids and their relatives. His observations provide a great amount of insight into the anatomical variation among these catfishes, although many currently recognized taxa were unknown at that time. However, his conclusions about relationships were based on an overall similarities among taxa, in which the systematic value of the primitive state of any given character was considered equal to that of the derived state.

# MATERIALS AND METHODS

## RELATIONSHIPS

The approach adopted here to elucidate the relationships of the studied taxa is cladistic, in the sense of Nelson and Platnick (1981), in which these authors expand on the methodology developed by Hennig (1966). Hypotheses of relationship are based on the identification of derived characters shared among members of a restricted group. The goal of this study was to nest taxa into an hierarchical arrangement of groups, with all groups sharing derived characters.

Derived characters were recognized by outgroup comparison, ontogenetic change, or both. Ontogenetic information was limited by the availability of specimens of a single species through a range of sizes. However, when more than one specimen was available for study, comparisons were made for size-related changes. A form of ontogenetic character that was used extensively in this study was the comparison of adult males to females and juveniles for sexually dimorphic changes. A discussion of these sexually dimorphic characters follows below. It was assumed here that the presence of a secondary sexual character in one sex is a derived character, and that the presence of similar characters in different species indicates relationship among those taxa.

## CLASSIFICATION

A classification of doradoid catfishes, excluding members of the family Doradidae, is presented here. The groupings have been made directly from the study of relationships study and are, therefore, based on the cladistic affinities of the taxa. Only monophyletic groups have been named, except in certain cases-for which an explanation is given. Groups above the generic level were provided with names, however, only when a family group name was already available. The term insertae sedis was used for genera that could not be placed at any level other than in a polychotomy with family-level taxa.

## RELATIONSHIPS OF DORADOID CATFISHES WITHIN THE SILURIFORMES

During the course of this study, a number of characters were examined and found to be derived within catfishes but of a greater level of generality than characters defining the Doradoidea. Although not of significance to our understanding of the relationships of doradoids or, more specifically, the Auchenipteridae, these characters are of interest to this study for two reasons: 1) the characters may in fact be characters of the Doradoidea that have been independently derived in a second catfish lineage; and 2) the characters may provide direction for fruitful avenues of research in the study of catfish relationships. Limitations of time and examinable material made it impossible to provide a thorough survey of the distribution of these characters among all catfishes. Instead, taxa observed to possess the characters are noted, as well as taxa in which the derived character is absent. It is recognized that the occurrence of the derived state of any particular character both within and outside of the Doradoidea is not sufficient evidence that it is not a valid character of that superfamily- and thus is present as a homoplasy in other catfish species. Similarly, the characters discussed here may be unrecognized 'catfish' characters that do not appear in all species. These errors cannot be recognized, however, until a well corroborated cladogram of all catfishes has been presented and the distributions of these characters compared.

Characters of this type are summarized in figure 41 along with characters used to define the Doradoidea.

## TERMS USED

When discussing attributes of Pectoral- or Dorsal-fin spines, directional terms refer to the spine in its erect, rather than reclined, position. Thus, serrations on the pectoral spine are typically found on the anterior and posterior edges, rather than the lateral and medial.

In one group of catfishes considered here, the anal fin has been rotated so that the fully erected rays point posteriorly or ventroposteriorly. To eliminate the need for two sets of terms in discussing directional relationships of the anal-fin rays, the modified fin is viewed as if it were not rotated. Thus, rays are described as being anterior or posterior to another, not dorsal or ventral.

Designating individual anal-fin rays and their parts is essential in this study. A strict anteroposterior counting scheme is unfeasible, inasmuch as small, unsegmented rays are not readily seen, especially in dissected specimens. Instead, the scheme adopted here counts branched rays anteroposteriorly and unbranched rays, which are located anterior to the branched rays, posteroanteriorly. Branched rays are designated with the letters BR; unbranched rays with UR. Thus, UR1 is immediately anterior to BR1, and UR2 is anterior to UR1.

The primary branches of branched rays are identified as anterior and posterior and designated as "a" and "p", respectively. Serrations on the posterior branch of the second branched ray of the anal fin would be identified as "BR2p serrations".

USE OF VERNACULAR NAMES

Throughout the text, the terms 'catfish' or 'catfishes' are used to delineate the natural group which has been variously called Nematognathi (e.g. Eigenmann and Eigenmann 1890, Mees 1974), Siluroidea (Fink and Fink 1981) and Siluriformes (e.g., Grande 1987). The monophyly of this group has been examined on numerous occasions and is not in question here. Neither is the correct name for this group, but for consistency, the term Siluriformes, or the informal adjective, siluriform, is adopted here. Family-level taxa have been assigned informal names corresponding with the truncated suffixes as follows: superfamily names end with -oid; family names end with -id; subfamily names with -in and tribe names with -ine. In the introduction, formal names proposed by, or used by, the author whose work is under discussion have been adopted. When the informal 'auchenipterid' is used in the Introduction, it refers to the family as delimited by Mees (1974) and Nelson (1984), which appears to be in wide use at present.

SEXUALLY DIMORPHIC CHARACTERS

Structures exhibiting sexual dimorphism have proven to be an important source of character information in doradoid catfishes. Most of the sexually dimorphic characters identified here are found only in adult males. Moreover, aquarium observations over a period of more than one year, suggest that some of characters are labile and manifest themselves only during periods of sexual activity. For periods as brief as a few weeks, the full range of sexually dimorphic characters are exhibited by males. Shortly thereafter, the individual returns to a non-dimorphic state with some of its sexually dimorphic characters no longer observable. Recognition of these characters within a taxon thus requires a preserved, sexually-active male specimen, but in many of the taxa discussed here, males in reproductive condition were unavailable. When the systematic position of any of these taxa is indicated by non-dimorphic characters, the dimorphic characters of that clade have been presumed to exist also in these taxa. For example, no adult male specimens of *Entomacorus benjamini*, the type species of *Entomacorus*, exhibit the sexually dimorphic traits characteristic of the tribe Auchenipterini. Several non-dimorphic characters, however, suggest a close relationship between *Entomacorus* and other auchenipterins. The dimorphic characters are hypothesized to be present in the species even though unobserved, or perhaps absent through secondary phylogenetic loss. Similarly, it is supposed that *Pseudepapterus hasemani* (Steindachner) and *P. cucuhyensis* Böhlke, now *Epapterus hasemani* and *E. cucuhyensis*, respectively, possess the same sexually dimorphic traits found in other species of *Epapterus*, although no dimorphic, adult specimens have been seen.

## MATERIAL EXAMINED

Specimens used extensively for character information in this study are listed below (Table 3). A number of specimens examined more superficially for external morphology at the collections of AMNH, CAS, USNM, ANSP, NMW, and UMMZ are not listed here. The extensive skeleton collection at AMNH includes representatives of most catfish families; these were examined in some detail early in the study. Except for the doradoids, these specimens are not listed below, unless specifically refered to in the text.

Because of the great number of species-level problems that remain unresolved within the Auchenipteridae, the species names used in discussions of anatomical structure are those under which the specimens have been cataloged and may be misidentified at the species level. In many cases, such as Auchenipterus nuchalis, Parauchenipterus galeatus, and Auchenipterichthys thoracatus, a single name is currently being used for what appears to be a number of distinct species. The proposed generic placement of the specimens examined is reflected by their designation in the list of materials examined (table 3), but no opinion is intended regarding the accuracy of the species identification. Illustrated material is identified by the generic name considered valid here, along with the specific name, if any, under which it is cataloged.

SPECIMEN PREPARATION

Osteological observations were made on both dry and cleared-and-stained specimens. Cleared-and-stained specimens were prepared following Taylor (1967), with the addition of appropriate steps for alcian blue staining of cartilage as described in Dingerkus and Uhler (1977). Freshly obtained, aquarium-trade specimens were often prepared as disarticulated cleared-and-stained specimens to permit more extensive observation of neurocranial details.

Osteological illustrations were made with a camera lucida attached to a Wild-M5 dissecting microscope. Details were added freehand when necessary. In the illustrations, fine stippling (either by hand or commercially-produced overlay) was used to represent bone; solid circles represent ligament; small open circles represent cartilage or, in the myological drawings, cut muscle; hatching indicates toothbearing surfaces; and broad crosshatching represents either cut or disarticulated bone.

## ABBREVIATIONS

Institutional abbreviations for the specimens are:

AMNH-American Museum of Natural History, New York;
ANSP-Academy of Natural Sciences, Philadelphia;
CAS-California Academy of Sciences, San Francisco;
IBN-Inventario Biologico Nacional, San Lorenzo, Paraguay
MBUCV-Museo de Biologia, Instituto de Zoologia Tropical, Universidad Central de Venezuela, Caracas;
MCZ-Museum of Comparative Zoology, Harvard University, Cambridge;
NMW-Naturhistorisches Museum, Vienna;
RMNH- Rijksmuseum van Natuurlijke Historie, Leiden;
UMMZ-University of Michigan Museum of Zoology, Ann Arbor;
USNM-National Museum of Natural History, Washington D. C.;
ZMA-Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Amsterdam.

Anatomical abbreviations used here are as follows:

| | |
|---|---|
| aBB | -accessory basibranchial cartilage |
| acc | -accessory dermal ossification |
| AFR | -anal-fin rays |
| APter | -fused anal-fin pterygiophore |
| art | -articular surface |
| BB2-4 | -basibranchial 2-4 |
| BBTP | -basibranchial toothplate |

| | |
|---|---|
| BO | -basioccipital |
| BR1-3 | -branched anal-fin rays 1-3 |
| BS | -basisphenoid process of parasphenoid |
| CB1-5 | -ceratobranchial 1-5 |
| CBTP | -ceratobranchial tooth plate |
| CHa | -anterior ceratohyal |
| CHp | -posterior ceratohyal |
| Cl | -cleithral spine |
| DS1-2 | -dorsal spine 1-2 |
| EB1-4 | -epibranchial 1-4 |
| Ep | -Epural |
| EpO | -epioccipital |
| EpS | -epioccipital spine |
| F | -frontal |
| FPts | -frontal-pterosphenoid |
| HHd | -dorsal hypohyal |
| HHv | -ventral hypohyal |
| HM | -hyomandibula |
| HS | -hemal spine |
| Hyp3-4 | -hypural 3-4 |
| Hy2-4 | -hypobranchial 2-4 |
| IOC | -infraorbital canal ossification |
| Lac | -lacrimal |
| LE | -lateral ethmoid |
| lig | -ligament |
| LL | -lateral line canal |

| | |
|---|---|
| lp | -lateral cartilagenous process of basipterygium |
| LPter | -laminar process of anal-fin pterygiophore |
| Max | -maxilla |
| mDeD | -depressor dorsalis muscle |
| ME | -mesopterygoid |
| mErD | -erector dorsalis muscle |
| Mes | -mesethmoid |
| Met | -metapterygoid |
| mInD | -inclinator dorsalis muscle |
| MR | -Müllerian ramus of complex centrum |
| N | -nasal |
| NM | -neuromast columns |
| of | -optic foramen |
| ol | -ossified ligament |
| OS | -orbitosphenoid |
| OsS | -os suspensorium |
| Pal | -palatine |
| Palvp | -ventral process of palatine |
| Par 5-6 | -parapophysis 5-6 |
| Pb2-3 | -pharyngobranchial 2-3 |
| PBTP | -pharyngobranchial tooth plate |
| Pel | -enlarged first pelvic-fin ray |
| PM | -premaxilla |
| PO | -prootic |
| Pre | -preopercle |

| | |
|---|---|
| PS | -parasphenoid |
| PT | -posttemporal |
| Pte | -pterotic |
| Pter | -anal-fin pterygiophore |
| Pt1-3 | -dorsal-fin pterygiophores 1-3 |
| Pts | -pterosphenoid |
| Q | -quadrate |
| Scu | -lateral-line canal scutes |
| SN | -supraneural |
| SO | -supraoccipital |
| Sph | -sphenotic |
| Sup | -suprapreopercle |
| tc | -transverse canals |
| Tr | -tripus |
| tri | -trigeminofascialis foramen |
| TrP | -transformator process of tripus |
| U | -urogenital pore |
| U2 | -second ural centrum |
| UC | -ural complex |
| uoc | -unossified cephalic lateral line canal |
| V1,5,6 | -vertebra 1, 5, or 6 |
| Vc | -compound vertebra |
| Vo | -vomer |

# RESULTS

Before presenting the character information analyzed in this study, the preferred hypothesis of relationships of the doradoid catfishes will be stated. This is done primarily to introduce taxonomic names that will be used in the discussion of character distributions. Defining characters for each of the named groups will be summarized in the systematic section, which follows the character analysis. Justification for the use of the names presented here is given later in the text. Only when a name presented here has a membership different from usage in Mees (1974), is the group membership mentioned. None of the family-level names is newly proposed.

The Doradoidea are hypothesized to be a monophyletic group consisting of three families: the Doradidae, the Centromochlidae, and the Auchenipteridae (fig. 1). Relationships within the Doradidae are outside of the scope of this study and have not been considered further.

The Centromochlidae are considered to be the sister group of the Auchenipteridae. The family Centromochlidae (fig. 2) is composed of six genera. Centromochlus is the sister group of an unnamed group (Genus A) consisting of species previously included in Tatia. The remaining species of Tatia are divided into two genera, one of which is unnamed (Genus B), that are sister groups. These two genera and their sister, Glanidium, form a second major clade of the family. The monotypic genus *Gelanoglanis* is placed in an unresolved trichotomy with these two clades.

The Auchenipteridae (fig. 3) are resolved into a basal polychotomy consisting of the monotypic genera *Pseudotatia*, *Tocantinsia*, and *Asterophysus*, and two subfamilies: the Trachycorystinae and the Auchenipterinae. The Trachycorystinae are composed of the genera *Trachycorystes*, *Liosomadoras*, and *Trachelyopterichthys*. I have not uncovered any character information that indicates the relationships of these genera.

Within the Auchenipterinae, one tribe, the Auchenipterini, is recognized. The genera *Auchenipterichthys* and *Pseudauchenipterus* are left in an unresolved polychotomy with this tribe, pending further resolution of their status.

The Auchenipterini consist of two multigeneric clades: the *Auchenipterus* group and the *Ageneiosus* group; and the genera *Trachelyichthys* and *Trachelyopterus*. The genus *Trachelyopterus* as used here includes *Parauchenipterus* (sensu Mees 1974). As indicated in fig. 4, *Trachelyopterus galeatus* is more closely related to *Trachelyopterus coriaceus* than to other species, including *T. amblops*, which Mees placed into his *Parauchenipterus*. Thus, the monophyletic group containing all species of Mees' *Parauchenipterus* also contains *T. coriaceus*, the type of the genus name with priority.

Trachelyichthys is considered to be the sister group of all other auchenipterins because it lacks most of the defining features of that group.

The Ageneiosus group includes Tetranematichthys (fig. 5) as the sister group of the only other genus recognized here, Ageneiosus. Relationships within the genus Ageneiosus are under study by another researcher and, therefore, greater resolution of the taxa within this tribe was not attempted here.

The Auchenipterus group (fig. 6) is composed of the genera Entomacorus, Auchenipterus, and Epapterus, with the latter two genera considered sister groups (but see the discussion of the genus Auchenipterus). Epapterus subsumes the genus Pseudepapterus, as the two included species of the latter genus, hasemani and cucuhyensis, have historically been joined on primitive characters and do not seem to share any derived characters.

## CHARACTER ANALYSIS

### Jaws and Suspensorium

J1) Hyomandibula rotated posteroventrally, with articular surface for quadrate posterior to articular facet for sphenotic (fig. 7A). Unique to Asterophysus. In all other doradoids and typically in catfishes, the hyomandibula is oriented anteroventrally, with its quadrate articulation anterior to its articulation with the neurocranium (fig. 7B-D).

J2) Quadrate with dorsomedially-directed lamina between articular surfaces for hyomandibula and metapterygoid. Laminar bone separates laminar portions of hyomandibula and metapterygoid and sutures to each of them (fig. 7D). In the Ageneiosus group. Primitively in doradoids, the dorsal surface of the quadrate is smoothly arched, and the hyomandibula sutures to the metapterygoid dorsal to the quadrate.

J3) Metapterygoid a conical, perichondral ossification with little or no laminar extension (fig. 7C). In the Centromochlidae. Typically in catfishes, the metapterygoid has a dorsomedially directed laminar sheet of bone which extends dorsal to the quadrate and sutures with a lamina of the hyomandibula.

J4) Ectoptergoid absent. Characteristic of the Doradoidea, but absent in a number of other catfishes. This is the entopterygoid of Regan (1911) and Chardon (1968). Both of these authors used the presence or absence of the entopterygoid in their family definitions. There is little question that this element, although modified from the primitive condition in catfishes, is homologous with the teleostean ectopterygoid (see Fink and Fink, 1981). Therefore, while the presence of the modified form may be defining for catfishes, its absence is defining for one or more groups within catfishes.

J5) Palatine expanded anteriorly, in adult males, with enlarged articular surface for maxilla (figs. 8, 9). Found in the _Auchenipterus_ group, the _Ageneiosus_ group, and "group a" species of the genus _Trachelyopterus_, all of which have ossified maxillary barbels in adult males. It is hypothesized that this character defines the Auchenipterini, and that its absence in some species of this tribe is a secondary loss. This absence is noted in groups 2 and 3 of the genus _Trachelyopterus_ and in the genus _Trachelyichthys_. In doradoids, the palatine is typically an elongate cylinder with cartilagenous articular surfaces anteriorly and posteriorly (fig. 10A). The shape of the catfish autopalatine varies considerably. Gosline (1975) and Howes (1983) have discussed the variation and the significance of this element in relation to maxillary barbel movement. No comment was made, in either study, however, regarding the condition found in the Auchenipterini.

J6) Palatine with posteriorly directed splint of bone ventrally (fig. 10B, C). In the Auchenipterus group. In all other doradoids, there is no such projection of bone, the ventral surface of the palatine being smoothly rounded. In the Auchenipterus group, a strong ligament runs from the palatine projection to the anterior face of the mesopterygoid.

J7) Premaxilla with dentition reduced to no more than a single row of small conical teeth. In Entomacorus and some of the examined species of Auchenipterus (fig. 12A, B). The absence of jaw dentition (J8, below) in Epapterus is presumed to be a further derivation of this character. Thus, reduction of jaw teeth may be a character defining the Auchenipterus group. In catfishes, the premaxillary dentition consists of several rows of conical teeth. Dentition patterns in catfishes vary considerably, but it seems that the primitive condition is the presence of bands of small conical teeth on both the premaxilla and dentary. Within the Doradoidea, reduced dentition is also found in most of the doradids with compressed heads, including Doras (Eigenmann 1925). Although a detailed phylogeny of the Doradidae has yet to be completed, it appears that, based on a number of characters including reduced dentition, that Doras is part of a restricted clade within the Doradidae. It is, therefore, hypothesized that the two groups have reduced their jaw dentition independently.

J8) Dentition absent from both dentary and premaxilla. A defining characteristic of the genus Epapterus. Epapterus is included in the Auchenipterus group, in which the dentition is reduced (character J7). Here, teeth are not known to develop at all, a condition otherwise known among catfishes only in Hypophthalmus.

J9) Tooth-bearing surface of dentary greatly expanded, accommodating large number of tooth rows. Found in Ageneiosus. The anterior margin of the tooth patch of the dentary in most catfishes is flush with the underlying bone. In Ageneiosus, the tooth patch extends in front of the bone.

J10) Teeth absent from palatines and vomer. In the Doradoidea and numerous other catfishes. The absence of teeth in the palate is found in a number of catfishes and has been ascribed previously to doradoids. Mees (1974), however, noted that vomerine teeth are present in large individuals of Tatia intermedia. I have not examined his specimens, but I suspect that this observation is of an aberrant individual, as I have never seen palatal teeth in any specimen of that species, nor in any other doradoid for that matter.

J11) Maxillary ossification elongate, extending far into maxillary barbel. In the Auchenipterus group and Gelanoglanis. In contrast, the doradoid maxilla typically consists of a short element which articulates basally with the palatine and extends into, and forms the base of, the maxillary barbel (fig. 10A). An elastin core extends from the hollowed-out distal end of the maxilla to the tip of the barbel. In both the Auchenipterus group and Gelanoglanis, however, the maxilla extends well into the maxillary barbel and is not continued by an elastin rod. The occurrence of this extended maxilla in Gelanoglanis is considered homoplasious with the similar condition in the Auchenipterus group.

J12) Abducted maxillary barbel directed laterally and dorsally. In the Auchenipteridae and Centromochlidae. Gosline (1975) discussed the range of movement for the catfish maxillary barbel. Generally, barbel movement consists of a sweep within a transverse plane, extending the barbel from its appressed position alongside the body to a forward position in front of the snout. Often, there is a component of the movement in which the barbel is also directed ventrally, resulting in an anteroventrally extended barbel. In both auchenipterids and centromochlids, the extended barbel can be anterodorsally directed so that its distal half is directed dorsally.

J13) Maxillary ossification extends distally into core of maxillary barbel, replacing elastin rod and transforming barbel into arc-shaped, rigid structure (figs. 9,11). The barbel rests appressed to the side of the head, curving below the eye. When erected, it extends out at right angles to the main axis of the body with its distal tip projecting dorsally. In the Auchenipterus group, the Ageneiosus group, and some species of Trachelyopterus, although in a modified form in Ageneiosus (J15, below). This increase in ossification occurs only in adult males and appears to be seasonal, inasmuch as aquarium-reared individuals of Ageneiosus sp. have been observed to grow, resorb, and regrow the barbel, within a single year (G. Eckstein, pers. comm. and pers. obs.). The surface of the maxillary barbel of adult males which undergo this increased ossification is strongly tuberculate dorsally.

J14) Maxillary barbel reduced in length, not extending posteriorly beyond snout. In Ageneiosus. Generally in doradoids, the maxillary barbel is as long as, or longer than, the head.

J15) Maxillary barbel of adult males with fully ossified core containing several tooth-like protuberances (fig. 9). In *Ageneiosus*. The character is considered to be a further modification of the maxillary barbel ossification described in J 13. Although the barbel is substantially shorter than that of other auchenipterids, it is completely ossified and is curved so that it projects dorsally when abducted.

J16) Maxillary barbel, when fully adducted, rests in groove in skin of the cheek, just ventral to eye (D. Curran, pers. comm.). In the Auchenipteridae and the Centromochlidae. In catfishes, the maxillary barbel, when fully retracted, is generally appressed to the cheek, but does not lie in a groove. In some members of the Pimelodidae (e.g. *Nannorhamdia* and *Nemuroglanis*), there is a groove similar to that of the Auchenipteridae. The occurrence of this condition in pimelodids is considered homoplasious, based on the highly corroborated evidence for a monophyletic Doradoidea.

J17) Dentary with two ventrally directed spurs near symphysis on which mental barbels articulate. In the *Auchenipterus* group. In other catfishes, the ventral surface of the tooth-bearing lower jaw element does not exhibit such spurs.

J18) Mental barbels in transverse row near symphysis of lower jaw. Common to the Auchenipterus group. Generally, mental barbels are found posterior to the symphysis of the dentary and most often obliquely situated, with the inner mental barbels more anteriorly placed.

J19) Mental barbels forming a single pair. Only in Tetranematichthys and Gelanolanis (Böhlke, 1980) among the doradoids. Generally, two pairs of mental barbels are found in catfishes, although more are known in several lineages (e.g. Callichthyidae and Aspredinidae). A single pair of mental barbels also defines the Asian catfish family Pangasiidae. Pangasiids, however, do not share any uniquely derived characters with doradoids. Thus, the loss of one pair of mental barbels is considered to be an independent occurence in each of these lineages.

J20) Premaxillae widely separated, not touching at midline (fig. 12D). In Gelanoglanis. Premaxillae are usually closely apposed or in actual contact along their mesial margins (figs. 12A-C, 14). In Gelanoglanis, the tooth-bearing elements are separated by at least one-half the length of the premaxilla.

J21) Premaxilla with posteriorly directed, toothless spur at lateral margin of tooth-bearing surface (fig. 12A, B). In the *Auchenipterus* group. In general, the catfish premaxilla is entirely covered with teeth on its ventral surface (figs. 12C,D, 14). Within the *Auchenipterus* group, the toothless spur is very short in *Entomacorus* (fig. 12A) and proportionally much longer in *Auchenipterus* (fig. 12B) and *Epapterus*.

J22) Mental barbels absent. In *Ageneiosus*. Doradoid catfishes generally have two pairs of mental barbels. As described in character J 19, *Gelanoglanis* and the sister group of *Ageneiosus*, *Tetranematichthys*, exhibit a single pair.

## Neurocranium

N1) Parasphenoid with dorsally expanded basisphenoid lamina which encloses optic foramen and excludes pterosphenoid (or pterosphenoid process of frontal, see N2) from anterior wall of foramen of trigeminal-fascialis complex (fig. 13). In the Auchenipterini, except *Trachelyichthys* and *Entomacorus*. Generally, in catfishes, the optic foramen is bounded posteriorly by the basisphenoid process of the parasphenoid and anteriorly by the orbitosphenoid (fig. 14). Often, the pterosphenoid forms at least part of the dorsal margin of the foramen. The pattern of ossifications surrounding the trigeminal-fascialis complex varies greatly among catfishes, but the pterosphenoid usually forms part of the anterior margin of the foramen. In the taxa listed above, a lamina of the parasphenoid extends between the pterosphenoid and the foramen.

N2) Pterosphenoid absent as independent element, apparently fused to ventral surface of frontal (fig. 13). In Trachelyopterus. Primitively, the pterosphenoid is a chondral bone dorsal to the orbitosphenoid and anterior to the chondral portion of the sphenotic. The frontal, a dermal bone, lies dorsal to the pterosphenoid. Species of Trachelyopterus, have a single element in the spatial arrangement that is equivalent to the frontal and pterosphenotic. The ventral margin of this element contacts the orbitosphenoid synchondrally, suggesting that at least part of the bone was derived from pterosphenoid material. Specimens examined during this study were all adult in which there is no indication of ontogenetic fusion.

N3) Epioccipital extends onto dorsal surface of neurocranium (figs. 14-19). Characteristic of the Doradoidea. In ostariophysans, the epioccipital forms the dorsolateral portion of the posterior neurocranium. In all doradoids, however, part of the epioccipital extends onto the dorsal surface of the neurocranium and is situated between the supraoccipital and the posttemporal.

N4) Epioccipital with posteriorly directed spinous process in form of elongate, flattened blade. In the Auchenipterinae. The epioccipital of catfishes typically has a short, conical, posteriorly directed spine. In auchenipterins and the doradid genus Pterodoras, the spinous process is elongate and, as described below, often forked.

N5) Epioccipital spine bifurcated distally. In the Auchenipterini, except Entomacorus, Pseudauchenipterus and Asterophysus. In the Auchenipterini (figs. 15, 17), the medial fork of the epioccipital spine usually contacts the parapophyses of the fifth and sixth centra (more fully described in character V10). In the other taxa with forked epioccipital spines, the medial fork is short (fig. 19), not extending to the vertebral column, and therefore not considered to be synapomorphous here.

N6) Frontals sutured along midline for entire length; anterior fontanelle absent. In Gelanoglanis. In all other doradoid catfishes, the frontals meet along the midline only posterior to the epiphysial bar (figs. 14-19). Anterior to that, a median gap in the frontals exists as the anterior fontanelle. In Gelanoglanis, this fontanelle is covered by the enlarged frontals.

N7) Epioccipital spine with medial fork broadly flattened, larger than lateral fork. Lateral fork with abrupt medially directed bend at tip. In the Ageneiosus group. In other species with forked epioccipitals, the forks are approximately equal in size, or the medial fork is smaller than the lateral. In species outside the Ageneiosus group, the lateral fork ends in a posteriorly directed point.

N8) Sphenotic expanded anteriorly, extending to anterior margin of frontal and excluding frontal from orbital margin (fig. 15). In Trachelyopterus, the Auchenipterus group, Asterophysus, and the Trachycorystinae. Outside of the Doradoidea, a similar condition is found in the Siluridae and Clariidae. Generally in catfishes, the frontal forms the dorsal border of the orbit.

N9) Sphenotic and pterotic excavated laterally, resulting in strongly concave lateral margin of neurocranium (fig. 16). In Glanidium. Generally in catfishes, the lateral margins of both of these bones are straight-sided and parallel to the long axis of the head (fig. 14), or only slightly concave (figs. 15, 17, 18).

N10) Frontal extended posteriorly, contacting anterior and lateral faces of supraoccipital, excluding sphenotic from contact with supraoccipital (fig. 17). In

Auchenipterus and Epapterus. In other auchenipterids, and generally in catfishes, the medial margin of the sphenotic contacts the supraoccipital.

N11) Vomer absent. Unique to Gelanoglanis. A vomer is present as a separate element in all other doradoids examined, and with few exceptions, in all catfishes. No evidence of a vomer was noted in either of the two specimens of Gelanoglanis that were examined.

N12) Transverse canals in supraoccipital and dermal component of dorsal-fin basal elements (fig. 18). Unique to Entomacorus. The function of these canals is unknown. The canals, however, are unrelated to canals found on the supraoccipital of a wide variety of catfishes that possess heavily ossified cranial roofing bones. In the latter case, two parallel canals open dorsally and extend posteriorly from the juncture between the frontal and supraoccipital. Posteriorly, the canals intersect a transverse canal which extends across the width of the supraoccipital. These canals appear to carry free neuromasts. The characteristic "$\pi$"- shaped arrangement of these canals has been noted previously by Eigenmann and Eigenmann (1890) and has been erroneously described as a species-specific characteristic of Parauchenipterus sp.

N13) Accessory dermal ossification at junction of frontal, sphenotic, and supraoccipital (fig. 18). Unique to Entomacorus. This ossification was first noted by Britski (1972) and it has been found in all specimens of Entomacorus. Positionally, it is equivalent to the parietal, an element that is absent as an independent ossification in catfishes (Fink and Fink, 1981). Therefore, the bone is considered a derived feature of Entomacorus and not a sympleisomorphy of primitive teleosts.

N14) Accessory dermal ossification at junction of sphenotic, pterotic, and supraoccipital (fig. 19). Unique to Asterophysus. As with the dermal ossification noted above (N13), the presence of an additional ossification on the dorsal roof of the neurocranium is considered to be derived within the catfishes. The positional difference between this bone and that of Entomacorus, in addition to other evidence indicating the relative position of these two taxa within the doradoid clade, argues for interpreting these elements as independently derived.

N15) Nasals forked, with accessory lateral tube directed anteriorly (fig. 9). In the Ageneiosus group. In other catfishes, the nasal is a tubular ossification surrounding the nasal canal of the cephalic lateral-line system (figs. 16, 18). Midway along the length of the bone, a branch of the canal exits laterally but remains unossified. In the Ageneiosus group, this side branch becomes ossified, giving the nasal a 'Y' shape.

N16) Orbitosphenoid of adult males with dorsal margins conjoined, forming a closed, cylindrical bone; horizontal shelf extending along lateral surface of orbitosphenoid (fig. 20). Unique to the Auchenipterus group. Typically, the orbitosphenoid is an unpaired, trough-shaped bone which is open dorsally (fig. 13-15). The formation of the orbitosphenoid described here provides an increased surface area and length for the musculature of the palatine-maxillary mechanism. Males of this group have ossified maxillary barbels and enlarged autopalatines that presumably require a larger muscle mass for movement.

N17) Parasphenoid keeled ventrally, at least in adult males. In the Auchenipterus group. In most catfishes, the parasphenoid is flat or slightly convex ventrally. As in the case of the orbitosphenoid shelf (N16), this modification of the parasphenoid apparently increases the surface area to accomodate the musculature of the palatine-maxillary mechanism.

N18) Vomer rounded anteriorly without angular lateral projections. In the Ageneiosus group. The typical catfish vomer is arrow-shaped anteriorly with posterolaterally directed arms attaching to the anterior end of the medial shaft. In *Ageneiosus* and *Tetranematichthys*, the anterior half of the vomer is either a broadly rounded mass without angular projections or a parallel-sided splint of bone without any anterior expansion.

N19) Supraoccipital concave dorsally in adult males, resulting in sloped nuchal region with dorsal fin elevated above dorsal surface of neurocranium (fig. 11). In the Auchenipterini. No similar sexual dimorphism has been noted in any other catfish.

## Lateral-line canal system and Infraorbital canal ossifications

I1) Four canal ossifications, including lacrimal, anterior to sphenotic (fig. 21A, B, I, J). In both the *Ageneiosus* group and the Doradidae. The homologies of infraorbital canal ossifications in catfishes have never been established. In the absence of a study of the relationship between ossification pattern and neuromast location, we are limited, at present, either to number of ossifications or grossly anomalous bones as sources of character information. Within doradoids, the number of ossifications varies greatly. In ostariophysans, the presumed primitive number of ossifications is six, including the lacrimal and dermosphenotic (Nelson, 1969). A dermosphenotic is never present in catfishes as an independent element; this bone, instead, is fused to the chondral sphenotic. This phylogenetic fusion is indicated by the presence of a branched canal of the cephalic lateral-line canal system typical of that found on the dermosphenotic. This fusion reduces the presumed primitive number of infraorbital elements to five. Thus, the reduction to four in both doradids and the *Ageneiosus* group must be considered derived. However, the preponderance of available evidence suggests that these two taxa are not closely related and, therefore, the character is considered homoplasious.

I2) Ventral process of lacrimal elongate, with spinous process extending ventrally from posterior rim of canal-bearing portion (figs. 21K, L). Unique to the *Auchenipterus* group. In other catfishes, the lacrimal canal extends along the length of the ventral process of the lacrimal bone.

I3) Four or five small ossifications lying anterior to ventral process of lacrimal (fig. 21G). Shared by *Auchenipterus* and *Epapterus*.

I4) First canal ossification beyond lacrimal flaired posteriorly, forming trumpet-shaped opening (fig. 21F). Unique to Ageneiosus. In all other catfishes examined, the canal ossifications near the lacrimal are tubular and of approximately equal size at both ends. The posterior end appears to be the junction of two canals, and this accounts for the enlarged size of the opening.

I5) Absence of small canal ossification just anterior to sphenotic (fig. 21A, B, E, G, I, J). In doradids, the Ageneiosus group, Asterophysus, and Trachelyopterichthys. Typically, the posterior margin of the orbit is bounded by two canal ossifications. The ventral ossification is the larger, extending along nearly the entire posterior margin of the orbit. The absence of the posterior-most ossification was determined by Britski (1972) to be a defining character of the family Doradidae. The distribution of this "loss" character indicates that it has been attained independently in several lineages.

I6) Posterior canal ossification remote from sphenotic, leaving an unossified length of infraorbital canal. Unique to Ageneiosus (fig. 21I, J). In no other doradoid catfishes is there a large gap between the last infraorbital canal ossification and the sphenotic. Typically, the entire canal is surrounded with ossifications (but see I7, below).

I7) Suborbital region of infraorbital canal without ossifications (fig. 21D, E, H). In the auchenipterid genera Trachelyopterichthys and Auchenipterichthys and the centromochlid, Tatia.

I8) Canal ossification anteroventral to sphenotic with broadly triangular laminar ossification which is strongly tuberculate (fig. 21E); remaining infraorbital ossifications oftern with row of conical denticulations along lateral surface. In the Trachycorystinae. Catfish infraorbital ossifications generally are limited to the canal-bearing portion and lack laminar extensions (Fink and Fink, 1981). Species within the families Doradidae and Clariidae provide notible exceptions to this.

I9) Lacrimal broadly joined along posteromedial face to lateral ethmoid and firmly joined at anterior tip to mesethmoid cornu (figs. 17, 18). Unique to the Auchenipterus group. Primitively, the lacrimal is either free or loosely joined to the lateral ethmoid and completely free from the mesethmoid.

I10) Mandibular ramus of lateral-line canal free from dentary. In Gelanoglanis. In all other catfishes, part or all of the mandibular ramus is fused to the lateral surface of the dentary bone.

I11) Lateral-line canal forked on caudal-fin base (fig.11). In the Auchenipteridae. Although not readily observed in all species examined, a forked canal is widely distributed within the Auchenipteridae and is considered characteristic of the family. Outside the Doradoidea, a forked canal has never been observed except in one species of *Pangasius*.

I12) Lateral-line canal sinusoidal along length of body, curves more pronounced anteriorly (fig. 11). In the Auchenipteridae. Generally, the lateral-line canal of catfishes is a straight tube situated along the horizontal myoseptum.

I13) Vertical rows of neuromast organs dorsal to lateral line along length of body (fig. 11). In the Auchenipteridae, but not known in the *Ageneiosus* group or the *Auchenipterus* group. The neuromasts often can be located by the lack of pigment surrounding the organ. Thus, the pattern of rows is most easily recognized in species with heavily pigmented bodies or those without complex pigment patterns. Outside the Doradoidea, a similar pattern of neuromasts is present in some species of the Ariidae (c.f. Bleeker, 1862b).

I14) Lateral-line canal with dorsally and ventrally directed branches at tip of anticlines and synclines, respectively, of sinusoidal waves. In *Auchenipterus* and *Epapterus*. These canal branches may extend in parallel oblique rows along the length of the body. In other auchenipterids, lateral-line canal pores are found on short branches off the main canal line. These branches, however, do not extend very far either dorsally or ventrally.

I15) A single series of scutes along sides of body (fig.22). In the Doradidae. The scutes appear to be expanded laminar bony plates of the lateral-line canal ossifications. The number and extent of the plates has been used for species recognition and generic definition (Eigenmann 1925). Although the form of the plates varies markedly, all of them seem to have at least one posteriorly directed spinous process in the vicinity of the lateral-line canal pore.

## Dorsal fin and supports

D1) First basal radial element of dorsal fin expanded dorsally to form rugose plate along dorsal margin, sutured along anterior margin to posterior margin of supraoccipital (figs. 14-19). Characteristic of the

Doradoidea, but absent in Ageneiosus and Gelanoglanis. Anterior to the pterygiophore of the second dorsal-fin spine in all catfishes is a median element that has been homologized with either a predorsal bone or the first fin-ray pterygiophore. Although the question of homology seems unsettled, I choose to equate this element with the first pterygiophore strictly as a matter of convenience. A dorsally expanded first pterygiophore occurs in a number of catfish lineages. Usually, it is found as a free element loosely or ligamentously associated with the succeeding pterygiophore and, often, with the convex or spinous posterior process of the supraoccipital. Outside the Doradoidea, in the Mochokidae, the element definitely does suture to the supraoccipital. That the similarity between the condition in the Mochokidae and Doradoidea indicates some affinity between the two groups cannot be dismissed. However, in the absence of a better understanding of the relationships of the doradoids among the various catfishes, the condition of the first pterygiophore may represent a synapomorphy of either the Doradoidea or of a more inclusive lineage.

D2) Basal radial of second dorsal-fin ray (Pt2) with dorsally expanded dermal component forming an "X", which sutures anterolaterally to supraoccipital and posttemporal, anteromedially to expanded first basal radial, and posteriorly to basal radial element of second dorsal-fin ray (figs. 16, 19). Characteristic of the Doradoidea but found in a modified form in Ageneisous (character D3). An expanded second basal radial is widespread and probably primitive for catfishes. Generally, however, the element is wedge-shaped, when viewed dorsally and is not sutured to the neurocranium. In the Mochokidae, the bone is usually broadly sutured along its entire anterior margin to either the supraoccipital or an expanded first pterygiophore.

D3) Entire anterior margin of dermal component of expanded basal radial of second dorsal-fin ray sutured to posterior margin of supraoccipital. In the Ageneiosus group. In other doradoids, the basal radial of the first element rests between the anterolateral processes of the second. In the Ageneiosus group, the first pterygiophore is either absent or lacks a dermal component and, therefore, lies entirely ventral to the expanded second element.

D4) Basal radial of third dorsal-fin ray (Pt3) with paired, dorsally expanded, dermal component lateral to articular surface of second dorsal spine; lateral extent of element generally recurved ventrally, following cross-sectional contour of body (figs. 16, 19). Characteristic of the Doradoidea. In catfishes, the basal radial element supports the modified second fin-ray, which is generally called the dorsal spine. The articular surface of this radial is generally much larger than that of the following rays, inasmuch as it supports a much larger spine. Primitively, the radial is completely sub-dermal, and lacks rugose dermal expansions lateral to the articular surface.

D5) Ligamentous attachments between the lateral process of the second dorsal-fin spine basal radial element, and the following: 1) epioccipital, 2) sixth vertebral rib, and 3) eighth neural arch. Characteristic of the Doradoidea. Expanded basal pterygiophore wings and associated ligaments are also found in members of the Mochokidae, Amphiliidae, and Sisoridae.

D6) Ligament extending between the second dorsal-fin spine radial and rib of sixth vertebra ossified (fig. 22). In the Doradidae. This ossification extends the entire length of the ligament and is firmly attached to both the rib and radial. A lateral-line canal passes through the ossified ligament laterally, giving the bone the appearance of an enlarged scute, a characteristic of the Doradidae. Nothing is known about the ontogeny of the ossification in this region, but one might speculate that the bone is compound, consisting of a superficial canal ossification that has fused with a deeper ossified ligament. In the Loricarioidea, the ligament is also ossified, and in all species except members of the Astroblepidae, the ossification appears as a dermal scute. Inasmuch as the Loricarioidea is a well defined natural group (Baskin 1972), I presume that the similarity of this condition to that in the Doradidae is a homoplasy.

D7) First dorsal spine with ventrally extended prongs projecting ventrolaterally, to level of basal radial (figs. 23B, 24C, D). Characteristic of the Doradoidea. The first dorsal fin-ray in catfishes is in the form of an unsegmented, heavily ossified, inverted 'V'-shaped bone that articulates with the first radial element (figs. 23A, 24A). The form, muscle and ligament attachments, and functional morphology of this element, as a part of the so-called dorsal-spine locking mechanism, has been described in detail by Alexander (1965). Generally, the anteroventral margins of this bone are broadly rounded and, when in the erect position, extend into an osseus cavity consisting of vertical or oblique lamina of the radial. In the Doradoidea, the ventral prongs are elongate, slender, and they posteriorly. The shape is similar to that in the Mochokidae (fig. 24B) and the sisorid genus Glyptosternon. Until a more broadly based study of these catfishes has been undertaken, it will not be possible to determine the phylogenetic significance of the similarities in question.

D8) Dorsal-fin spine depressor muscle passes anteriorly beneath fin-spine basal radial and inserts on ventral surface of expanded first basal radial. The tendinous origin of this muscle forms a sheath which surrounds the ventral prongs of the first dorsal spine (fig. 24C, D). Unique to the Doradoidea. Depressor muscles of fin rays in teleosts typically originate on the posterior surface of the basal radial element of the ray to which the muscle is inserted and to the anterior margin of the next basal radial (Winterbottom 1974). In catfishes, the same pattern exists for all fin rays, including the spinous anterior ones (fig. 24A, B). The condition described above for doradoids is unlike anything previously observed, and should be given additional attention. Muscle contraction appears to act on both the first and second fin spines, but its precise action on the first is unclear. Within the doradoids, two patterns of muscle attachment are observed. In auchenipterids, centromochlids, and some doradids, all fibers of the retractor muscle are reoriented (fig. 24D), and fibers are found both lateral and medial to the ventral prongs of the first fin spine. In some doradids, (fig. 24C), the deep fibers of the retractor muscle exhibit the primitive catfish orientation and only the lateral fibers reoriented. In addition, the lateral fibers are found only medial to the dorsal fin spine. In these two respects the arrangement of muscle fibers appears to be represent a transitional state between the general catfish condition and the condition found in the remaining doradoids.

D9) Dorsal-fin spine sexually dimorphic; in males elongate and exhibits increased spinulation, at least seasonally (fig. 11). Unique to the Auchenipteridae. Such an increase in length, diameter, and spinulation is known to me only among auchenipterids. From observations of a species of Ageneiosus maintained in an aquarium, it is clear that these striking dimorphic changes are reversible. They are correlated with changes in the maxillary barbel (Character J11), but the level of generality of the fin-spine enlargement appears to be greater than that of the maxillary barbel enlargement. It is not known at present whether sexual dimorphism of the dorsal fin exists in a number of auchenipterid genera, including Pseudotatia, Trachelyichthys, Asterophysus, Tocantinsia, Pseudepapterus, and Trachycorystes. However, except for Asterophysus, I have been able to examine only presumably immature specimens of these. One of the two Asterophysus batrachus syntypes is an adult male (NMW 47515) without any obvious difference in dorsal fin-spine size from that of the nearly equal-sized female syntype (NMW 47516). Some form of sexual dimorphism is expected in Trachycorystes, as this is clearly evident in Liosomadoras and Trachelyopterichthys (Ferraris and Fernandez 1987). In Trachelyopterus, dimorphic development of the dorsal fin in adult males is known for several species that I place in species group 1. The remaining species appear to show little or no dimorphism in both dorsal fin and maxillary barbels. The lack of development of these characters is presumed to be a secondary loss within the genus and is, therefore, treated as a further derivation of this character. Although the positions of some of these genera within the Auchenipteridae are unresolved, and they may, in reality, form the sister group of the clade in which sexual dimorphism of the dorsal spine does occur. However, for the present, I choose here not to use the absence of information on this character as evidence of true absence; I believe that the sexual dimorphism is likely to be a synapomorphy of the family Auchenipteridae.

D10) Dorsal-fin spine in mature males slightly to strongly sinusoidal with laterally recurved spinules originating from anterior midline of spine, often arranged in basal and distal clusters (fig. 11). Defining for the Auchenipterini. In non-auchenipterin doradoids, anterior spinules on the second dorsal-fin spine, if present, are oriented anteriorly, not recurved.

D11) Dorsal-fin spine in mature males with single row of spinules extending posteriorly from posterior midline of distal half of spine. In the Trachycorystinae (Ferraris and Fernandez, 1987) and Auchenipterichthys.

D12) Dorsal-fin spine in adult males capable of hyper-erection, with distal tip pointed anteriorly or anterodorsally. In the Auchenipterini. In all other catfishes, the erected dorsal spine can be extended only to a vertical position, with its tip directed dorsally. This limitation of the movement of the spine also occurs in female and juvenile specimens, and can be tested in both preserved and living specimens.

D13) Dorsal-fin rays feeble; second spine short; branched rays vestigial, rays fewer than 5. In Epapterus and Trachelyopterichthys taeniatus. Inasmuch as the reduced dorsal fin is exhibited in only the single species of the Trachycorystinae, its presence in T. taeniatus is considered to be independently derived from that in Epapterus.

## Anal fin

A1) Anterior rays of anal fin enlarged and thickened in adult males. Shared by the Centromochlidae and the Auchenipteridae. Rays UR1, BR1, and BR2 are usually markedly larger in males than in females. The nature of the enlargement is important in defining a number of lineages, as described below. Enlargement of anal-fin rays is not otherwise known in catfishes.

A2) Anal fin elongate, with at least 16 rays and usually more than 20. Found in all members of the Auchenipterinae. In doradids and centromochlids, anal-fin rays are usually 12 or less (Britski 1972). This is also true for catfishes in general and is presumed to be the primitive condition for otophysans. The pronounced elongation of the anal fin along with an enlarged epioccipital spine (character N4) defines the sub-family Auchenipterinae. Among doradoids, only members of the genus Trachelyopterichthys also have elongated dorsal fins. The two species of this genus, however, share several characters with member of the Trachycorystinae; thus, the elongate anal fin is considered homoplasious in the two lineages.

A3) In adult males, urogenital pore located at distal tip of anterior margin of anal fin (fig. 11A) in females, urogenital opening enlarged; at maturity, male urogenital tube grows from base of anal fin, forming elongate tube attached firmly to anterior margin of fin. In the Auchenipteridae, although absent in Entomacorus (fig. 26) and not observed as yet in several other genera. In other catfishes, the urogenital openings of both males and females, which are of similar size and shape, are located at the base of the anal fin. External examination of the urogenital pores of catfishes other than the auchenipterids has demonstrated that the sexing ofindividual fish is possible (e.g. Mayden et al. 1980, for Noturus alabater). In no other catfishes, however, does the male urogenital pore extend to the distal margin of the anal fin.

A4) Urogenital tube of adult males slender and emerging from hood-like flap of skin that covers urogenital base anteriorly (fig. 25). In the Centromochlidae. As described above (Character A3), the urogenital pore in most catfishes is a relatively inconspicuous structure located between the anus and the anal-fin base.

A5) Anal-fin basal radials obliquely slanted and not interdigitated with hemal spines, at least in adult males. Defining for the Centromochlidae. In all other catfishes and teleosts in general, the anal-fin basal radials are more or less vertical in orientation at their bases and extend into spaces between the hemal spines. In centromochlids, the pterygiophores (at least those of adult males) are strongly obliquely oriented and do not interdigitate with the hemal spines.

A6) Anal-fin pterygiophores obliquely slanted and not interdigitated with hemal spines in females and juveniles. In Centromochlus and Gelanoglanis. As described above, obliquely slanted anal-fin rays are considered derived within the Centromochlidae. In both Centromochlus and Gelanoglanis, this condition is not sexually dimorphic, but occurs in all individuals. As described more fully in the generic account of Gelanoglanis, the occurrence of this condition in the two groups is considered independent rather than synapomorphous.

A7) Anal-fin basal elements fused into single plate-like structure in adult males. In Centromochlus (fig. 27), Genus a, and Epapterus blomhi (Vari et al. 1984). Typically, the anal-fin basal elements remain separate in catfishes, even if enlarged. In Centromochlus, all basal elements are fused, whereas in Epapterus blohmi, only the anterior-most elements are involved. The differences in morphology, as well as the considerable amount of conflicting character information, suggest that the occurrence in these taxa is independent.

A8) Posteriormost 4 or 5 basal radials of anal fin with enlarged lamina on vertical process. In Auchenipterus and Epapterus (fig. 28). In catfishes, the anal-fin basal radials, except for the most posterior ones, generally consist of a single rod-like process.

A9) UR1 and first branched anal-fin ray (BR1) of adult males with paired retrorse spinules posterolaterally on distal segments (fig. 27). Shared by Centromochlus and Genus a of the Centromochlidae

A10) Ultimate unbranched anal-fin ray (UR1) longer than other rays and curved posteriorly at distal tip. In Genusa.

A11) UR1 with antrorse spinule on anterior margin of each distal segment; first branched anal-fin ray with anteriorly directed, blunt, retrorse projections on segments of anterior-branch (fig. 29A, BR1a). In Tatia and Genus b.

A12) Anal fin of adult males with large fleshy keel anterior to rayed portion. UR2 curved posteriorly and BR1 curved anteriorly so that three enlarged rays converge distally (fig. 29B); remaining rays rudimentary and crowded together. In Genus b of the Centromochlidae.

A13) UR1 and BR1 enlarged and elongated but otherwise unmodified; remaining anal-fin rays distinctly shorter, giving fin margin a lobed appearance (fig. 29C). In Glanidium.

A14) Anal fin with expanded anterior margin of penultimate unbranched fin-ray (UR2) bound tightly to antipenultimate unbranched ray (UR3) by dense connective tissue. In Glanidium, Tatia, and Genus b. The two rays are bound together so that they appear to move as a unit with only slight amounts of anteroposterior motion possible. A great amount of lateral movement is possible, however, and this suggests that the fairly rigid fin may be used as a clasping device or perhaps a conduit for sperm transfer. In nonreproductive, aquarium specimens, the fin has never been observed to move in any manner.

Caudal fin and supports

C1) Caudal fin obliquely truncate with unbranched rays not substantially thicker or longer than branched ones; hemal spines of PU3-PU7 expanded distally, reaching margin of caudal peduncle and supporting lower caudal fin rays. In the Trachycorystinae, the genera Auchenipterichthys, Trachelyichthys, Tetranematichthys, and some species of Ageneiosus and Trachelyopterus. The primitive condition in catfishes, including the Doradoidea, is a forked caudal fin with a single, thickened, unbranched ray dorsal and ventral to the shorter, branched ones. In species with this caudal fin configuration, only the first two or three pre-ural hemal spines contribute to the support of the caudal-fin rays (fig. 30A).

C2) More than 8 lower branched caudal-fin rays; first ventral unbranched caudal-fin ray inserted opposite tip of hemal spine of PU4 or PU5 (fig. 30B). In Trachelyichthys, Asterophysus, Tetranematichthys, and a restricted clade of Trachelyopterus. The primitive condition of branched caudal-fin rays in doradoid catfishes is 7 dorsally and 8 ventrally with the lower principal caudal-fin ray inserting opposite PU2. The presumed primitive condition for catfishes is 8 branched rays in each lobe of the fin (Lundberg and Baskin 1969), a condition found only in Diplomystes. Widespread among catfishes, however, is the condition described above for doradoids: 7 plus 8 branched rays. As noted in character C1, all of these taxa have obliquely truncate caudal fins. Taylor (1969) noted a correlation between an increased number of branched rays and larger body size in the round-tailed ictalurid Noturus. He suggested that the increase was due to the continual branching of lower caudal rays throughout the ontogeny of the fishes. Lundberg and Baskin (1969) indicated that this ontogenetic increase may negate the systematic value of the character. On the contrary, it seems that there is good reason to consider this an excellent source of information. A small series of specimens from the Parana drainage of Paraguay, identified as Parauchenipterus galeatus (UMMZ 207572), showed a distinct trend of increasing lower branched fin rays from 10 to 12 (Table 4). A second species from the same collection with similar-sized individuals had approximately one fewer ray. In both species, the lowest number of rays exceeded the presumed primitive doradoid number. Although the increase is limited to species with a obliquely truncate caudal fin, not all taxa possessing a fin of that shape exhibit an ontogenetic increase in rays, and this suggests an affinity among those that do.

C3) First unbranched ray of ventral portion of caudal fin articulates with hemal spine of PU4-PU6 (fig. 30B). In

_Auchenipterichthys_, _Trachelyichthys_, _Trachelyopterus_, _Trachelyopterichthys_, and _Tetranematichthys_. In catfishes, the first unbranched ray is usually found opposite the parhypural (fig. 30A). However, in auchenipterins with obliquely truncate caudal fins, the lower portion of the fin is displaced ventrally leaving the first unbranched ray opposite one of the expanded hemal spines, usually anterior to PU4 (character C1).

C4) Second ural centrum (U2) a full half centrum (fig. 30C). In _Entomacorus_. In nearly all other catfishes, U2 is reduced to a tiny ossicle attached to the proximal end of Hypural 3 (Lundberg and Baskin 1969). A fully formed half centrum is found in several catfishes outside of the Doradoidea (Lundberg and Baskin, 1969, Vari and Ortega, 1986), but in doradoids it is found only in _Entomacorus_.

C5) Complex ural centrum with ventrally directed spur on hypuropophysis (fig. 30C). In the _Auchenipterus_ group. In all other doradoids, the hypuropophysis is in the form of a lcw arch with no spur-like projection.

C6) Caudal fin with upper lobe longer than lower; caudal peduncle highly compressed, depth not less than body depth at anal fin (fig. 25). In _Tatia_. In other doradoid catfishes with forked caudal fins, the lobes are approximately equal in size and the caudal fin is preceded by a distinct caudal peduncle.

C7) Hypuropophysis of type B (Lundberg and Baskin, 1969). In the Ageneiosus group. The caudal skeleton of doradoids, other than Ageneiosus, exhibit hypurapophyses belonging to type C of Lundberg and Baskin (1969), characterized by a continuous horizontal shelf that extends from the second preural centrum onto the fused lower hypural plate. In type B, the hypurapophysis extends only partially onto the hypurals, for a distance equal to the presumed extent of hypural 2. Lundberg and Baskin (1969) found this condition to be uncommon in other catfishes, being present only in the Cetopsidae and Cranoglanis.

## Pelvic fins and supports

PV1) Basipterygium with anterolaterally directed, cartilaginous lateral process just anterior to articulation of first ray (fig. 31). Characteristic of the Doradoidea. In all catfishes, the posterior and lateral margins of the pelvic girdle are bordered by a slender ridge of cartilage with which the rays articulate. In doradoids, the anterolateral end of this cartilage is expanded. Shelden (1937) illustrated this extension of cartilage in doradoids and a plotosid, Plotosus arab, and he termed the mass the lateral process of the basipterygium. The presence of this lateral process in doradoids and plotosids is considered to be homoplasious.

PV2) First pelvic fin ray an elongate, flattened paddle in adult males. Unique to Entomacorus (fig. 26). Sexual dimorphism of the pelvic fin rays in unknown in doradoids, except for Entomacorus and Centromochlus (character PV2a, below). The peculiar modification of the pelvic fin in E. gameroi was first noted by Mago-Leccia (1984). With its segments flattened and broader than long, the fin ray looks like a paddle. The segments become longer distally, but become narrow abruptly near the tip. The dorsal surface of the ray is covered with papillae similar to those covering the maxillary barbel. When abducted fully, the distal segments curve medially, None of the available specimens of E. benjamini shows any sign of sexual dimorphism. Britski (1972) suggested that this species does not exhibit any dimorphism, but there is no indication that the specimens he examined were mature.

PV3) Pelvic fin with 6 or more branched rays. Found in the Doradidae, Trachycorystinae, and widely among auchenipterid genera. Lundberg (1970) and Grande (1987) have suggested that the primitive pelvic-fin configuration for catfishes consists of a pelvic splint and 6 rays (presumably consisting of 1 unbranched and 5 branched rays, here indicated by the formula s,i,5). If this is true, it must be considered a previously unrecognized synapomorphy for the Siluriformes, inasmuch as other otophysans generally have six or more branched rays. Doradoids lack a pelvic splint, leaving the presumed primitive ray formula for the group as i,5. This formula applies to all the centromochlids and to Trachelyopterus as well. All other doradoid taxa have a greater number of pelvic-fin rays. Doradids, Ageneiosus, and the genera Pseudotatia and Tocantinsia have 6 branched rays; auchenipterines, trachycorystines, Trachelyichthys, Auchenipterichthys, and Pseudauchenipterus all have 8 or more rays. Because of the wide distribution of this derived fin-ray count within the Doradoidea, the possession of a high number of pelvic fin-rays cannot be used unequivocally to unite taxa. Instead, the high counts are considered to be independently derived in each of the lineages.

PV4) Basipterygium convex dorsally; internal and external anterior processes directed obliquely-ventrally, with external processes more ventral; laminar bone between anterior processes also dorsally convex (fig. 31A). In the Auchenipterus group. In all other doradoids and widespread among other catfishes as well, the basipterygium is a flat element oriented in a nearly horizontal plane.

PV5) Anterior unbranched pelvic-fin ray longest, remaining rays progressively shorter posteriorly. In the Auchenipterus group. In other doradoids, the pelvic fin is rounded with its anterior unbranched ray equal to or shorter than the longest ray. In auchenipterids and males of Centromochlus heckelii, the anterior ray is longest.

PV6) Pelvic fins joined by extension of interradial membrane to ventral midline of body. In a restricted clade of the genus Epapterus. In no other doradoid does the inner pelvic-fin ray have a membrane connecting it with the body.

## Pectoral fin and supports

P1) Mesocoracoid arch of pectoral girdle absent. Characteristic of the Doradoidea. Regan (1911) noted the absence of the mesocoracoid in his discussion of the doradoids. Chardon (1968) apparently misinterpreted Regan when he claimed that a mesocoracoid arch was present in all Neotropical doradoid families.

P2) Pectoral spine elongate, that is, greater than head length, with feeble serrae posteriorly and none anteriorly. In Centromochlus. Primitively, the doradoid pectoral spine is bounded anteriorly and posteriorly by relatively stout serrae, and the spine is equal to or shorter than the length of the head.

P3) Pectoral spine with anterior serrae twice as numerous as posterior ones (fig. 32A) and much shorter. In centromochlid Genus a. In all other doradoids with serrated pectoral spines, the ratio of anterior to posterior serrae is 1:1. Mees (1974) noted the similarity in the serration pattern of pectoral spines between his Tatia altae and T. perugiae; he suggested that these forms should be considered subspecies to indicate their close relationship.

P4) Anterior pectoral-spine serrae directed perpendicular to the long axis of the spine (fig. 32B). In Tatia. The anterior serrations of most other doradoids, and catfishes generally, are directed obliquely toward the distal edge of the fin. (but see P6).

P5) Anterior pectoral-spine serrae directed basally (fig. 32C). In Tocantinsia.

P6) Anterior pectoral-spine serrae of adult males curved ventrally with tips directed ventrally or posteroventrally (fig. 32D). In Entomacorus. Recurved tips of pectoral serrae are otherwise unknown in catfishes.

P7) Anterior pectoral spine serrations absent. In the Ageneiosus group, the genera Pseudauchenipterus, Gelanoglanis, Auchenipterus, and Epapterus, and Trachelyopterus coriaceus. The distribution of this apparent loss of serrations suggests that this occurred independently several times.

P8) Cleithrum without posteriorly directed spine in adults. In Ageneiosus. A cleithral spine is typically present in catfishes and is present in all doradoids except Ageneiosus. Among the specimens available, a cleithral spine could be seen in one juvenile specimen of Ageneiosus marmoratus, but the spine was absent in a larger specimen.

P9) Third pectoral-fin basal radial expanded distally, supporting a large number of fin rays. In the Ageneiosus group. Typically the third basal radial is a rod-like ssification with its basal and distal ends approximately equal in size.

P10) Third pectoral-fin radial absent. In Gelanoglanis and Tatia cruetzbergi. In all other doradoids, the third pectoral-fin radial is present, although sometimes modified, as in it is the Ageneiosus group (P9).

## Hyoid and gill-arch elements

G1) First and second hypobranchials strongly concave anteriorly; mesial end of cartilaginous tip of each bone located further anteriorly than the lateral end of the bone (fig. 33). In the Ageneiosus group In other doradoids, and generally in catfishes, the anterior margins of the hypobranchials are straight and the elements are perpendicular to the long axis of the body.

G2) Accessory basibranchial cartilage located between the third and fourth basibranchials (fig. 34). In the Auchenipteridae, but often quite small. In catfishes, the basibranchial series develops from two cartilages. The anterior cartilage is situated in the region of hypobranchials 1 through 3 and often becomes ossified as two perichondral bones situated between the second and third, and third and fourth pairs of hypobranchials. These ossifications are termed the second and third basibranchials, respectively. The second cartilage of the basibranchial series is situated posterior to the third basibranchial ossification and, in doradoids, is often in the form of a broadly flattened plate (BB4 in figs. 33-35). This cartilage, which never ossifies in catfishes, is termed the fourth basibranchial. In the Auchenipteridae, an extra cartilage forms along the anterior edge of the fourth basibranchial plate. The cartilage appears to be an anterior extension of the fourth basibranchial, but is present, with few exceptions, as an independent element. No other catfish examined by me has ever had a structure similar to this.

G3) Mesial tip of first epibranchial larger than that of second epibranchial (fig. 33), usually covering that element dorsally. In the Ageneiosus group. In other catfishes including all other doradoids, the mesial tips of the first and second epibranchials are nearly identical in size and form. The two elements are bound together so that the first is just anterior to the second, but in the same dorso-ventral plane.

G4) Gill rakers long and closely spaced. In the Auchenipterus group (Britski 1972). In other doradoids, gill rakers either are quite short, with space between succeeding rakers greater than their length, or are absent.

G5) Pharyngobranchial toothplate elongate, extending anteriorly to below an elongated third pharyngobranchial ossification (fig. 35). In Asterophysus. Typically the single upper gill-arch tooth plate in catfishes is round or slightly oval and rests below the fourth pharyngobranchial element.

G6) Second and third basibranchials rudimentary, remote from greatly enlarged fourth basibranchial cartilage (fig. 35A). In Asterophysus. The size relationships between these elements of the basibranchial series are unusual, compared with the more typical arrangement for catfishes seen in figures 33 and 34. The virtual absence of the anterior basibranchials and the large plate-like fourth basibranchial resemble the condition in the Asian catfishes Chaca (Brown and Ferraris, In Press) In both of these genera, the mouths and oral cavities are exceptionally large, and the species are known to consume large fish as prey. It is possible that basibranchial development is retarded in relation to this feeding mode.

G7) Urohyal with medial projection directed dorsally and extending between hypohyals. In the Ageneiosus group. Similar projections of the urohyal are found in a number of catfish families, such as the Hypophthalmidae and some species of the Pimelodidae, but in general, the catfish urohyal lies wholly ventral to the hypohyals so that the latter are closely apposed along the midline.

G8) Anterior ceratohyal sutured to ventral hypohyal along ventromedial surface (fig. 36A). In the Ageneiosus group. In other doradoids, the two hyoid elements are joined along their lateral surfaces, leaving the medial aspect of the two bones separated by a substantial block of cartilage (fig. 36B).

## Vertebral column

V1) Neural arch of complex centrum sutured to exoccipital (fig. 13). Defining for Doradoidea. In all other catfishes, the neural-arch lamina of the complex centrum extends anteriorly dorsal to the first centrum and closely apposes or contacts the posterior end of the neurocranium at the exoccipitals. Wherever contact is made, the ossifications are separated by cartilage. In all doradoids, the anterior margin of the neural arch forms an interdigitated suture with the exoccipital.

V2) Transformator process of tripus a ventrally recurved lamina that projects medially and clamps onto tunica externa of swimbladder (fig. 37). In the Doradoidea, but also found in the aspredinid genus Agmus and in one specimen of the schilbeid Pseudeutropius garua (NMW 44360). The primitive condition of the catfish tripus includes a transformator process with a slender medially directed curve (fig. 38). The process penetrates the tunica externa [as illustrated in Chardon (1968, p. 93, fig. 8)].

V3) Transformator process of tripus, in adults, with enlarged, recurved lamina which is not oriented horizontally (fig. 39). In _Ageneiosus_, except _A. nigricollis_. This appears to be a further modification of the doradoid transformator process; during the ontogeny of at least one species, _A. marmoratus_, it can be observed to change from the typical doradoid configuration to the one found only in adult _Ageneiosus_. In adult specimens of _A. nigricollis_, a species without an encapsulated swimbladder, the tripus retains the typical doradoid condition.

V4) Os suspensorium reduced to a disc-shaped nodule suspended by a ligamentous fan to the tripus and complex centrum (fig. 40). Defining for the Doradoidea. The os suspensorium is a splint of bone extending anteroventrally from the ventral surface of the transverse process of the complex centrum. The tip of the os is an expanded nodule to which a ligamentous sheath is attached. In all doradoids, the osseus shaft is absent in adults. However, in a small specimen of _Pseudauchenipterus_ (USNM 226107), a very thin shaft of bone was still visible.

V5) Tripus expanded anteriorly; broadly ovoid attachment for ligamentous connection among Weberian ossicles (fig. 37). In the Auchenipterus group. In all other doradoid catfishes, the anterior end of the tripus is slightly, if at all, expanded.

V6) Anterior process of complex-centrum transverse process flattened forming a two-dimensional lamina [called the Müllerian ramus (Tavolga, 1962)], not ligamentously joined to posttemporal. In the Doradoidea and the families Mochokidae, Malapteruridae, Ariidae, and Pangasiidae (but not in Pangasius suchii, Pers. obs.). The distal tip of the transverse process is expanded (fig. 40) and broadly contacts the anterior end of the swimbladder. This ramus, along with its associated muscles, has been called the elastic spring apparatus and has been shown to have a sound-generating function by Tavolga (1962). There is considerable variation in the form of the apparatus, along with the derivation of the muscular attachments associated with it. The questions concerning the homology of this structure in all of these lineages is beyond the scope of this study inasmuch as the problem can only be addressed within the context of a broad study of catfish-family relationships. It is assumed that the Müllerian ramus is characteristic of the Doradoidea, but it could turn out to be a synapomorphy at a higher level of generality.

V7) Elastic spring apparatus relatively feebly developed in adults. In Ageneiosus except A. nigricollis. This character has been used widely to define the family Ageneiosidae without the genus Tetranematichthys or the genus Ageneiosus when Tetranematichthys in included within the family Ageneiosidae. Neither level of generality appears to be correct, however, inasmuch as at least one species, Ageneiosus nigricollis, has a well developed apparatus. Ontogenetic evidence of change from the typical doradoid condition to the condition described here was found in two specimens of Ageneiosus marmoratus. The smaller individual (100 mm SL) showed the doradoid condition but with signs of the beginning of swimbladder encapsulation. The larger individual had a fully enclosed swimbladder with a proportionally smaller Müllerian ramus. Thus, the character defines a restricted clade within the genus Ageneiosus that is corroborated by at least two additional characters: a reoriented tripus and an encapsulated swimbladder.

V8) Tip of Müllerian ramus produced posteriorly, extending deep into the lumen of the swimbladder. In Centromochlus. In other doradoids, the osseus tip of the Müllerian ramus is a flattened disc that rests on the anterior surface of the swimbladder.

V9) Swimbladder encapsulated by thin osseus lamina of ventral process of complex centrum. In Ageneiosus, but not A. nigricollis and probably other species placed by Eigenmann and Allen (1942) in the genus Tympanopleura. The osseus capsule is in the shape of a cornucopia, with a larger circular opening anterolaterally and a more restricted opening posterolaterally. The absence of an encapsulated swimbladder was used by Eigenmann (1912) to justify the creation of the genus Tympanopleura. However, the unencapsulated swimbladder in several species of Ageneiosus is considered to be a primitive feature and not, by itself, an indication of a natural group within the Ageneiosus.

V10) Parapophyses of fifth and sixth vertebrae directed perpendicular to long axis of vertebral column (fig. 40) and either sutured or bound by strong ligament to medial arm of epioccipital spine (see character N5). Characteristic of the Auchenipterini, but absent in Entomacorus and further modified in one clade of the genus Trachelyopterus (V11). In catfishes, the parapophyses of the fifth and sixth centra generally are oriented in an oblique, posterior direction. In the auchenipterines, the parapophyses are transverse and expanded into a "T" or "Y" shape with the arms extending antero- and posterolaterally from the centrum. The suturing of the parapophyses to each other and to the epioccipital further reinforces the structural integrity of the head-complex centrum, by eliminating all lateral movement from the basioccipital to the seventh centrum.

V11) Parapophysis of centrum 5 absent or reduced to a rudiment. In a restricted clade of the genus Trachelyopterus that contains groups 2 and 3. In other doradoids, the fifth parapophysis is either a slender posterolaterally directed rod or, as described in V10, a laterally expanded process. In the species of Trachelyopterus with a reduced parapophysis, a short rounded knob projects laterally from the centrum. It is attached to a ligament that runs both anteriorly toward the epioccipital spine, as well as posteriorly to the parapophysis of the sixth centrum. Thus, the ligament appears to be a further modification of the ossified condition described above.

V12) Pleural ribs contorted basally, wrapping around neck in parapophysis (fig. 40). Characteristic of the Doradoidea. Typically, the base of such a rib is straight and the bone tapers gradually to form a rounded basal tip. It is ligamentously attached to the ventral surface of the distal tip of the parapophysis, usually in a proximodistally oriented groove. In contrast, the base of the doradoid rib spirals dorsally and medially from the main axis of the shaft, thereby surrounding a constriction of the distal end of the parapophysis.

Other

O1) Abdomen keeled between pelvic fin and anus. In the Auchenipterus group. An acutely keeled abdomen is rarely found within catfishes and not at all in the Doradoidea except the Auchenipterini.

O2) Adipose dorsal fin absent. In Trachelyopterichthys, Trachelyichthys, Trachelyopterus coriaceus, and a restricted clade within Epapterus. The adipose dorsal fin in catfishes has been found to be a labile structure that is prone to disappear within lineages and even within populations (Vari and Ortega, 1986). Within the Doradoidea, an adipose fin is typically present, and there is little indication of any intraspecific loss of fin. P. Miranda Ribeiro (1968a) provided evidence that one of the defining characters of the genus Ceratocheilus A. Miranda Ribeiro, namely the absence of an adipose fin, was an example of individual variation. In each of the lineages listed above, however, an adipose dorsal fin is absent in all known specimens. Available evidence suggests that the loss of an adipose fin has occured repeatedly in the Auchenipteridae. Although Trachelyopterichthys taeniatus was first described as a member of Trachelyopterus on the basis of the absence of an adipose fin by Kner (1858). However, the species was soon removed from that genus by Bleeker (1862b).

03) Eyes directed ventrolaterally. In the Auchenipterus and Ageneiosus groups. Generally, the eyes of catfishes are directed laterally or dorsolaterally. In Auchenipterus, Ageneiosus, and their relatives, alone among doradoids, the eyes are more ventrally positioned and can be seen readily when viewed from below.

# SYSTEMATICS OF DORADOID CATFISHES

## SUPERFAMILY DORADOIDEA BLEEKER 1858

phalanx Doradini Bleeker 1858, p. 48.

cohors Euanemini Bleeker 1858, p. 49.

phalanx Trachelyopterini Bleeker 1858, p. 49.

stirps Pseudauchenipterini Bleeker 1862a, p. 6.

phalanx Centromochli Bleeker 1862a, p. 7.

phalanx Astrophysi [sic] Bleeker 1862a, p. 7.

phalanx Ageneoisi Bleeker 1862a, p. 14.

stirps Auchenipterini Bleeker 1862a, p. 14.

family Trachycorystidae Miranda Ribeiro, A. de, 1911, p. 352

DIAGNOSIS: Siluriform catfishes with the following derived characters: 1) tripus with expanded posterior (=transformator) process, 2) exoccipitals sutured to neural arch material of complex centrum, 3) depressor muscle of second dorsal-fin spine with at least some fibers wrapping around ventral process of first dorsal-fin spine, 4) pelvic-girdle basipterygium with expanded cartilage anterolaterally, 5) os suspensorium reduced to independent nodule, free from complex-centrum parapophysis, and 6) nuchal shield consisting of two expanded pterygiophores sutured to posterior margin of neurocranium.

Within the Doradoidea, the families Centromochlidae and Auchenipteridae are considered sister groups. This clade is defined by the shared presence of the following four characters: 1) grooved cheek for reception of retracted maxillary barbel (D. Curran, pers. comm.), 2) sexually dimorphic enlargement of at least some of the anterior anal-fin rays, 3) depressor muscle origin of second dorsal-fin spine on the lateral surface of basal projections of first dorsal-fin spine, and 4) tip of abducted maxillary barbel directed dorsally.

COMMENTS: The name Doradoidea and its variants have been used since Günther (1864) to designate a group containing, at least, the Doradidae, Auchenipteridae, and Ageneiosidae. The name dates from Bleeker's (1858) usage for the phalanx Doradini, which was restricted to members of the current Doradidae, but placed by Bleeker near the callichthyids rather than other doradoids. In the same publication, the family-level names Euanemini and Trachelyopterini were proposed for other groups of doradoid fishes. Günther (1864) served as the first revisor of these names and placed all auchenipterids, ageneiosids, and doradids, along with mochokids other than Mochokus, into his Doradina.

The Doradoidea, as treated here, does not include the Mochokidae. Chardon (1968) included the Mochokidae in his Doradoidae [sic], and Lundberg (pers. comm.) has expressed the view that the mochokids are the nearest relatives of the doradoids. The scope of this study does not include an analysis of the relationships of doradoids within the catfishes, and no opinion is expressed here regarding either the nearest relative of the doradoids or Chardon's placement of the Mochokidae.

## FAMILY DORADIDAE BLEEKER 1858

phalanx Doradini Bleeker 1858, p. 48.

DIAGNOSIS: Doradoid catfishes With: expanded ossifications of the lateral-line canal system in the form of overlapping scutes, each with a recurved hook located mid-laterally; scute that is ventral to the expanded pterygiophore of the second dorsal spine extends from the notched posteroventral margin of the pterygiophore to the lateral surface of distal tip of sixth vertebral pleural rib and ligamentously joined to both bones; infraorbital series reduced to 3 elements between the lacrimal and sphenotic; pelvic fins with 6 branched rays.

TYPE GENUS: Doras Valenciennes 1840

COMMENTS: The family Doradidae lies outside the scope of this study, and details of its relationships and nomenclature will not be considered further. There has been no comprehensive treatment of the Doradidae since Eigenmann (1925) reviewed the family.

The monotypic genus Werthemeria Steindachner (1877) has been considered a member of the Auchenipteridae by Eigenmann and Eigenmann (1890) and subsequent authors. Britski (1972) examined one of the two syntypes of the type species, W. maculata, and concluded that it was a doradid and not an auchenipterid. My observations on the second syntype are in complete agreement with this finding. Werthemeria possesses all of the diagnostic characters of the Doradidae. The lateral body scutes, however, are small and restricted to the caudal peduncle. As the presence of scutes has been the most widely used character for the family, the apparent absence of scutes naturally kept Werthemeria from being considered a doradid.

## FAMILY CENTROMOCHLIDAE BLEEKER 1862

phalanx Centromochli Bleeker 1862a, p. 7.

DIAGNOSIS: Doradoid catfishes with: anal-fin rays and basal radials rotated posteroventrally and oriented nearly parallel to vertebral axis (at least in adult males); male urogenital pore emerges from swollen basal structure at anal-fin origin; and metapterygoid a perichondral ossification with little or no laminar ossification and separated from hyomandibula.

TYPE GENUS: Centromochlus Kner 1858.

INCLUDED GENERA: Centromochlus, Tatia, Glanidium, Gelanoglanis, and two unnamed genera.

COMMENTS: This family is easily recognized by the short anal-fin base and one of its diagnostic characters, the peculiar orientation of the anal fin, especially in adult males, in which the fin is not only rotated but also immediately preceded by a swollen sack-like structure.

Unfortunately, no studies of the soft anatomy associated with the anal fin or the reproductive system of these fishes have been made. It is likely that this region of the body will reveal additional character information.

Centromochlus and one unnamed group (Genus a) are considered sistergroups based on the shared presence of two characters: 1) paired retrorse spinules found posterolaterally on distal segments of last unbranched and first branched anal-fin rays of adult males; and 2) anal-fin pterygiophores of adult males which are fused into a single element.

Glanidium is considered the sister group of Tatia plus Genus b, based on the shared presence of an expanded anterior margin of the penultimate unbranched anal-fin ray, to which the antipenultimate unbranched ray is tightly bound by dense connective tissue.

Gelanoglanis is retained as a monotypic genus, placed in a basal polychotomy of the Centromochlidae. Gelanoglanis is currently known only from the type series and an additional small series of specimens (D. J. Stewart and J. Baskin, pers. comm.) which I have not seen.

The present arrangement of species (summarized in table 6) is quite unlike any previously proposed because it reflects previously unrecognized similarities, primarily of the anal fin-ray anatomy of adult males. Males of all species have yet to be seen, and thus the generic assignment of some species remains problematical.

When possible, other evidence (e. g., sphenotic shape and pectoral fin spinulation) has been used to assign species to a particular genus. The species in this category are listed below, by the name originally used, which is preceded by an asterisk.

*Centromochlus gyrinus Eigenmann and Allen

Centromochlus gyrinus Eigenmann and Allen, 1942, p. 118, pl. 5, fig. 4, (type locality Peru: Iquitos, brook near Río Itaya).

*Tatia reticulata Mees

Tatia reticulata Mees, 1974, p. 90, fig. 25, (type locality British Guiana: Rupununi River at Karanambo).

*Centromochlus schultzi Rössel

Centromochlus schultzi Rössel, 1962, p. 27, figs. 1-2, (type locality Brazil: Rio Xingu).

*Tatia simplex Mees

Tatia simplex Mees, 1974, p. 90, fig 25, (type locality Brazil: Matto Grosso, Rio das Mortes).

GENUS CENTROMOCHLUS KNER 1858

Centromochlus Kner, 1858, p. 430 (reprint p. 60), (type species Centromochlus megalops Kner, 1858, by subsequent designation of Bleeker, 1862a, p.7).

DIAGNOSIS: Centromochlids with elongate, slender pectoral- and dorsal-fin spines which exceed the length of the head; pectoral-fin spines smooth anteriorly, feebly serrate posteriorly; anal fins of females with rotated and crowded pterygiophores, similar to the arrangement characteristic of centromochlid males; enlarged tip of Müllerian ramus a bulbous projection which extends posteriorly into the swim bladder.

TYPE SPECIES: Centromochlus megalops Kner, 1858, by subsequent designation of Bleeker, 1862a

INCLUDED SPECIES:

Centromochlus heckelii (Filippi)

Auchenipterus Heckelii Filippi, 1853, p. 166 [reprint p. 4], (type locality Rio Napo).

Centromochlus megalops Kner, 1858, p. 430, pl.8, fig. 24. (type locality Colombia: Bogota).

Centromochlus Steindachneri Gill, 1870, p. 95, (type locality Upper Rio Amazonas or Rio Napo).

Centromochlus existimatus Mees

Centromochlus existimatus Mees 1974, p. 50, figs. 8 and 9, (type locality Brazil: Rio Amazonas at Manaus).

COMMENTS: The elongate pectoral spines found in the species of this genus have long been used to distinguish Centromochlus from the remaining auchenipterids. Species of Centromochlus were thought by Mees (1974) not to be sexually dimorphic in anal-fin ray morphology, a characteristic, which if true, would certainly set the species apart from other auchenipterids. Dimorphism, however, does occur, and adult males exhibit anal-fin rays as described in the diagnosis of the genus.

When *Centromochlus* was allied with other auchenipterid species, the alliance included all, or nearly all the other species of the Centromochlidae, as recognized here. At no time was the close relationship between *Centromochlus* and the species of *Genus a* recognized.

The synonymy under *Centromochlus heckelii* and the recognition of *C. existimatus* follows Mees (1974). D. J. Stewart (pers. comm.) is of the opinion that at least one additional species exists in the upper Amazon drainage. I have not pursued species-level questions concerning this distinctive genus. *Centromochlus existimatus* is sexually dimorphic in pelvic-fin ray shape: Pelvic fins of females do not extend to anal fin base and they have rounded margins while in males, the first (unbranched) ray is longest, with a tapered margin. No evidence of similar dimorphism was noticed in *C. heckelii*.

DISTRIBUTION: Species of this genus appear to be limited to the main rivers of the Rio Amazonas and Rio Orinoco drainages.

## GENUS A

DIAGNOSIS: Centromochlids with: last unbranched anal fin ray (UR 1) elongate, fin margin hooked; and pectoral-fin spine with numerous, closely spaced serrae along anterior margin, anterior serrae twice as numerous as posterior ones.

INCLUDED SPECIES:

*Centromochlus altae* Fowler, 1945, p. 109, fig. 7-10, (type locality Colombia: Río Caqueta drainage at Morelia).

*Centromochlus Perugiae* Steindachner, 1882, p. 178, (type locality Ecuador: Canelos).

Genus A sp. 1 (Venezuela)

Genus A sp. 2 (Colombia)

COMMENTS: Mees (1974) suggested that the species *C. altae* and *C. perugiae* should be grouped together as sub-species within his large genus *Tatia* without indicating the reason for this action. His illustrations of the two species (figs. 14, 15, and 17) clearly show the two characteristics that appear to be diagnostic for the genus.

DISTRIBUTION: Species of this genus are known from tributary streams of the Rio Amazonas and Río Orinoco drainages along the northeastern margin of the Andes.

## GENUS *TATIA* MIRANDA RIBEIRO 1911

*Tatia* Miranda Ribeiro, A. de, 1911, p. 360 (type species *Centromochlus intermedius* Steindachner, 1877, by subsequent designation of Gosline, 1945, p. 10).

DIAGNOSIS: Centromochlids with: sexually dimorphic caudal peduncle and caudal fin; males have highly compressed caudal peduncles which seem never to be less deep than body; upper caudal fin lobe distinctly longer than the lower in males.

TYPE SPECIES: Centromochlus intermedius Steindachner, 1877, by subsequent designation of Gosline, 1945.

INCLUDED SPECIES:

Glanidium aulopygia (Kner)

Centromochlus aulopygius Kner, 1858., p. 432 [reprint p. 62], pl. 8, fig. 25, (type locality Brazil: Rio Guaporé).

Tatia intermedia (Steindachner)

Centromochlus intermedius Steindachner, 1877, p. 664, footnote 1, [offprint p. 106] (type locality Brazil: Pará, Marabitanos).

Tatia dunni (Fowler)

Centromochlus dunni Fowler, 1945, p. 111, figs. 11-13, (type locality Colombia: Río Caqueta drainage at Morelia).

Tatia galaxias Mees

Tatia galaxias Mees, 1974, p. 86, figs. 13, 23, (type locality Venezuela: Caño Quiribana, of Río Orinoco).

Tatia sp. (Venezuela)

COMMENTS: Tatia is hypothesized to be the sister group of Genus B, (below) based on the shared presence, in adult males, of an antrorse spinule on the anterior margin of each of the distal segments of the last unbranched anal-fin ray (UR1) and an anteriorly directed, blunt, retrorse projection on the anterior-branch segments of the first branched anal-fin ray (fig. 29B, BR1a).

The limits of the genus have varied greatly. Gosline (1945) restricted *Tatia* to the two species for which it was originally proposed. Britski (1972) argued that the characters separating *Tatia* and *Glanidium* graded inperceptibly together, and this prompted him to synonymize the two. Mees (1974), on the other hand, thought of *Tatia* as distinct and greatly added to the membership of the genus by the addition of new species and the removal of several species from *Centromochlus*.

DISTRIBUTION: Widespread through the Amazon and Orinoco drainages and into the Guianas.

## GENUS B

DIAGNOSIS: Centromochlids with 1) anal-fin margin of adult males acutely pointed, and 2) UR1 and BR1 rays longest and subsequent branched rays rudimentary.

INCLUDED SPECIES:

*Centromochlus creutzbergi* Boeseman, 1953, p. 7, fig. 1c, (type locality Suriname: Djaikreek).

*Tatia brunnea* Mees, 1974, p. 84, figs 10d, 21, (type locality Suriname: Compagnie Kreek).

*Glanidium neivei* Ihering, 1930, p. 99, pl. 13, fig. 1, (type locality Brazil: Est. de São Paulo, Rio Piraciacaba, Piraciaba).

*Tatia* sp. (Venezuela)

COMMENTS: These species were placed by Mees (1974) in his genus <u>Tatia</u>. While Genus b is considered to be the sister group of <u>Tatia</u>, it is put in a separate genus in recognition of the two distinct lineages. Anal fins of adult males of species in this group are proportionally smaller than in other centromochlid genera.

DISTRIBUTION: This genus appears to be limited to drainages north and south of the Rio Amazonas.

## GENUS <u>GLANIDIUM</u> LÜTKEN 1874

<u>Glanidium</u> Lütken, 1874, p. 31 [offprint p. 3] (type species <u>Glanidium albescens</u> Lütken, 1874, by monotypy).

<u>Gephyromochlus</u> Hoedeman, 1961, p. 135 (type species <u>Centromochlus (Gephyromochlus) leopardus</u> Hoedeman, 1961, by monotypy)

DIAGNOSIS: Centromochlids with: anal-fin unbranched rays and first branched ray (BR 1) enlarged and elongated but otherwise unmodified; remaining anal-fin rays distinctly shorter, fin margin lobed; Sphenotic and pterotic excavated laterally, resulting in strongly concave lateral margin of neurocranium (fig. 16).

TYPE SPECIES: <u>Glanidium albescens</u> Lütken 1874, by monotypy

INCLUDED SPECIES:

<u>Glanidium albescens</u> Lütken

<u>Glanidium</u> <u>albescens</u> Lütken, 1874, p. 31, (type locality Brazil: Minas Geraës, Rio del Velhas cum affluentibus).

Glanidium melanopterum Miranda Ribeiro

Glanidium melanopterum Miranda Ribeiro, A. de, 1918, p. 643, (type locality Brazil: Sao Paulo, Piquete).

Glanidium cesarpintoi Ihering

Glanidium cesarpintoi Ihering, 1928, p. 46. (type locality Brazil: Rio Mogi-Guassu).

Glanidium leopardum (Hoedeman)

Centromochlus (Gephyromochlus) leopardus Hoedeman, 1961, p. 135, (type locality French Guiana: Litany R. at Aloiké).

Glanidium catharinensis Miranda Ribeiro

Glanidium catharinensis Miranda Ribeiro, P. de, 1962, p. 3, fig. 2, (type locality Brazil: Estado de Santa Catharina, Rio do Branco do Norte, Municipio de Tubarao).

Glanidium punctatum (Mees)

Tatia punctata Mees, 1974, p. 88, figs. 10c, 24, (type locality Suriname: creek between Kabel and Lombeé).

Glanidium concolor (Mees)

Tatia concolor Mees, 1974, p. 84, figs. 10g, 22, (type locality Suriname: Coppename River, at headwaters).

Glanidium sp. (Paraguay)

COMMENTS: The limits of the genus have varied as authors have shuffled species between the genera Tatia and

Centromochlus. Details of such movements can be found in the accounts of the two genera.

DISTRIBUTION: Widely distributed along river systems of coastal Brazil and the Guianas, but not recorded from the Amazon drainage.

GENUS GELANOGLANIS BÖHLKE 1980

Gelanoglanis Böhlke, 1980, p. 152 (Type species Gelanoglanis stroudi Böhlke, 1980, by original designation).

DIAGNOSIS: Centromochlida with: single pair of mental barbels; premaxillae widely separated, not joined at midline; maxilla elongate, extending into core of maxillary barbel beyond eye; pectoral spine serrated on medial surface only; mesopterygoid reduced to a tiny rounded nodule; vomer absent; infraorbital and nasal ossifications absent; anterior fontinelle absent, frontals broadly joined at midline; quadrate not sutured to either hyomandibula or metapterygoid; mandibular lateral-line canal ossifications separate from dentary; first dorsal-fin pterygiophore absent; transformator process of tripus without reflexed flap; elastic spring apparatus reduced; anal-fin pterygiophores of females crowded together; and anterior serrations of pectoral spine absent.

TYPE SPECIES: Gelanoglanis stroudi Böhlke, 1980, by original designation.

INCLUDED SPECIES:

*Gelanoglanis stroudi* Böhlke

*Gelanoglanis stroudi* Böhlke, 1980, p. 152, fig. 1, (type locality Colombia: Meta, Río Metica).

COMMENTS: *Gelanoglanis* is a highly distinctive centromochlid characterized by its highly compressed head and large mouth. The only currently described species, *G. stroudi*, appears to mature at a small size, as specimens of less than 26 mm SL show sexual dimorphism.

*G. stroudi* is rare in collections. Only part of the type series (including two alizarin-stained specimens) was available to me, and my observations were limited to what could be learned from the already stained specimens and the external morphology of alcoholic specimens.

Nevertheless, *Gelanoglanis* is confidently placed in the Centromochlidae, as it shows all the characteristics defining the family. The anal fin of adult males is rotated so that the rays point posteriorly and the fin is preceded by a flap of skin from which the urogenital tube emerges. Anal-fin rays of males are larger than those of females, but there is no indication of distortion of any segments of the enlarged rays. The metapterygoid is an elongate perichondral ossification with only a little laminar ossification along its posterior margin. The laminar portion is distinctly separate from the hyomandibula.

The relationships of *Gelanoglanis* within the

Centromochlidae, however, are problematical. In the absence of any modifications of the segments of the anal fin-rays in adult males, it may be argued that Gelanoglanis is the sistergroup of all other centromochlids. The crowded anal-fin pterygiophores of females, however, resembles that of Centromochlus.

DISTRIBUTION: The only published account is the description of the species from the Río Meta system of Colombia. Additional specimens in the possession of Jonathan Baskin and Don Stewart are evidently from different localities.

FAMILY AUCHENIPTERIDAE BLEEKER 1862 (1858)

cohors Euanemini Bleeker 1858, p.49
phalanx Trachelyopterini Bleeker 1858, p. 49
stirps Pseudauchenipterini Bleeker 1862a, p. 6
phalanx Astrophysi [sic] Bleeker 1862a, p. 7
phalanx Ageneoisi Bleeker 1862a, p.14
stirps Auchenipterini Bleeker 1862a, p. 14
family Trachycorystidae Miranda Ribeiro, A., 1911, p. 352

DIAGNOSIS: Doradoid catfishes with genital tube of adult males located at distal tip of anterior margin of anal fin, and females with enlarged urogenital opening at the base of anal fin; anterior anal-fin rays elongated and thickened in adult males, appearing to function as an intromittant organ [Ihering (1937) called is a pseudopenis] dorsal-fin spine of adult males larger than that of females and possessing proportionally larger serrae; pelvic fin usually with 6 or more branched rays; lower gill arch skeleton with accessory basibranchial cartilage between third and fourth element; lateral line with a series of columns of free neuromasts dorsal to lateral-line canal; and, lateral-line canal branched on caudal-fin base.

TYPE GENUS: Auchenipterus Valenciennes 1840

INCLUDED TAXA: subfamilies Trachycorystinae and Auchenipterinae, and genera Pseudotatia, Tocantinsia, and Asterophysus.

COMMENTS: Except for Entomacorus, species in this family exhibit a modification of the male genital pore that is unique among catfishes. The distally located male pore, along with the thickened anterior anal-fin rays, appear to be used as an intromittant organ for depositing sperm into the genital tract of the female. Ihering (1937) first suggested that some auchenipterids practiced internal fertilization and he provided evidence that females of at least one species had the capability of storing sperm for several months. More recently, Burgess (1982) illustrated the copulation sequence of another species, Trachelyopterus insignis (Steindachner), and the copulation of an unnamed species of Ageneiosus has been illustrated by Köpke (1986). Currently unpublished observations on the copulation of the same species of Ageneiosus made by Ginny Eckstein (pers. comm.) indicate that the copulatory sequence may take several minutes, but that it does not involve the immediate deposition of eggs. Inasmuch as no other information on the breeding behavior of these fishes is available, the universality of internal fertilization in this family must remain to some extent speculative.

Accessory lateral-line neuromast rows are found in a number of species but seem to be absent in several taxa, most notably in all members of the Auchenipterus and Ageneiosus groups. This curious character distribution is interpreted as a secondary loss in these groups.

The Auchenipteridae, as delimited here, differs from previous usage by the inclusion of those species traditionally placed in the family Ageneiosidae and in excluding the Centromochlidae, as defined above. Ageneiosus and its sister-genus Tetranematichthys are considered highly derived forms of one lineage within the Auchenipteridae. To continue to accord that group family status, under the constraint of dealing only with monophyletic taxa, would necessitate the creation of several additional small families.

Eigenmann and Eigenmann (1890) adopted Bleeker's (1862a) Auchenipterini as a subfamily of the Doradidae, instead of the older Euanemini (Bleeker 1858). Since Euanemus was synonymized into Auchenipterus by Eigenmann and Eigenmann (1890), the name Euanemini has never been used. According to article 40b of the Code of Zoological Nomenclature, (ICZN, 1985) continuous use of a junior family-level synonym adopted prior to 1961, is sufficient to justify the continued use of the younger name. The younger name then takes the date of the senior synonym for purposes of priority, which, in this case, requires the name Auchenipterinae to compete only with Trachelyopterini (Bleeker 1858). Eigenmann and Eigenmann (1890) placed Trachelyopterus and Auchenipterus into their Auchenipterinae, thereby acting as first revisor and establishing Auchenipteridae as the appropriate name for this taxon.

GENUS PSEUDOTATIA MEES 1974

Pseudotatia Mees, 1974, p.105 (type species Pseudotatia parva Mees, 1974, by original designation).

DIAGNOSIS: An auchenipterid, but without diagnostic characters of either subfamily. Recognized only by the presence of primitive characters for the family, including 6 branched pelvic-fin rays; 8 branched rays in lower lobe of forked caudal fin; infraorbital bones without dermal granulations; epioccipital with short, posteriorly directed process and, therefore, without osseous connection between the epioccipital and parapophyses of fifth and six centra; parasphenoid without expanded basioccipital process; and pterosphenoid present as an independent ossification.

TYPE SPECIES: *Pseudotatia parva* Mees, 1974, by original designation

INCLUDED SPECIES:

*Pseudotatia parva* Mees

*Pseudotatia parva* Mees, 1974, p. 105, fig. 29, (type locality Brazil: Joazeiro, Rio São Francisco).

COMMENTS: The genus *Pseudotatia* was created by Mees (1974) for a species he considered to be close to *Tatia*, but with enough differences to make inclusion in that genus untenable. There are clear indications in the description, however, that *Pseudotatia parva* does not belong near *Tatia* but, instead, near members of the Auchenipteridae.

The genus is represented by the type species, *P. parva*, which, in turn, is known only from the type series. Among the specimens of the type series is a 45-mm Sl male, in which the urogenital tube extends nearly the entire length of the anterior margin of the anal fin. This specimen shows no other indications of sexual dimorphism, however, and this precludes further resolution of the affinities of the species.

DISTRIBUTION: Known only from the type locality on the Rio Sao Francisco, Brazil.

## GENUS *ASTEROPHYSUS* KNER 1858

*Asterophysus* Kner, 1858, p. 402, (Type species *Asterophysus batrachus* Kner 1858, by monotypy).

Astrophysus Bleeker 1858, p. 356 (Unwarranted replacement name for Asterophysus Kner, 1858, therefore having the same type species: Asterophysus batrachus).

DIAGNOSIS: An auchenipterid with the hyomandibula oriented nearly vertically, resulting in an elongated maxilla, dentary, third pharyngobranchial, and pharyngobranchial tooth-plate ossifications; posteriormost infraorbital ossification absent; neurocranium with accessory dermal ossification at junction of sphenotic, pterotic, and supraoccipital.

TYPE SPECIES: Asterophysus batrachus Kner 1858, by monotypy

INCLUDED SPECIES:

Asterophysus batrachus Kner

Asterophysus batrachus Kner, 1858, p. 403 [offprint p. 33], pl. 5, fig. 13, (type locality Brazil: Marabitanos).

COMMENTS: The cavernous mouth and unusual body form of this distinctive auchenipterid has been used to set the genus apart from all other species. Bleeker (1862a) first emphasized its distinctiveness by placing it in a separate phalanx, the Astrophysi [sic]. Britski's branching diagram of the doradoids placed Asterophysus as the sister group of all auchenipterids and centromochlids except his Ageneiosidae. Although I disagree with Britski's placement of Ageneiosus and its relatives, as well as that of the centromochlids, my disposition of Asterophysus is not substantially different from his. Neither Britski nor

I found any derived characters that *Asterophysus* shares with any part of the Auchenipteridae. In both of our studies, however, only small individuals of *Asterophysus* have been examined. It is possible that adult morphology will prove useful in determining the relationships of this taxon.

DISTRIBUTION: Known only from the Rio Negro system of Brazil and Venezuela and, more recently, the Rio Orinoco drainage.

## GENUS *TOCANTINSIA* MEES 1974

*Tocantinsia* Mees 1974, p. 108, (type species *Tocantinsia depressa*, Mees, 1974, by original designation)

DIAGNOSIS: An auchenipterid with retrorse serrations on both lateral and medial surface of pectoral spine.

TYPE SPECIES: *Tocantinsia depressa*, Mees, 1974, by original designation.

INCLUDED SPECIES:

*Tocantinsia piresi* (Miranda Ribeiro)

*Glanidium piresi* Miranda Ribeiro, A. de, 1920, p. 14, pl. 15-17, (type locality Brazil: Rio S. Manoel).

*Tocantinsia depressa* Mees, 1974, p. 108, fig. 30, (type locality Brazil: Goias, Rio Tocantins near Piexa).

COMMENTS: Synonymy of *T. depressa* with *T. piresi* follows Mees (1984). Inasmuch as the paratypes *Tocantinsia depressa* that I have examined are most probably not members of the Centromochlidae, Glanidium piresi must be removed from that family.

Placement of Tocantinsia into the Auchenipteridae is somewhat problematical, however, because only a superficial examination of the apparently juvenile paratypes could be made and no adult specimens were available. T. piresi does not exhibit any of the derived characters of the Doradidae. The juveniles show no sexually dimorphic features of the urogenital region, thus leaving a grooved cheek as the only observable character to place the species within the Auchenipteridae/Centromochlidae. A forked lateral-line canal system on the caudal-fin base is the only character that suggests some affinity with the Auchenipteridae. In the absence of material for a more thorough examination, the genus is placed insertae sedis in that family.

DISTRIBUTION: Known only from the Rio São Manoel and Rio Tocantins in Brazil.

SUBFAMILY TRACHYCORYSTINAE MIRANDA RIBEIRO 1911

family Trachycorystidae Miranda Ribeiro, A. de, 1911, p. 352.

DIAGNOSIS: Auchenipterids with: enlarged serrae on posterior margin of dorsal-fin spine of adult males; denticulations on suprapreopercle, preopercle and last infraorbital; loss of small ossicle between large posterior infraorbital and sphenotic/dermosphenotic;

broad, depressed head with protruding lower jaw; and nine or more pelvic-fin rays.

TYPE GENUS: Trachycorystes Bleeker

INCLUDED GENERA: Liosomadoras, Trachycorystes, and Trachelyopterichthys

COMMENTS: Relationships within the Trachycorystinae are vague. Of the three genera recognized, Trachelyopterichthys, with two species, is diagnosed by its elongate body form. The monotypic Liosomadoras is distinguished by its bold color patterning and strongly denticulate cleithral spine. Nominal species retained in Trachycorystes are undefined by shared derived characters but, rather, are retained in the genus for convenience.

A high number of pelvic-fin rays is not unique to this subfamily but is considered a derived character in this group because of the corroboration of other characters of the subfamily.

A. Miranda Ribeiro's (1911) creation and definition of the family Trachycorystidae has little in common with its present delimitation. He proposed that the family include all the auchenipterids and centromochlids except for the Auchenipterus group and the Ageneiosus group, each of which were assigned family rank. Miranda Ribeiro's name was adopted by Ihering (1937) for species having "oviducal" or internal fertilization. As described above, this character is more general than originally thought and is considered now to be defining for the entire family Auchenipteridae.

P. Miranda Ribeiro (1968b) further restricted usage of the name to a group of three genera, Trachycorystes, Tetranematichthys, and Auchenipterichthys, which here are considered to be related only at the familial level.

## GENUS TRACHYCORYSTES BLEEKER 1858

Trachycorystes Bleeker, 1858, p. 208 (type species Auchenipterus trachycorystes Valenciennes, 1840, by absolute tautonomy).

DIAGNOSIS: Trachycorystins not belonging to either Liosomadoras or Trachelyopterichthys.

TYPE SPECIES: Auchenipterus trachycorystes Valenciennes, 1840, by absolute tautonomy, of Bleeker, 1858.

INCLUDED NOMINAL SPECIES:

Trachycorystes trachycorystes (Valenciennes)

Auchenipterus trachycorystes Valenciennes, in Cuvier and Valenciennes, 1840, p. 214, pl. 437 (type locality putatively Brazil).

Trachycorystes typus Bleeker, 1862a. p. 6, (an unjustified replacement name for Auchenipterus trachycorystes Valenciennes, thus taking the same type and type locality as that name).

Trachycorystes obscurus (Günther)

Auchenipterus obscurus Günther 1864, p. 195, (type locality British Guiana: Essequibo River).

*Trachycorystes cratensis* Miranda Ribeiro, 1937

*Trachycorystes cratensis* Miranda Ribeiro, A. de, 1937, p.55, (type locality Brazil: Ceará, Rio Granjeiro).

*Trachycorystes* sp. 1

*Trachycorystes trachycorystes*: Mees, 1974 (Brazil)

COMMENTS: The genus *Trachycorystes*, as here defined, differs from the broad usage of most earlier authors. Mees (1974) restricted the genus to one species, *T. trachycorystes*, and removed all other species to *Parauchenipterus*, which I include in the genus *Trachelyopterus*. Virtually all accounts of *Trachycorystes* refer to some species or another of *Trachelyopterus*, and this has resulted in a certain amount of nomenclatural confusion, especially with the introduction of the family name Trachycorystidae (A. Miranda Ribeiro, 1911). Specimens of *Trachycorystes* are rare in collections and few are available for study. Thus, the species names listed here may represent a single species, as thought by Mees (1974), although *T.* sp. 1 appears to differ substantially from the types of *T. obscurus* and *T. trachycorystes*.

DISTRIBUTION: Known from the Lower Rio Amazonas, the Rio Orinoco, and coastal drainages of the Guianas and Brazil.

## GENUS *LIOSOMADORAS* FOWLER 1940

*Liosomadoras* Fowler, 1940, p. 226, (type species *Liosomadoras morrowi* Fowler, 1940, by original designation).

DIAGNOSIS: Trachycorystines with: strongly denticulate cleithral spine and bold color pattern on the body, reminiscent of the pattern of a jaguar.

TYPE SPECIES: *Liosomadoras morrowi* Fowler, 1940 [=*Arius oncinus* Schomburgk], by original designation

INCLUDED SPECIES:

*Liosomadoras oncinus* (Schomburgk)

*Arius oncina* Schomburgk, 1841, p. 173, (type locality Rio Padauiri).

*Arius oncinus* Schomburgk, 1841, pl. 4, (type locality Rio Padauiri).

*Liosomadoras morrowi* Fowler, 1940.p. 226, (type locality Peru: Río Ucayali basin, at Contamana)

COMMENTS: The placement of the genus *Liosomadoras* has been one of the more controversial aspects of doradid relationships in recent years. On the basis of spinulations on the cleithral spine, Fowler (1940) described his *L. morrowi* as a doradid, although it lacked lateral scutes. Gosline (1942) considered *Liosomadoras* as an example of a gradation between the doradids and auchenipterids, and he concluded that these two groups should not be retained as separate entities. Britski (1972) assigned Schomburgk's *oncinus* to the genus

Glanidium, although he was unable to examine any specimens.

The continued use of the generic name Liosomadoras for this species is a reflection of the poor resolution of relationships within the subfamily Trachycorystinae. The distinctive Trachelyopterichthys forms a monophyletic group within the subfamily, but available evidence requires that the two other genera be placed in a polychotomy with it.

Specimens of Liosomadoras had been quite rare until recently, and this made the assignment of the species difficult. Mees's (1978) search for specimens of Schomburgk's Arius oncina yielded only five museum specimens. Recent importation of the species in the aquarium fish trade has changed this situation and made the species readily available for study.

DISTRIBUTION: Scattered through the Rio Amazonas drainage of Brazil and Peru. Aquarium specimens are said to come from the region around Manaus.

## GENUS TRACHELYOPTERICHTHYS BLEEKER 1862

Trachelyopterichthys Bleeker, 1862b, p. 402 (type species Trachelyopterus taeniatus Kner, 1858, by original designation).

DIAGNOSIS: Trachycorsytins with elongated, compressed bodies and anal fin with more than 50 rays.

TYPE SPECIES: Trachelyopterus taeniatus Kner, 1858, by original designation.

INCLUDED SPECIES:

Trachelyopterichthys taeniatus (Kner)

Trachelyopterus taeniatus Kner, 1858, p. 434 [reprint p. 64], pl 8, fig 26, (type locality Brazil: Rio Guaporé).

Trachelyopterichthys anduzei Ferraris and Fernandez

Trachelyopterichthys anduzei Ferraris and Fernandez, 1987, p. 257, (type locality: Venezuela, Río Orinoco).

COMMENTS: Trachelyopterichthys differs from other members of the Trachycorystinae and basal auchenipterids in body form. The post-anal region is greatly elongated with a concommitant increase in anal-fin rays. The entire posterior portion of the fish is compressed and the fish swims with an anguilliform motion atypical for doradoids. Elongation of the body also appears to be derived in the Auchenipterus group, although not to the extent exhibited by Trachelyopterichthys. The hypothesis of relationships of auchenipterids presented here, however, suggests that the elongation is independent in these two lineages.

The two species included in this genus differ in degree of development of the dorsal-fin rays and associated spine. T. taeniatus has a diminutive fin, which has been suggested, along with the absence of an adipose dorsal fin, to be derived characters shared with Epapterus. Available evidence, however, suggests that the absence of an adipose dorsal fin is characteristic of only one clade within Epapterus, and that the reduction of the dorsal fin

is limited to one species within _Trachelyopterichthys_.
DISTRIBUTION: The genus is known from the Rio Amazonas basin and the Río Orinoco.

## SUBFAMILY AUCHENIPTERINAE BLEEKER 1862 (1858)

cohors Euanemini Bleeker 1858, p.49
phalanx Trachelyopterini Bleeker 1858, p. 49.
stirps Auchenipterini Bleeker 1862a, p. 14
stirps Pseudauchenipterini Bleeker 1862a, p. 6
phalanx Astrophysi [sic] Bleeker 1862a, p. 7
phalanx Ageneoisi Bleeker 1862a, p.14

DIAGNOSIS: Auchenipterids with elongate anal fin, and long, posteriorly projecting epioccipital process.
INCLUDED TAXA: The tribe Auchenipterini and the unassigned genera _Pseudauchenipterus_ and _Auchenipterichthys_.
COMMENTS: The Auchenipterinae, as defined here, has not been recognized previously.

## GENUS _AUCHENIPTERICHTHYS_ BLEEKER 1862

_Auchenipterichthys_ Bleeker, 1862a, p. 7 (type species _Auchenipterus thoracatus_ Kner, 1858, by original designation).

DIAGNOSIS: Auchenipterins with: elongate unbranched epioccipital spine; elongated anal-fin base, obliquely oriented caudal fin; and 8 to 10 branched pelvic-fin rays; but lacking bifurcated epioccipital spine and other derived characters of the Auchenipterini.

TYPE SPECIES: Auchenipterus thoracatus Kner, 1858, by original designation

INCLUDED SPECIES:

Auchenipterichthys thoracatus (Kner)

Auchenipterus thoracatus Kner, 1858, p. 425, pl. 7, figs., 22, 22a, 22b, (type locality Brazil: Rio Guaporé).

Auchenipterichthys longimanus (Günther)

Auchenipterus longimanus Günther, 1864, p. 195, (type locality: Brazil: Pará, Rio Capim).

Auchenipterichthys coracoideus (Eigenmann and Allen)

Trachycorystes coracoideus Eigenmann and Allen, 1942, p. 120, (type locality: Peru: Iquitos).

Auchenipterichthys sp. (Peru)

COMMENTS: The genus is poorly defined by osteological characters but appears to be natural. All species possess a laterally placed, large eye and a caudal fin that is either obliquely truncate or only slightly emarginate. One male specimen from AMNH 12700 has an exceptionally long dorsal fin-spine with a single row of serrae along its posterior margin. The spine is very similar in appearance to the dimorphic male spines in Trachelyopterichthys and Liosomadoras of the Trachycorystinae. The specimens shows no other evidence of secondary sexual dimorphism, and other specimens examined show no dimorphism other than urogenital modifications. Thus, the significance of the resemblance between *Auchenipterichthys* and the Trachycorystinae is unknown.

DISTRIBUTION: Widely distributed along the Rio Amazonas and Rio Orinoco drainages.

GENUS *PSEUDAUCHENIPTERUS* BLEEKER 1862

*Pseudauchenipterus* Bleeker, P., 1862a, p. 6, (type species *Silurus nodosus* Bloch, 1794, by original designation).

DIAGNOSIS: Auchenipterins with seven branched pelvic-fin rays, and pectoral-fin spines with serrations on posterior surface only.

TYPE SPECIES: *Silurus nodosus* Bloch, 1794, p. 35, pl. 368, fig 1, by original designation.

INCLUDED NOMINAL SPECIES:

*Pseudauchenipterus nodosus* (Bloch)

*Silurus nodosus* Bloch, 1794, p. 35, pl. 368, fig. 1, (type locality "Tranquebar").

*Pseudauchenipterus furcatus* (Valenciennes)

*Auchenipterus furcatus* Valenciennes, in Cuvier and Valenciennes, 1840, p. 211, (type locality: French Guiana and Suriname)

*Pseudauchenipterus jequitinhonhae* (Steindachner)

*Auchenipterus* (*Pseudauchenipterus*) *jequitinhonhae* Steindachner, 1877, p. 647 [offprint p. 89], pl 6, fig, 1, 1a, (type locality: Brazil, Rio Jequintinhonhae).

Pseudauchenipterus affinis (Steindachner)

Auchenipterus (Pseudauchenipterus) affinis Steindachner, 1877, p. 651, [offprint p. 93] (type locality Brazil: São Matheos).

Pseudauchenipterus flavescens (Eigenmann and Eigenmann)

Felichthys flavescens Eigenmann and Eigenmann, 1888, p. 152, (type locality Brazil: Rio São Francisco).

Pseudauchenipterus guppyi (Regan)

Auchenipterus guppyi Regan, 1906, p. 387, pl. 23 (incorrectly labelled and cited in text), (type locality Trinidad).

Pseudauchenipterus nigrolineatus Fowler

Pseudauchenipterus nigrolineatus Fowler, 1911, p.434 (type locality Venezuela: Pedernales).

Pseudauchenipterus aguilerae (Fernández-Yépez)

Silvaichthys aguilerae Fernández-Yépez, 1973, 5 unnumbered pages. (type locality Venezuela: Gulf of Paria).

COMMENTS: The genus Pseudauchenipterus has been widely recognized, although Mees (1974) questioned whether the species found in southeastern Brazil should be considered congeneric with those north of the Amazon. There is little morphological evidence to support the monophyly of the genus. All species are without serrations along the anterior margin of the pectoral-fin spines. No specimens of the southeastern Brazilian species were available for osteological examination in order to determine whether the branched epioccipital spine exists there.

DISTRIBUTION: Coastal rivers and associated estuaries from east of the Maracaibo basin of Venezuela to the Rio Doce of southeastern Brazil. *Pseudauchenipterus* is the only group of doradoids found in estuarine waters. Taylor (1977) reports *P. nodosus* to be common in brackish river mouths. Records of the genus from the Peruvian Amazon appear to be based solely on Fowler's (1940, p. 232) account of a specimen from Contamana, ANSP 103414, which is an *Auchenipterichthys* and not a *Pseudauchenipterus*.

## TRIBE AUCHENIPTERINI 1862 (1858)

cohors Euanemini Bleeker 1858, p.49

phalanx Ageneoisi Bleeker 1862a, p.14

stirps Auchenipterini Bleeker 1862a, p. 14

DIAGNOSIS: Auchenipterines with medial fork of branched epioccipital spine either sutured or ligamentously bound to transversly oriented parapophyses of fifth and sixth vertebrae.

INCLUDED TAXA: The genera *Trachelyichthys*, *Trachelyopterus*, *Auchenipterus*, *Epapterus*, *Tetranematichthys*, and *Ageneiosus*.

COMMENTS: A restricted clade of the Auchenipterini, consisting of all genera listed above except *Trachelyichthys*, is defined by the following characters: enlarged basioccipital process of parasphenoid that forms both optic foramen and anterior and ventral walls of

Trigeminofascialis complex fissure; anteriorly expanded palatine, becoming robust and contorted in adult males; progressive distal ossification, in adult males, of elastin core of maxillary barbel and formation of papillose dorsal surface on fully ossified barbel; elongation and sinusoidal deformation of second dorsal fin spine, with development of basal and distal clusters of serrae anteriorly, in adult males; dorsal-fin spine of dimorphic males capable of being hypererected and directed anterodorsally.

GENUS *TRACHELYICHTHYS* MEES 1974

*Trachelyichthys* Mees, 1974, p. 111, (type species *Trachelyichthys decaradiatus* Mees, 1974, by original designation).

DIAGNOSIS: Auchenipterini with large, laterally placed eyes that exceed snout length in diameter; and no adipose dorsal fin.

TYPE SPECIES: *Trachelyichthys decaradiatus* Mees, by original designation.

INCLUDED SPECIES:

*Trachelyichthys decaradiatus* Mees

*Trachelyichthys decaradiatus* Mees, 1974, p. 112, (type locality British Guiana: Rupununi, Karanambo area).

*Trachelyichthys exilis* Greenfield and Glodek

*Trachelyichthys exilis* Greenfield, and Glodek, 1977, p.49, figs. 2, 5, (type locality Peru: Río Mamon).

*Trachelyichthys* sp. 1. (Venezuela: Río Orinoco).

COMMENTS: This little known genus was first noted by Britski (1972) under the manuscript name "Pseudotrachlyopterus" for a single species "P. hossnei." Britski placed this fish into his Centromochlinae, based on the relatively short sphenotic which does not preclude the frontal from the orbital margin. *Trachelyichthys* possesses, however, characters that are restricted to the Auchenipteridae and the Auchenipterini, and it is, therefore, now placed within that tribe here.

DISTRIBUTION: The described species are from the Guianas and Peruvian Amazon. Britski (1972) reported specimens of one species from a large stretch of the Rio Amazonas; and an apparently undescribed species has been collected recently from the Río Orinoco.

## GENUS *TRACHELYOPTERUS* VALENCIENNES 1840

*Trachelyopterus* Valenciennes, in Cuvier and Valenciennes, 1840, p. 220 (type species *Trachelyopterus coriaceus* Valenciennes, 1840, by monotypy).

*Parauchenipterus* Bleeker 1862a, p.7 (type species *Silurus galeatus* Bloch [= *Silurus galeatus* Linnaeus, 1758], by original designation).

DIAGNOSIS: Auchenipterines with pterosphenoid fused with frontal; parapophysis of fifth vertebral centrum reduced or absent; and ligmentous connection between epioccipital and expanded parapophyses of fifth and sixth centra.

TYPE SPECIES: Trachelyopterus coriaceus Valenciennes, by monotypy

INCLUDED NOMINAL SPECIES:

Group 1

Trachelyopterus amblops (Meek and Hildebrand)

Trachycorystes amblops Meek and Hildebrand, 1913, p.77, (type locality: Panama: Río Tuyra, Marrigante).

Trachelyopterus fisheri (Eigenmann)

Trachycorystes fisheri Eigenmann, 1916, p. 82, (type locality Colombia: Río Sucio)

Trachelyopterus insignis (Steindachner)

Auchenipterus insignis Steindachner 1878. p. 89, (type locality Colombia: Río Magdalena).

Trachelyopterus magdalenae (Steindachner)

Auchenipterus Magdalenae Steindachner 1878, p. 89, (type locality Colombia : Río Magdalena).

Trachelyopterus peloichthys (Schultz)

Trachycorystes insignis peloichthys Schultz, 1944, p. 236, pl. 4A, (type locality Venezuela: Lake Maracaibo drainage, Río Agua Caliente).

Trachelyopterus teaguei (Devincenzi)

Trachycorystes teaguei Devincenzi, in Devincenzi, and Teague 1942, p. 37, pl. 5, fig. 1,2. (type locality Uruguay: Río Queguay).

Trachelyopterus badeli (Dahl)

Trachycorystes insignis badeli Dahl, 1955, p. 13, (type locality Colombia: Río Sinu).

Group 2

Trachelyopterus coriaceus Valenciennes

Trachelyopterus coriaceus Valenciennes, in Cuvier and Valenciennes, 1840, p. 221, pl. 438, (type locality French Guiana: Cayenne).

Trachelyopterus maculosus Eigenmann and Eigenmann

Trachelyopterus coriaceus maculosus Eigenmann and Eigenmann, 1888, p. 157, (type locality Brazil: Porto do Moz) [a junior subjective synonym of T. coriaceus Valenciennes].

Group 3

Trachelyopterus galeatus (Linnaeus)

Silurus galeatus Linneaus 1766, p. 503, (type locality "in America australi").

Trachelyopterus immaculatus (Valenciennes)

Auchenipterus immaculatus Valenciennes, in Cuvier and Valenciennes, 1840, p. 218, (type locality: French Guiana: Cayenne).

*Trachelyopterus maculosus* (Valenciennes)

*Auchenipterus maculosus* Valenciennes, in Cuvier and Valenciennes, 1840, p. 216, (type locality French Guiana: Cayenne).

*Trachelyopterus punctatus* (Valenciennes)

*Auchenipterus punctatus* Valenciennes, in Cuvier and Valenciennes, 1840, p. 219, (type locality probably Brazil).

*Trachelyopterus ceratophysus* (Kner)

*Auchenipterus ceratophysus* Kner 1858, p. 427, pl. 7, fig. 23. (type locality Brazil: Rio Negro, Rio Branco, and Rio Guaporé).

*Trachelyopterus robustus* (Günther)

*Auchenipterus robustus* Günther, 1864, p. 197, (type locality British Guiana: Demarara).

*Trachelyopterus lacustris* (Lütken)

*Auchenipterus lacustris* Lütken, 1873, p. 20, [offprint p. 3], (type locality Brazil: Minas Gerais, Rio das Velhas, and Lagoa Santa).

*Trachelyopterus glaber* (Steindachner)

*Auchenipterus glaber* Steindachner, 1877, p. 655, [offprint p. 97] footnote 1, (type locality British Guiana: Demarara).

Trachelyopterus striatulus (Steindachner)

Auchenipterus (Pseudauchenipterus) striatulus Steindachner, 1877, p. 656, pl. 5, [offprint p. 98] (type locality Brazil: Rio Doce and Campos, on the Rio Paraiba).

Trachelyopterus brevibarbis (Cope)

Auchenipterus brevibarbis Cope, 1878, p. 676, (type locality Peru: Río Amazon probably near Pebas).

Trachelyopterus isacanthus (Cope)

Auchenipterus isacanthus Cope, 1878, p. 677, (type locality Peru: "Amazon" (probably Rio Maranon).

Trachelyopterus analis (Eigenmann and Eigenmann)

Trachycorystes analis Eigenmann and Eigenmann, 1888, p. 156, (type locality Brazil: Arary).

Trachelyopterus porosus (Eigenmann and Eigenmann)

Trachycorystes porosus Eigenmann, and Eigenmann, 1888, p. 154, (type locality Brazil).

Trachelyopterus albicrux (Berg)

Trachycorystes albicrux Berg, 1901, p. 130, (type locality: Río de la Plata, near the mouth of Río Santiago).

Trachelyopterus paseae (Regan)

Auchenipterus paseae Regan, 1906, p. 387, pl. 24 (figure incorrectly labeled and cited in text), (type locality Trinidad).

*Trachelyopterus leopardinus* (Borodin)

*Trachycorystes leopardinus* Borodin, 1927, p. 3, fig. 2, (type locality Brazil: Rio São Francisco, Minas Gerais).

*Trachelyopterus jokeannae* (Hoedeman)

*Trachycorystes jokeannae* Hoedeman, 1961, p. 138, (type locality: French Guiana, Ile de Cayenne, Rorata stream).

COMMENTS: The connections between the medial process of the epioccipital spine and the fifth parapophysis that is characteristic of the Auchenipterini are further modified in this group, with the parapophysis reduced to either an anteriorly directed rudiment or absent altogether. The absence of this parapophysis is not unique among the Doradoidea: both *Megalodoras* and *Orinocodoras* of the Doradidae also share the condition. In *Trachelyopterus*, however, the ossified parapophysis is replaced by a strong ligament that connects to the epioccipital spine either directly or *via* the ligament which runs between the epioccipital and the sixth vertebral parapophysis. That this condition defines a monophyletic group is corroborated by the two additional characters listed above.

*Trachelyopterus* can be divided into three groups of species. Group 1 contains all species which are members of *Trachelyopterus* but lack any derived characters that would unite them with other species in the genus. Thus, group 1 does not form a natural group within the genus. Group 2 consists of _T. coriaceus_ and its junior subjective synonym _T. maculatus_ and is defined by the absence of an adipose dorsal fin and the absence of anterior pectoral-fin spine serrations. Group 3 comprises all the remaining species and is defined by the presence of more than 8 branched fin-rays associated with the fused lower hypural element of the ural complex and the absence of an ossified parapophysis of the fifth centrum. Groups 2 and 3 are thought to be sister groups through their reduction or absence of secondary sexual dimorphism and the absence of ossified barbels in adult males.

Most members of this genus had been placed in the genus _Trachycorystes_ until Mees (1974) correctly pointed out that _T. trachycorystes_ and its relatives belonged to a different lineage from most of the included species, and that an available generic name for the remaining species was _Parauchenipterus_. _Trachelyopterus_ was retained as a distinct genus and separated from _Parauchenipterus_ on the basis of its absence of an adipose dorsal fin.

The retention of _Parauchenipterus_ would require the continued use of _Trachelyopterus_ as a monotypic genus for _T. coriaceus_, and the creation of additional generic names for the species making up group 1. While _T. coriaceus_ is distinctive in not having an adipose dorsal fin and in possessing a pectoral-fin spine devoid of serrations anteriorly, its evident relationship to the species that Mees placed into _Parauchenipterus_ cannot be ignored.

Although a detailed study of the relationships among the species of Trachelyopterus are beyond the scope of this study, T. coriaceus is evidently more closely related to some species of Mees's Parauchenipterus than species of group 3 are to species of group 1 (fig. 44). Thus, any group that contains all species of Parauchenipterus must include T. coriaceus.

Although a large number of specimens of Trachelyopterus are available, representatives of many of the nominal species were not examined. Inclusion of these species within the genus or within one of the three species groups of the genus is based on literature accounts of the species and, to some degree, on Mees's (1974) synonymy of Parauchenipterus galeatus. Although I believe that several forms Mees considers as variants of P. galeatus are, in reality, good species, his synonymy of these species supports my characterization ofthem as members of the species-group 3.

The type specimen of Trachelyopterus coriaceus maculosus was distinguished from T. coriaceus by spots along the body (Eigenmann and Eigenmann 1888). However, all of the specimens of T. coriaceus that were available to the Eigenmanns are in an advanced state of deterioration and show no evidence of any pigmentation. The same is true for the holotype of T. coriaceus. Fresh specimens of Trachelyopterus all show reticulating patterns of dark brown on a lighter brown background, which could be interpreted as spots if the specimens were partially faded. In all other respects, the holotype of T. coriaceus maculosus is identical with T. coriaceus and it is, therefore, considered to be a member of that species.

DISTRIBUTION: Trachelyopterus has the broadest geographic distribution of any genus in the family, rivaled only by Ageneiosus. Species occur from Panama to the La Plata system, including both the major river drainages and the Atlantic coastal drainages from the Guianas to southeast Brazil. Within the genus, groups 2 and 3 are widely distributed in the Guianas, the Rio Amazonas and the La Plata system, but they are absent west of the Andes. The basal species of group 1, have a more limited and unusual distribution. A different species has been described from each of the TransAndean Carribean drainages from Lake Maracaibo westward to the Río Sinu of Colombia and north to southern Panama. In addition, a single species that appears to belong to this group, T. teaguei, is found in the the Río Uruguay system.

## AGENEIOSUS GROUP

DIAGNOSIS: Auchenipterini with the following characters: eyes ventrolaterally positioned; quadrate with broadly expanded lamina which separates the hyomandibula from metapterygoid; vomer with reduced anterior process; second dorsal-fin pterygiophore sutured along its entire anterior margin to supraoccipital; parapophyses of fifth and sixth centra broadly expanded, fifth sutured to expanded medial fork of epioccipital spine anteriorly and to sixth posteriorly; urohyal with dorsally directed process situated between the hypohyals; expanded distal tip of third pectoral-fin radial supports an unusually large number of rays; nasal with anteriorly directed, elongated lateral branch forming a 'y'; hypobranchials 1 and 2 arched, concave anteriorly, with medial tips far anterior to anterolateral margin; epibranchial 1 expanded dorsomedially and overlapping epibranchial 2; anterior ceratohyal sutured to ventral hypohyal along ventromedial surface; autopalatine with articular facet at oblique angle to long axis; and infraorbital bone anteroventral to the eye funnel-shaped.

In addition to the derived characters listed above, the Ageneiosus group may be recognized by having a relatively primitive neurocranium with its sphenotics small and not expanded along the lateral margin of the frontal.

TYPE GENUS: Ageneiosus LaCépède 1803

INCLUDED GENERA: Ageneiosus LaCépède and Tetranematichthys Bleeker.

## GENUS TETRANEMATICHTHYS BLEEKER 1858

Tetranematichthys Bleeker, 1858, p. 357 (type species Ageneiosus quadrifilis Kner, 1858, by monotypy).

DIAGNOSIS: Genus of the Ageneiosus group with: single pair of mental barbels and obliquely truncate caudal fin.

*Tetranematichthys* adult males retain an elongated ossified, toothless, barbel, which is considered a primitive auchenipterin character that is further derived in *Ageneiosus*.

TYPE SPECIES: *Ageneiosus quadrifilis* Kner, Bleeker 1858, p. 357, by monotypy.

INCLUDED SPECIES:

*Tetranematichthys quadrifilis* (Kner)

*Ageneiosus quadrifilis* Kner, 1858, p. 442 (reprint p. 72), pl. 9, fig. 29, (type locality Brazil: Rio Guaporé).

COMMENTS: The diagnostic features of this monotypic genus are those of its type species. While clearly a member of the Ageneiosini, this genus lacks the derived characters of *Ageneiosus* and is considered to be the sister group of *Ageneiosus*.

DISTRIBUTION: Rio Guaporé and Rio Negro of Rio Amazonas drainage and Río Orinoco.

## GENUS *AGENEIOSUS* LACEPEDE 1803

*Ageneiosus* LaCépède 1803, p.132, (type species *Silurus armatus* LaCépède by subsequent designation of Eigenmann and Eigenmann 1890, p. 299).

*Ceratorhynchus* Agassiz, in Spix and Agassiz, 1829, p. 10 (type species *Ceratorhynchus militaris* Agassiz in Spix and Agassiz, 1829 [= *Ageneiosus armatus* LaCépède], by monotypy).

Hypothalmus Schomburgk 1841, p. 191, (type species Hypothalmus dawalla, Schomburgk, 1841, by monotypy)

Davalla Bleeker 1858, p. 58, (type species Hypophthalmus Davalla [sic] (= Hypothalmus dawalla) Schomburgk, 1841 by monotypy).

Pseudageneiosus Bleeker 1862a, p. 14 (type species Ageneiosus brevifilis Valenciennes, in Cuvier and Valenciennes, 1840, by original designation).

Tympanopleura Eigenmann 1912, p. 203, (type species Tympanopleura piperata Eigenmann, 1912, by original designation).

DIAGNOSIS: Auchenipterini with: expanded tooth-bearing surface of dentary and maxilla; anteriorly flared infraorbital ossification; cleithrum without posteriorly directed spine in adults (although spine may be present in juveniles); reduced maxillary barbel; no mental barbels; and, in adult males, tooth-like projections on ossified maxillary barbel.

TYPE SPECIES: Silurus armatus LaCépède by subsequent designation of Eigenmann and Eigenmann 1890

INCLUDED NOMINAL SPECIES:

Ageneiosus inermis (Linnaeus)

Silurus inermis Linnaeus, 1766, p. 503, (type locality Suriname).

Ageneiosus armatus LaCépède

Silurus militaris Bloch, 1794, p.19, pl. 362. [Junior primary homonym of Silurus militaris Linnaeus, 1766].

Ageneiosus armatus LaCépède, 1803, p. 133, (type locality Suriname).

Ageneiosus militaris Valenciennes, in Cuvier and Valenciennes, 1840, p. 232, [unwarranted replacement name for Ageneiosus armatus LaCépède, 1803, therefore taking the same type specimen and type locality].

Ageneiosus brevifilis Valenciennes

Ageneiosus brevifilis Valenciennes, in Cuvier and Valenciennes, 1840, p. 242, (type locality Cayenne)

Ageneiosus dawalla (Schomburgk)

Hypothalmus dawalla Schomburgk, 1841, p. 191, (type locality Guiana)

Hypothalmus davalla Schomburgk, 1841, pl. 9

Ageneiosus ucayalensis Castelnau

Ageneiosus ucayalensis Castelnau, 1855, p. 49, pl. 17. fig. 2 (type locality Peru: Río Ucayali).

Ageneiosus dentatus Kner

Ageneiosus dentatus Kner, 1858, p. 441 [reprint p. 71], (type locality Suriname).

Ageneiosus axillaris Günther

Ageneiosus axillaris Günther, 1864, p. 431, (type locality Suriname).

Ageneiosus sebae Günther

Ageneiosus sebae Günther, 1864, p. 192, (type locality Suriname).

<u>Ageneiosus valenciennesi</u> Bleeker

<u>Ageneiosus militaris</u> Valenciennes, 1847 (type locality Rio Puty). [Junior primary homonym of <u>Ageneiosus militaris</u> Valenciennes 1840].

<u>Ageneiosus valenciennesi</u> Bleeker, 1864, p. 150, [replacement name for <u>Ageneiosus militaris</u> Valenciennes 1847 therefore taking the same type and type locality].

<u>Ageneiosus porphyrus</u> Cope

<u>Ageneiosus porphyrus</u> Cope, 1869, p. 404, (type locality Suriname).

<u>Ageneiosus pardalis</u> Lütken

<u>Ageneiosus pardalis</u> Lütken, 1875, p. 190, (type locality Venezuela: Caracas).

<u>Ageneiosus caucanus</u> Steindachner

<u>Ageneiosus caucanus</u> Steindachner, 1880, p.61 [offprint p. 9], pl. 6, fig. 1-1a (type locality Colombia: Río Cauca).

<u>Ageneiosus brevis</u> Steindachner

<u>Ageneiosus brevis</u> Steindachner, 1881, p. 16 (type locality Rio Amazonas).

<u>Ageneiosus atronasus</u> Eigenmann and Eigenmann

<u>Ageneiosus atronasus</u> Eigenmann and Eigenmann, 1888, p. 149 (type locality unknown).

<u>Ageneiosus vittatus</u> Steindachner

<u>Ageneiosus vittatus</u> Steindachner 1908, p. 64 (type locality Brazil: Rio Purus).

<u>Ageneiosus virgo</u> Posada

<u>Ageneiosus virgo</u> Posada, 1909, p. 295, (type locality Colombia: Río Magdelana).

<u>Ageneiosus therzinae</u> Steindachner

<u>Ageneiosus therzinae</u> Steindachner, 1909, p. 341, (type locality Brazil: Rio Parnaiba).

<u>Ageneiosus parnaguensis</u> Steindachner

<u>Ageneiosus parnaguensis</u> Steindachner 1910, p. 399, (type locality Brazil: Piauí, lake Parnaqua).

<u>Ageneiosus guianensis</u> Eigenmann

<u>Ageneiosus guianensis</u> Eigenmann 1912, p. 204, pl. 21, fig. 2 (type locality British Guiana: Demarara River at Wismar).

<u>Ageneiosus piperata</u> (Eigenmann)

<u>Tympanopleura piperata</u> Eigenmann, 1912, p. 203, pl. 20, fig. 3, (type locality British Guiana: Essequibo River at Crab Falls).

<u>Ageneiosus marmoratus</u> Eigenmann

<u>Ageneiosus marmoratus</u> Eigenmann, 1912, p. 206, pl. 22, fig. 1 (type locality British Guiana: Potaro River of Essequibo River).

Ageneiosus rondoni A. Miranda Ribeiro

Ageneiosus rondoni A. Miranda Ribeiro, 1914, p. 12, pl. 1, fig. 3, pl. 2 fig. 3-4, (type locality Brazil: Rio Negro at Manaus).

Ageneiosus ogilviei Fowler

Ageneiosus ogilviei Fowler, 1914, p. 266, fig. 15, (type locality British Guiana: Rupununi River).

Ageneiosus madeirensis Fisher

Ageneiosus madeirensis Fisher, 1917, p. 426, pl. 42, and fig. 4, (type locality Bolivia: San Joaquin).

Ageneiosus melanopogon A. Miranda Ribeiro

Ageneiosus melanopogon A. Miranda Ribeiro, 1917, p. 51 (type locality, Brazil: Rio Solimões).

Ageneiosus polystictus Steindachner

Ageneiosus polystictus Steindachner, 1917, p. 84, (type locality Brazil: Rio Negro, at mouth).

Ageneiosus alta (Eigenmann and Myers)

Tympanopleura alta Eigenmann, and Myers, in Myers, 1928, p. 85, (type locality Peru: Río Maranon, at Iquitos).

Ageneiosus uruguayensis Devincenzi

Ageneiosus uruguayensis Devincenzi, 1933, p. 3, pl. 1, (type locality Uruguay: Río Uruguay).

Ageneiosus nigricollis (Eigenmann and Allen)

Tympanopleura nigricollis Eigenmann and Allen, 1942, p. 139, Pl. 5, fig. 2,3, Pl. 6, fig. 3 (type locality Peru: Iquitos).

_Ageneiosus freiei_ Schultz

_Ageneiosus freiei_ Schultz 1944, p. 240, (type locality Venezuela: Lake Maracaibo).

_Ageneiosus barranquerensis_ Risso and Risso

_Ageneiosus barranquerensis_ Risso and Risso, 1964, p.11, pl. 2, fig. 1-3, (type locality Argentina: Riacho Barranquerensis of Río Paraná).

_Ageneiosus gabardinii_ Risso and Risso

_Ageneiosus gabardinii_ Risso and Risso, 1964, p. 12, pl. 3, fig. 1, pl. 6 fig. 4, (type locality Argentina: Río Paraná at Corrientes)

_Ageneiosus marquesi_ Risso and Risso

_Ageneiosus marquesi_ Risso and Risso, 1964, p. 20, pl. 6, fig. 1-3, & 5, (type locality Argentina: Río Paraná).

COMMENTS: Species of this genus, with the exception of _Ageneiosus nigricollis_, are further diagnosed by the presence, in adult specimens, of an encapsulated swim bladder, reduced and reoriented Müllerian ramus of the complex-centrum parapophysis, and expanded and obliquely oriented ventral lamina of the tripus transformator process. Sexually dimorphic specimens of _Ageneiosus nigricollis_ lack these characters, as do juvenile _Ageneiosus marmoratus_ (85 mm SL) and _A. caucanus_ (68 mm SL). In a somewhat larger _A. marmoratus_ ( 170 mm SL), however, the beginnings of bladder encapsulation can be seen, as evidenced by laminar bone projecting ventrally from the complex centrum. Although this process seems to start to appear at a large size in A. marmoratus, fully formed swim bladder encapsulations have been found in A. ucayalensis at 120 mm SL and A. guianensis at 92 mm SL, a size range similar to that of adult A. nigricollis. Thus, while absolute size and maturity may be important in determining the presence of these characters, their absence in the adult A. nigricollis specimens examined indicates that swimbladder encapsulation never occurs in that species. In the absence of evidence to suggest that A. nigricollis has, as its closest relative, a species possessing these characters, the former is considered to be the sister group of all other species of Ageneiosus.

The genus Tympanopleura Eigenmann (1912) was created for T. piperata, a species lacking an encapsulated swimbladder. However, as Eigenmann stated in his description of the species, the types may be only juveniles in which encapsulation has not yet occurred. I have not examined any adult specimens of this species to determine whether the three derived characters shared by species other than A. nigricollis are present at a later state in the ontogeny of T. piperata. In the absence of this information, the three species described as Tympanopleura piperata, T. nigricollis, and T. alta are considered to be species of Ageneiosus that lack the derived characters of a more restricted Ageneiosus clade and do not, by themselves, constitute a natural group that warrants a separate genus.

Ceratorhynchus Agassiz is an unwarranted replacement name for Ageneiosus, as C. militaris is also for A. armatus LaCépède. Thus, both the genus and species names are objective synonyms of those of LaCépède. The placement of Davalla and Pseudageneiosus in the synonymy of Ageneiosus reflects current usage and not any observations or decisions of my own.

The type species of Ageneiosus is somewhat problematical, and the following summary of the history of the name is needed to explain the previously unrecognized solution. The genus was created by Lacépède (1803) for two species, Silurus inermis Linnaeus (1766) and Ageneiosus armatus Lacépède (1803), and did not include any indication of a type species. A. armatus, however, is itself somewhat problematical inasmuch as it appears, at first glance, to be a replacement name for Linnaeus'(1758) Silurus militaris, an Asian ariid catfish, which LaCépède included in the synonymy of A. armatus. The LaCépède description of A. armatus, however, better fits a fish that Bloch (1794, p. 19, fig. 362) misidentified as Silurus militaris Linnaeus. Inasmuch as LaCépède's synonymy also includes Bloch's description, A. armatus is actually a composite of two species. There has been, to my knowledge, no explicit choice of a lectotype for A. armatus, and I choose one here, selecting the specimen described and figured by Bloch, to be associated with the name _A. armatus_.

Recognizing the problem that had developed from Bloch's and, especially, LaCépède's misidentification, Valenciennes (in Cuvier and Valenciennes, 1840) proposed that Bloch's specimen be given the name _Ageneiosus militaris_, which is an unwarranted replacement name, and, therefore, a junior objective synonym of _Ageneiosus armatus_ LaCépède.

The first type species designation for _Ageneiosus_ is that of Bleeker (1862a). Therein, he designated "_Ageneiosus militaris_ Bl[eeker] = _Silurus militaris_ Bloch" as the type. As such, this designation could be considered valid, based on the creation of a new species name, for a previously misidentified specimen, and the simultaneous designation of a type species (International Code of Zoological Nomenclature (ICZN 1985) Art 70c(i)). Previously, however, Bleeker (1858) had clearly indicated his knowledge of Valenciennes' proposed solution of the species-level problem by the statement "_Ageneiosus militaris_ Bl[eeker]= _Ageneiosus militaris_ Valenciennes = ...= _Silurus militaris_ Bloch". Therefore, Bleeker's use of the name _Ageneiosus militaris_ cannot be construed as the proposal of a new name for the species. That being the case, the name _Ageneiosus militaris_ cannot compete for type-species status, as it was not an available name at the time _Ageneiosus_ was first proposed (ICZN, 1985, art. 69a). It also cannot qualify as a type designation under

ICZN art. 70c(i) (as discussed above) and, therefore, Bleeker's designation of the type species is invalid.

Eigenmann and Eigenmann (1890, p. 299) cited the type of Ageneiosus as "Ageneiosus armatus type = Silurus militaris Bloch". This appears sufficient as a type designation for Ageneiosus, despite the reference to the unavailable name of Bloch.

Jordan's (1917, p. 66) widely cited designation of "A. armatus LaCépède = S. militaris Linnaeus" as the type of Ageneiosus, which action would have resulted in Ageneiosus becoming a genus in the family Ariidae and a junior subjective synonym of Osteogeneiosus Bleeker, postdates that of Eigenmann and Eigenmann (1890).

Thus, it appears that Eigenmann and Eigenmann (1890) first designated a type species for Ageneiosus in a way that conforms with the ICZN rules and is unambiguously associated, by my above-recorded lectotype designation, with Neotropical catfishes related to the species described and illustrated by Bloch.

DISTRIBUTION: Species of Ageneiosus are known from most of the major drainages in South America and have been reported from scattered coastal drainages. Along with species of Trachelyopterus discussed above, two species of Ageneiosus have been reported in TransAndean drainages.

## *AUCHENIPTERUS* GROUP

DIAGNOSIS: Auchenipterines with: eyes located ventrolaterally on head; mental barbels aligned transversely at symphysis of lower jaw, immediately ventral to paired bony spurs of dentary; maxillary ossification elongated, extending deeply into core of barbel; palatine with posteriorly directed spur on the ventral surface; vomer with ventral keel (at least in adult males); gill rakers longer than intervening spaces; lacrimal broadly sutured to lateral ethmoid dorsally, and with elongate ventral process that extends ventral to infraorbital-canal pore; infraorbital canal with series of small ossicles just posterior to lacrimal; tripus with enlarged anterior edge, in shape of flat oval; basipterygium convex dorsally; pelvic fin with elongated first ray; complex ural centrum with ventrally-directed spur on hypuropophysis; ventral surface of abdomen produced into an acute keel between pelvic fin insertion and anus.

TYPE GENUS: *Auchenipterus* Valenciennes 1840, p. 207 (type species *Auchenipterus nuchalis* Val. [=*Hypophthalmus nuchalis* Spix in Spix and Agassiz 1829], by subsequent designation, Bleeker 1862b, p. 15.)

INCLUDED GENERA: *Entomacorus*, *Auchenipterus*, and *Epapterus*.

COMMENTS: *Auchenipterus* and *Epapterus* are more closely related to each other than either is to *Entomacorus*, as determined by the shared presence of: sphenotic excluded from contact with the supraoccipital by posterior and lateral expansions of the frontals; two pairs of ventrally directed bony spurs near the symphysis of the dentaries; and, in adult males, a cylindrical orbitosphenoid and the fusion of segments of the last (UR1) unbranched anal-fin ray into an unsegmented, stiffened rod.

## GENUS ENTOMACORUS EIGENMANN 1917

Entomacorus Eigenmann 1917, p. 403 (type species Entomacorus benjamini Eigenmann, 1917, by monotypy).

DIAGNOSIS: auchenipterines with: deep canals in supraoccipital, supraneural, and first dorsal-spine pterygiophore elements; accessory dermal bone present on dorsal surface of neurocranium posterior to frontals and medial to sphenotics; vomer keeled; caudal skeleton with separate second ural centrum; pectoral-fin spines of mature males with anterior serrations ventrally recurved; no prolongation of urogenital pore in adult males; mature males with enlarged first pelvic-fin ray, distal segments expanded and flattened, forming paddle-like structure.

TYPE SPECIES: Entomacorus benjamini Eigenmann, 1917, by monotypy

INCLUDED SPECIES:

*Entomacorus benjamini* Eigenmann 1917, p. 403, pl. 41, (type locality Bolivia: San Joaquin).

*Entomacorus gameroi* Mago Leccia, 1984, p. 217, (type locality: Venezuela: Guarico, Río Apurito mouth at Río Apure, near San Fernando de Apure, Río Orinoco basin).

COMMENTS: Inclusion of the genus *Entomacorus* within the Auchenipterinae is somewhat problematical. Sexually dimorphic males of *E. benjamini* are unknown, but males of *E. gameroi* are not uncommon and have been figured by Mago-Leccia (1984). *E. gameroi* males do not exhibit the prolongation of the urogenital pore which is one of the characters that defines the family. Inasmuch as the other characteristics of the family are present, the absence of the elongated urogenital pore is considered a secondary loss. Internal fertilization may not occur in this species, or the insemination process may involve the unusual elongated first pelvic-fin ray found in mature males.

Inclusion of *Entomacorus* in the tribe Auchenipterini is also problematical. The epioccipital process is not bifid posteriorly and, thus, there is no medial process connecting the epioccipital to the parapophyses of the fifth and sixth vertebrae. The basisphenoid process of the parasphenoid does not show the derived expansion described for this lineage. However, inasmuch as all other characters of the tribe are present in the genus, the absence of these characters is considered to be a secondary loss.

DISTRIBUTION: Entomacorus benjamini is known only from the Rio Guaporé drainage of Bolivia and E. gameroi from the llanos (savannahs) of Venezuela.

GENUS AUCHENIPTERUS VALENCIENNES 1840

Auchenipterus Valenciennes, in Cuvier and Valenciennes, 1840, p. 207 (type species "Auchenipterus nuchalis Val." [=Hypophthalmus nuchalis Spix in Spix and Agassiz, 1829], by subsequent designation, Bleeker 1862b, p. 15.)

Euanemus Müller and Troschel, in Müller, 1842, p. 320 (type species Euanemus colymbetes Müller and Troschel, in Müller 1842, by monotypy).

Ceratocheilus A. Miranda Ribeiro, 1918, p. 664 (type species Ceratocheilus osteomystax A. Miranda Ribeiro, 1918, by original designation [preoccupied by Ceratocheilus Wesché, 1910]).

Osteomystax Whitley, 1940, p. 242 (Substitute name for Ceratocheilus A. Miranda Ribeiro and therefore taking the same type species, Ceratocheilus osteomystax A. Miranda Ribeiro, 1918).

DIAGNOSIS: See Comments, below.

TYPE SPECIES: "Auchenipterus nuchalis Val." [=Hypophthalmus nuchalis Spix, in Spix and Agassiz, 1829], by subsequent designation, Bleeker 1862b, p. 15.)

INCLUDED NOMINAL SPECIES:

Hypophthalmus nuchalis Spix, in Spix and Agassiz, 1829, p. 17, pl. 17, (type locality Brazil: Rio Amazonas).

Auchenipterus dentatus Valenciennes, in Cuvier and Valenciennes, 1840, p. 210, (type locality French Guiana: Cayenne).

Euanemus colymbetes Müller and Troschel, in Müller, 1842, p. 320, (type locality: Suriname).

Euanemus brachyurus Cope, 1878, p. 676, (type locality: Peru: Amazon).

Auchenipterus fordicei Eigenmann and Eigenmann, 1888, p. 151, (type locality Brazil: Coari).

Euanemus nigripinnis Boulenger, 1895, p. 524. (type locality Paraguay).

Auchenipterus brevior Eigenmann, 1912, p. 202, (type locality British Guiana: Potaro River at Tumatumari).

Auchenipterus demerarae Eigenmann, 1912, p. 202, pl. 21, fig. 1, (type locality British Guiana: Demarara River at Wismar).

Auchenipterus ambyiacus Fowler, 1915, p. 222, fig. 6, (type locality: Peru: Río Ambyiacu).

Ceratocheilus osteomystax A. de Miranda Ribeiro, 1918, p. 644, pl. 1, (type locality Brazil: Goias, Rio Vermelho at Santa Rita das Antas).

Auchenipterus paysanduanus Devincenzi, 1933, p. 2, (type locality: Uruguay: Río Uruguay, Paysandu).

COMMENTS: There are no known derived characters by which the species included here can be defined in the absence of the species placed in the genus Epapterus. There are, however, no characters that specifically refute an hypothesis of the monophyly of this group. Their inclusion of these species in this, the type genus of the tribe, was necessary in order to permit the recognition of the clearly monophyletic genus Epapterus (discussed below). A close examination of the species of Auchenipterus may reveal that some species are more closely related to Epapterus than to other species of Auchenipterus. Until a study is undertaken at this level, the status of the name Epapterus must remain tentative.

Mees (1974) synonymized most of the nominal species of Auchenipterus under A. nuchalis but he acknowledged that two additional species names may be valid. The great individual variation in meristics, which Mees observed and attributed to intraspecific variation, appears to be organized into discrete geographical units, and these groups probably deserve to be named. At this time, however, the limits of each species and the oldest available name for each has yet to be completely determined, Thus, all available names are listed here without attempting to evaluate them.

The type species of Auchenipterus was listed by Mees (1974) as Hypophthalmus nuchalis Spix, by original designation of Valenciennes, 1840. Although Valenciennes discussed the development of his new generic name for Spix's species, there is no indication that he considered nuchalis as the type for the genus, as currently required. Bleeker (1858) came to a similar conclusion, inasmuch as he restricted the use of the name Auchenipterus to a group that did not include H. nuchalis, which he put into Euanemus. Later, however, Bleeker (1862a) synonymized Euanemus under Auchenipterus and chose nuchalis as the type. This action appears to be the first selection of a type for the genus.

DISTRIBUTION: Auchenipterus is found in the Guianas, the Amazon and Orinoco drainages, and the La Plata system.

## GENUS EPAPTERUS COPE 1878

Epapterus Cope, 1878, p. 677 (type species Epapterus dispilurus Cope, 1878, by monotypy).

Pseudepapterus Steindachner, 1915, p. 199 (type species Auchenipterus (Pseudepapterus) hasemani Steindachner, 1915, by monotypy).

DIAGNOSIS: Members of the Auchenipterus group with: absence of jaw teeth; diminutive dorsal fin, consisting of four or fewer short and slender rays and a feeble spine. A subgroup consisting of E. dispilurus, E. blohmi, E. chaquensis, and E. sp.A can be defined by the shared presence of pelvic fins joined together across ventral midline by extensions of interradial membrane.

TYPE SPECIES: Epapterus dispilurus Cope, 1878, by monotypy.

INCLUDED SPECIES:

*Epapterus dispilurus* Cope

*Epapterus dispilurus* Cope, 1878. p. 677, (type locality Peru: Rio Amazonas, probably at Nauta).

*Epapterus longipinnis* Steindachner, 1882. p.17, (type locality Brazil: Javari).

*Epapterus hasemani* (Steindachner)

*Auchenipterus (Pseudepapterus) hasemani* Steindachner, 1915, p. 199, (type locality Brazil: Pará).

*Epapterus cucuhyensis* (Böhlke)

*Pseudepapterus cucuhyensis* Böhlke, 1951, p. 38, fig. 1, (type locality Brazil: Rio Negro, at Cucui).

*Epapterus chaquensis* Risso and Risso

*Epapterus chaquensis* Risso and Risso, 1962, p. 5, figs. 1-3, (type locality Argentina: Chaco, Laguna del Golf, Resistencia).

*Epapterus blohmi* Vari, Jewett, Taphorn, and Gilbert

*Epapterus blohmi* Vari et al., 1984, p. 463, figs. 1, 6a, (type locality Venezuela: Guacimos, Guarico State).

*Epapterus* sp. a (Venezuela)

COMMENTS: The genus *Epapterus* forms a natural group most closely related to members of the genus *Auchenipterus*. As stated in the account of that genus, the validity of the genus name *Epapterus* may change when the relationships of species currently placed in *Auchenipterus* are resolved. Should *Auchenipterus nuchalis*, the type species of

Auchenipterus, be found to be more closely related to the species of Epapterus than to other species of Auchenipterus, the name Epapterus may be relegated to synonymy.

The generic name Pseudepapterus was proposed by Steindachner as a subgeneric name for a single species that he considered to be close to Epapterus, but distinct from it in the possession of an adipose dorsal fin. Böhlke (1951) discovered a second species with an adipose fin, and a third is unnamed at present. The presence of an adipose dorsal fin, however, is considered a primitive character for the genus. Furthermore, the three species do not share any derived characters, and one of the three is more closely related to other species of Epapterus. Thus, the genus Pseudepapterus seems not be a natural group, but, forms part of the genus Epapterus, instead.
DISTRIBUTION: Species of Epapterus are found in the Amazon, Orinoco, and La Plata drainages.

# DISCUSSION

## SYSTEMATIC CONCLUSIONS

The family Auchenipteridae, as most generally delimited, is not a monophyletic group. Species of the Ageneiosidae are more closely related to Auchenipterus than are many species that have traditionally been put in the Auchenipteridae. If we accept the constraint that a classification must be based on monophyletic groups and that named taxa include all members of a lineage, the Auchenipteridae must either include Ageneiosus and its relatives, or the auchenipterids must be split into a number of different families. The approach adopted here partkaes of both of these solutions.

The Auchenipteridae has been expanded to include all species previously included in the Ageneiosidae (Table 5). The family is redefined on a series of morphological characters, including modifications of the reproductive system for internal fertilization. While internal fertilization in these catfishes has been recognized previously (e. g. Ihering, 1937, and P. Miranda Ribeiro, 1968b), it has been considered to be restricted to only part of the family. Miranda Ribeiro correctly pointed out that a classification based on modes of reproduction is inherently weak, inasmuch as little is known about the biology of many of the species that are available to a systematist only as preserved specimens. However, several morphological characteristics some associated with and others independent of, the reproductive biology of auchenipterids serve to define the lineage. Thus, placement of a given specimen in the family can be achieved without observing its reproductive activities, as required by the scheme of Ihering.

As a part of the Auchenipteridae, a lineage consisting of *Ageneiosus* plus *Tetranematichthys* is still recognized as a monophyletic group, but within the tribe Auchenipterini. The distinctions that have led authors in the past to recognize these fishes as a separate family have overshadowed the number of derived characters that *Ageneiosus* and *Tetranematichthys* share with *Auchenipterus* and its relatives, characters that are not exhibited in several auchenipterid genera.

A second major clade of the Auchenipteridae, the *Auchenipterus* group, has been widely recognized. Typically, three genera are included: *Auchenipterus*, *Epapterus*, and *Pseudepapterus*. As indicated in the systematic section, *Pseudepapterus* cannot be recognized as a natural group in the absence of *Epapterus*, and has, therefore, been synonymized. The close relationship between *Entomacorus* and the *Auchenipterus* group has not been noticed previously. As explained above, this appears to be due to the surprising number of reversals of derived characters in *Entomacorus*.

As defined here, the Auchenipteridae includes only part of the group as proposed by Britski (1972) and Mees

(1974). Excluded from membership are the Centromochlidae, a group that has been recognized by some workers as either an auchenipterid subfamily (Britski, 1972), or as a separate family (P. Miranda Ribeiro, 1968b), although with a membership that differs from the one proposed here. Membership in the Centromochlidae is most easily recognized by the modified anal-fin of adult males in which the fin rays are posteriorly directed and compressed, and the entire fin suspended beneath the body on a swollen peduncle. In addition, the metapterygoid is reduced in size and not broadly sutured to the hyomandibula. Otherwise, centromochlids do not show any derived characters, so that, strictly speaking, recognition is limited to adult males. Unlike the situation in the Auchenipteridae, internal fertilization has not been observed in centromochlids and quite likely does not occur in the family. Modifications of the male anal fin are not accompanied by an enlargement of the female urogenital pore, so that sperm transfer seems unlikely. Instead, the male fin may serve either as a sperm-directing conduit for precise deposition during spawning or as a clasping organ for more efficient external fertilization.

Thus, the auchenipterids and centromochlids each form natural groups that, most likely, have different modes of reproduction, a situation that I think is best recognized at the familial level.

Britski's Centromochlinae is characterized by an orbital margin bordered by the frontal, a characteristic considered here to be primitive for doradoid catfishes. Using this character, Britski's grouping contains not only the centromochlids (as recognized here), but the genera *Pseudauchenipterus*, *Entomacorus*, and *Trachelyichthys*, all of which belong in the Auchenipteridae.

Relationships among species placed in the Centromochlidae have differed markedly with various authors (Table 6). The inclusiveness of *Centromochlus* and *Glanidium* have changed as species have been shifted into and out of a third genus, *Tatia*. Although Britski (1972) considered *Tatia* as merely a part of *Glanidium*, Mees (1974), in contrast, elevated it and put most of the centromochlid species into it. Consideration of the newly discovered source of character information, concerning the male anal-fin rays should help to stabilize the limits of these genera.

The enigmatic species *Gelanoglanis stroudi* has been removed from the position of insertae sedis in the Auchenipteridae. Böhlke (1980) recognized its relationship to the so-called auchenipterids, was unable to place the species with confidence near any existing taxa. There seems little doubt that it belongs in the Centromochlidae, at some as yet undetermined level.

Finally, much of the systematics of the auchenipterids and centromochlids remains unresolved. The position of a number of genera has been left in limbo inasmuch as clear evidence for their placement has yet to be found. Several genera, including Asterophysus, Tocantinsia, and Pseudotatia, are known from very few individuals and their anatomy is still largely unknown. A number of species in this group were not available during this study and had to remain unplaced, or tentatively located in the systematic scheme presented here. As much of the systematics of both the auchenipterids and centromochlids is, at present at least, based on sexually dimorphic characters, adult males are essential to real progress in the systematics of the group.

# TABLES

Table 1. Diagnostic characters for the families of the superfamily Doradoidae (from Chardon, 1968).

| | Mochokidae | Auchenipteridae | Doradidae | Ageneiosidae |
|---|---|---|---|---|
| Elastic spring mechanism of Weberian complex | present | present | present | transformed |
| Lateral body plates | absent | absent | present | absent |
| Mesocoracoid | lost | present | present | present |
| Air bladder | large & free | large & free | large & free | reduced & encapsulated |
| Entopterygoid (=Mesopterygoid) | present | absent | absent | absent |
| Ossification between Supraoccipital and first dorsal fin pterygiophore | present | present | present | absent |
| connection between epiotic and fourth [sic] parapophysis | ligamentous | ossified | ossified | ossified |

Table 2. Summary of diagnostic character information for three families of doradoid catfishes provided by Britski (1972).

| | Doradidae | Auchenipteridae | Ageneiosidae |
|---|---|---|---|
| ossified plates along lateral line | present | absent | absent |
| suprapreopercle | absent | present | present |
| infraorbitals | 3 | 3-9 | 3 |
| sexual dimorphism | absent | present | present |
| mental barbels | 2 pairs | 2 pairs | 0-1 pair |
| nuchal plate | present | usually present | absent |

Table 3. Specimens examined for comparative anatomical study of Auchenipterid relationships. Species are grouped by generic placement as proposed here. Species names, however, refer to the name currently assigned to the catalog number and not necessarily to the species. C&S refers to both alizarin red/alcian blue and alizarin red (only) cleared and stained fishes; A - preserved specimens examined for external details only; Skel - dry skeletal preparations; D - dissected alcoholic specimens. Types are designated by H, S, or P, following the name, for holotype, syntype(s) or paratype(s), respectively.

| Taxon | Catalog number | Number of specimens | Nature of material |
|---|---|---|---|
| | CENTROMOCHLIDAE | | |
| Gelanoglanis | | | |
| Gelanoglanis stroudi (P) | ANSP 142941 | 1 | C&S |
| Gelanoglanis stroudi (P) | ANSP 142940 | 1 | C&S |
| Centromochlus | | | |
| Centromochlus heckelii | AMNH 55406 | 16 | C&S,D |
| Centromochlus existimatus | AMNH 55407 | 3 | A |
| Centromochlus existimatus | USNM 261447 | 1 | A |
| Genus a | | | |
| Tatia altae | AMNH 55411 | 1 | A |
| Tatia sp. | INHS 69553 | 20 | A, D |
| Glanidium | | | |
| Glanidium albescens (S) | ZMUC 335,338 | 2 | A |
| Glanidium ribieroi | AMNH 37924 | 1 | A |
| Tatia punctata (P) | ZMA 105.525 | 3 | A |
| Glanidium leopardus | RMNH 28576 | 1 | C&S |
| Glanidium leopardus | ZMA 105.854 | 12 | C&S,A |
| Glanidium melanopterum | MCZ 36187 | 3 | A |
| Tatia concolor (P) | ZMA 106.209 | 2 | A |
| Tatia | | | |
| Tatia intermedia | ZMA 105.791 | 2 | A |
| Tatia galaxias | AMNH 78898 | 4 | D, C&S |
| Tatia sp.(Venezuela) | AMNH 74442 | 1 | D |
| Tatia sp.(Venezuela) | AMNH 74443 | 2 | C&S |
| Genus b | | | |
| Glanidium sp. | AMNH 74441 | 1 | C&S |
| Tatia brunnea (P) | ZMA 105.851 | 3 | A, C&S |
| Tatia creutzbergi | ZMA 105.859 | 1 | C&S |
| Glanidium neivai | IBN 703 | 1 | A |

Table 3. Continued.

| | | | |
|---|---|---|---|
| | AUCHENIPTERIDAE | | |
| Asterophysus | | | |
| Asterophysus batrachus (S) | NMW 47515-6 | 2 | A, radiograph |
| Asterophysus batrachus (S) | ANSP 158294 | 2 | A, C&S |
| Pseudotatia | | | |
| Pseudotatia parva (P) | FMNH 57807 | 13 | A, C&S |

Table 3. Continued.

| | | | |
|---|---|---|---|
| Tocantinsia | | | |
| Tocantinsia depressa (P) | CAS 6590 | 1 | A |
| Tocantinsia depressa (P) | CAS 13398 | 1 | A |
| | Trachycorystinae | | |
| Trachycorystes | | | |
| Trachycorystes sp. | USNM 273044 | 1 | C&S |
| Trachycorystes obscurus (S) | BMNH 1864.1 .21.13 | 1 | A |
| Trachycorystes trachycorystes | AMNH 78899 | 2 | C&S, D |
| Auchenipterus trachycorystes (H) | MNHN A.9422 | 1 | Skin |
| Liosomadoras | | | |
| Liosomadoras oncinus | AMNH 78900 | 4 | C&S, Skel |
| Trachelyopterichthys | | | |
| Trachelyopterichthys taeniatus | AMNH 78901 | 2 | Skel, C&S |
| Trachelyopterichthys anduzei (H) | MBUCV-V-14627 | 1 | A |
| | Auchenipterinae | | |
| Auchenipterichthys | | | |
| Auchenipterichthys thoracatus | AMNH 21642 | 1 | C&S |
| Auchenipterichthys sp | AMNH 78902 | 1 | C&S |
| Pseudauchenipterus | | | |
| Pseudauchenipterus nodosus | USNM 273045 | 5 | C&S |
| Pseudauchenipterus nodosus | AMNH 78903 | 3 | A, C&S |
| Pseudauchenipterus nodosus | AMNH 3782 | 8 | A, C&S |
| Pseudauchenipterus sp. | USNM 226107 | 1 | C&S |
| | Auchenipterini | | |
| Trachelyopterus | | | |
| Trachelyopterus coriaceus | UMMZ 117605 | 1 | A |
| Trachelyopterus coriaceus | ZMA 107.828 | 4 | A |
| Trachelyopterus coriaceus | MCZ 7070, 7371,7338 | 1 | C&S |
| Trachelyopterus coriaceus | AMNH 78904 | 1 | Skel |
| Trachelyopterus coriaceus maculatus (H) | MCZ 7337 | 1 | A |
| Trachycorystes insignis badeli | USNM 175292 | 2 | A |
| Trachycorystes fisheri | AMNH 5332 | 1 | C&S |
| Trachycorystes amblops | USNM 273047 | 2 | C&S |
| Trachycorystes galeatus | AMNH 78905 | 1 | C&S |

Table 3, Continued.

| | | | |
|---|---|---|---|
| Parauchenipterus galeatus | UMMZ 207075 | 29 | Skel |
| Parauchenipterus galeatus | UMMZ 207572 | 17 | A |
| Parauchenipterus striatulus | AMNH 8675 | 1 | C&S |
| Trachelyichthys | | | |
| Trachelyichthys exilis | AMNH 78906 | 3 | C&S |
| Trachelyichthys sp. | MBUCV-V-14975 | 6 | A |
| Auchenipterus group | | | |
| Auchenipterus | | | |
| Auchenipterus nuchalis | UMMZ 207566S | 3 | Skel |
| Auchenipterus nuchalis | AMNH 3866 | 1 | C&S |
| Auchenipterus demararae | AMNH 78907 | 1 | C&S |
| Auchenipterus demararae | AMNH 12949 | 2 | C&S, Skel |
| Auchenipterus sp. | AMNH 55352 | 2 | C&S |
| Auchenipterus sp. | AMNH 37381 | 3 | C&S |
| Entomacorus | | | |
| Entomacorus gameroi | AMNH 55404 | 4 | C&S |
| Entomacorus gameroi | ANSP 158849 | 3 | A |
| Entomacorus benjamini | AMNH 78908 | 1 | C&S |
| Entomacorus benjamini | UMMZ 204709 | 4 | A |
| Epapterus | | | |
| Epapterus blohmi | USNM 260638 | 3 | C&S |
| Epapterus blohmi | USNM 263115 | 1 | C&S |
| Pseudepapterus hasemani | USNM 274480 | 1 | A |
| Pseudepapterus cf. P. hasemani | ANSP 139502 | 1 | A |
| Epapterus chaquensis | UMMZ 207136 | 1 | A |
| Ageneiosus group | | | |
| Ageneiosus | | | |
| Ageneiosus marmoratus | AMNH 78909 | 2 | Skel, C&S |
| Ageneiosus ucalayensis | AMNH 3844 | 1 | C&S |
| Ageneiosus brevifilis | AMNH 56229 | 1 | Skel |
| Ageneiosus guianensis | AMNH 55349 | 2 | C&S, D |
| Ageneiosus caucanus | AMNH 11395 | 1 | C&S |
| Ageneiosus sp (Venezuela) | AMNH 78910 | 3 | C&S |
| Ageneiosus nigricollis | AMNH 78911 | 4 | C&S, D |
| Tetranematichthys | | | |
| Tetranematichthys quadrifilis | AMNH 74444 | 4 | C&S, A |

Table 3, Continued.

| | | | |
|---|---|---|---|
| | DORADIDAE | | |
| Doras lipophthalmus | AMNH 74489 | 5 | D, skel |
| Doras cf. D. leporhinus | AMNH 78912 | 1 | D |
| Platydoras costatus | AMNH 78913 | 1 | D |
| Pterodoras granulosus | AMNH 78914 | 1 | Skel |
| Pterodoras angeli | AMNH 78915 | 1 | C&S |
| Rhinodoras dorbignyi | AMNH 78916 | 1 | C&S |
| Megalodoras irwini | AMNH 56306SD | 1 | Skel |
| Astrodoras asterifrons | AMNH 40183 | 1 | C&S |
| Hemidoras carinatus | AMNH 12946 | 1 | C&S |
| Doras hancocki | AMNH 12945 | 1 | C&S |
| Anduzedoras microstomus | AMNH 74491 | 2 | C&S |
| Hildadoras sp. | AMNH 55906 | 2 | Skel |
| Acanthodoras sp. | AMNH 55907 | 1 | Skel |
| | MOCHOKIDAE | | |
| Synodontis sp. | AMNH 55333 | 4 | C&S |
| Synodontus njassae | AMNH 55409 | 2 | D |
| Microsynodontis batesii | AMNH 11741 | 1 | C&S |
| Mochokus niloticus | AMNH 55403 | 1 | C&S |
| Mochokus niloticus | USNM 229657 | 1 | C&S |
| Mochokiella paynei | AMNH 78917 | 1 | D |
| Chiloglanis deckerii | AMNH 14289 | 1 | C&S |
| Euchilichthys dybowskii | AMNH 6690 | 1 | C&S |
| | ICTALURIDAE | | |
| Ictalurus punctatus | AMNH 55927 | 3 | Skel |
| | DIPLOMYSTIDAE | | |
| Diplomystes chilensis | AMNH 55318 | 1 | C&S |
| | ARIIDAE | | |
| Arius felis | AMNH 78920 | 6 | C&S |
| Bagre bagre | AMNH 20718 | 2 | C&S |
| Genidens genidens | AMNH 20725 | 2 | C&S |
| | PANGASIIDAE | | |
| Pangasius suchii | AMNH 78918 | 2 | C&S |
| Pangasius suchii | AMNH 55632 | 1 | Skel |
| | SISORIDAE | | |
| Glyptosternon sinense | AMNH 10265 | 2 | D |
| | ASPREDINIDAE | | |
| Agmus lyriformes | AMNH 78919 | 1 | Skel |
| | SCHILBEIDAE | | |
| Pseudeutropius garua | NMW 44360 | 1 | D |
| | CHACIDAE | | |
| Chaca bankanensis | AMNH 77377 | 12 | C&S, Skel |

Table 4. Caudal fin-ray number as a function of body size in a sample of <u>Parauchenipterus galeatus</u> (UMMZ 207572) from Paraguay.

| Standard length | Number of branched fin-rays associated with lower half of hypural plate | | |
|---|---|---|---|
| | 10 rays | 11 rays | 12 rays |
| 60-89 mm | 5 | 1 | 0 |
| 90-119 | 3 | 2 | 0 |
| 120-159 mm | 2 | 3 | 1 |

Table 5. A classification of the families Auchenipteridae and Centromochlidae.

Centromochlidae
- *Centromochlus*
- Genus a
- *Glanidium*
- *Tatia*
- Genus b
- *Gelanoglanis*

Auchenipteridae
- insertae sedis
  - *Pseudotatia*
  - *Tocantinsia*
  - *Asterophysus*
- Trachycorystinae
  - *Trachycorystes*
  - *Liosomadoras*
  - *Trachelyopterichthys*
- Auchenipterinae
  - insertae sedis
    - *Auchenipterichthys*
    - *Pseudauchenipterus*
  - Auchenipterini
    - *Trachelyichthys*
    - *Trachelyopterus*
    - *Ageneiosus*
    - *Tetranematichthys*
    - *Auchenipterus*
    - *Epapterus*
    - *Entomacorus*

Table 6. Comparison of generic placement of species within the Centromochlidae

| Eigenmann 1910 | Gosline 1945 | Fowler 1951 | Mees 1974 | here |
|---|---|---|---|---|
| **Centromochlus** | | | | |
| oncinus | oncinus | OUT | | |
| heckelii | heckelii | heckelii | heckelii | heckelii |
| (megalops) | (megalops) | (megalops) | (megalops) | (megalops) |
| steindachneri | steindachneri | steindachneri | (steindachneri) | (steindachneri) |
| | | | *existimatus | existimatus |
| perugiae | perugiae | perugiae | To Tatia | To Genus A |
| | | *altae | To Tatia | " |
| aulopygius | To Tatia | | | |
| intermedius | To Tatia | | | |
| | *gyrinus | gyrinus | To Tatia | |
| | | *dunni | To Tatia | |
| **Genus A** | | | | perugiae |
| | | | | altae |
| **Glanidium** | | | | |
| albescens | albescens | albescens | albescens | albescens |
| | *ribeiroi | ribeiroi | ribeiroi | ribeiroi |
| | *cesarpintoi | cesarpintoi | (cesarpintoi) | ? |
| | *melanopterum | melanopterum | melanopterum | melanopterum |
| | *piresi | piresi | piresi | OUT |
| | *neivai | ? | To Tatia | |
| | | | *catharinensis | ? |
| | | | *leopardus | leopardus |
| | | | | punctata |
| | | | | concolor |
| **Tatia** | | | | |
| | | | perugiae | ToCentromochlus |
| | | | altae | ToCentromochlus |
| | aulopygia | aulopygia | aulopygia | aulopygia |
| | intermedia | intermedia | intermedia | intermedia |
| | | | (dunni) | dunni |
| | | | *galaxias | galaxias |
| | | | *gyrinus | ? |
| | | | *schultzi | ? |
| | | | *reticulata | ? |
| | | | *simplex | ? |
| | | | *concolor | to Glanidium |
| | | | *punctata | " " |
| | | | *brunnea | to Genus B |
| | | | *creutzbergi | " " |
| | | | neivai | " " |
| Genus B | | | | |
| | | | | brunnea |
| | | | | creutzbergi |
| | | | | neivai |

Note: Underlined names are type species; parentheses indicate names in synonymy of name above; asterisks indicate a species described since previous publication; OUT indicates removal from the centromochlids.

FIGURES

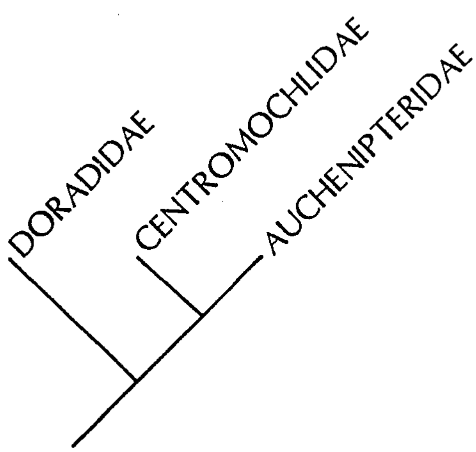



Fig. 1. Cladogram of the hypothesized relationship among the families of the superfamily Doradoidea.

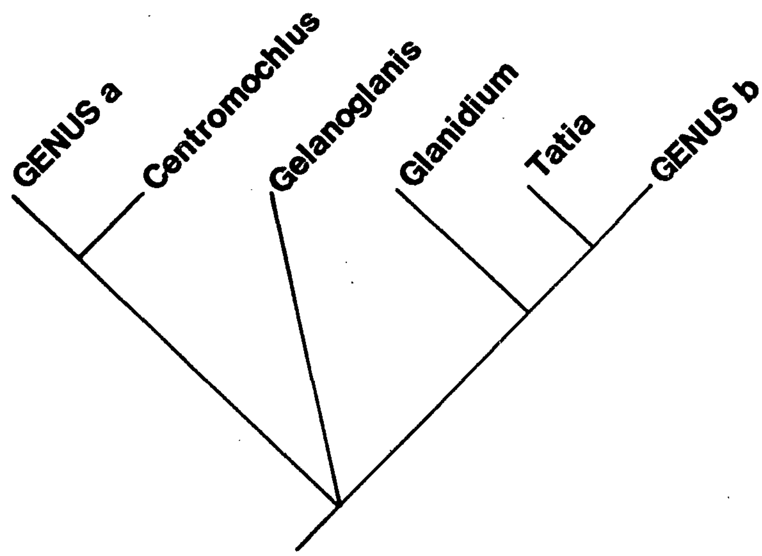



Fig. 2. Cladogram of hypothesized relationships for the genera of the family Centromochlidae.

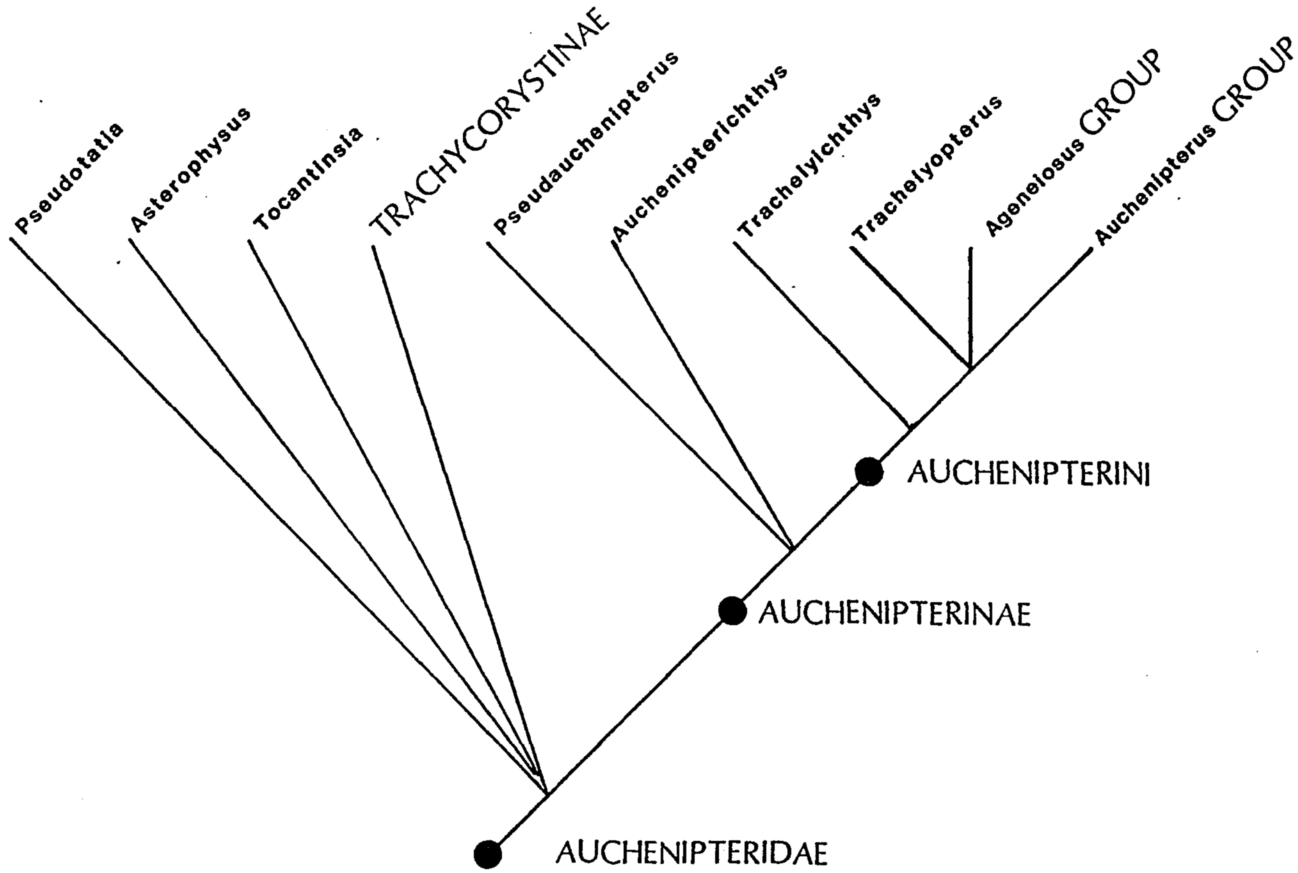



Fig. 3. Cladogram of the hypothesized relationships for the family Auchenipteridae.

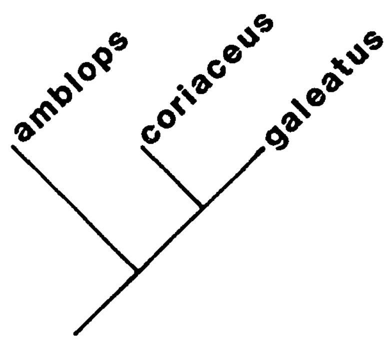



Fig. 4. Cladogram showing the relationships for three species of the genus *Trachelyopterus*.

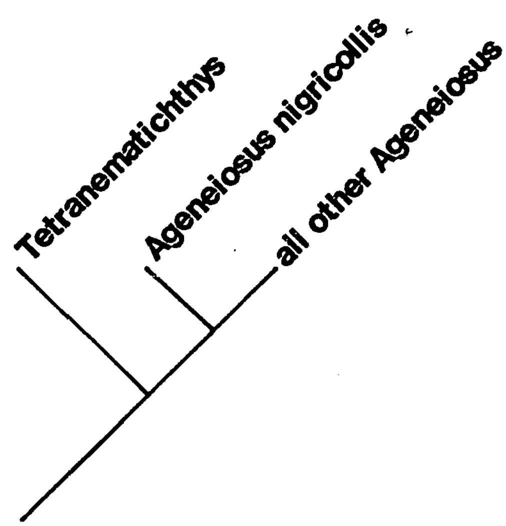



Fig. 5. Cladogram showing the hypothesized relationships of the Ageneiosus group.

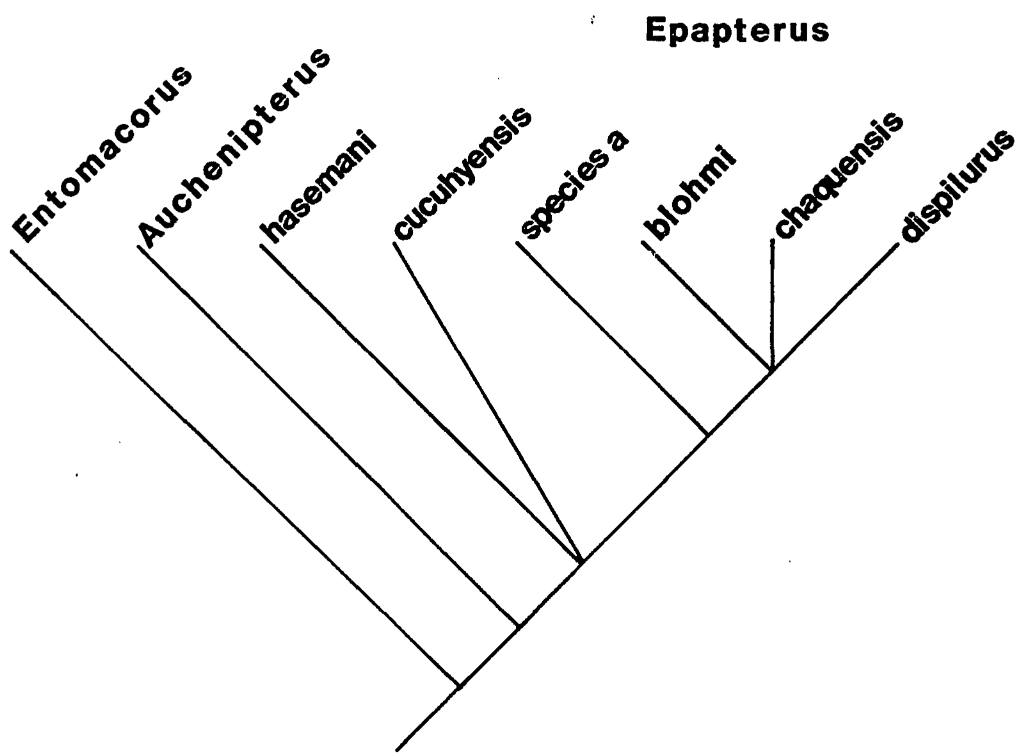



Fig. 6. Cladogram of the relationships of the genera of the *Auchenipterus* group and of species of the genus *Epapterus*.

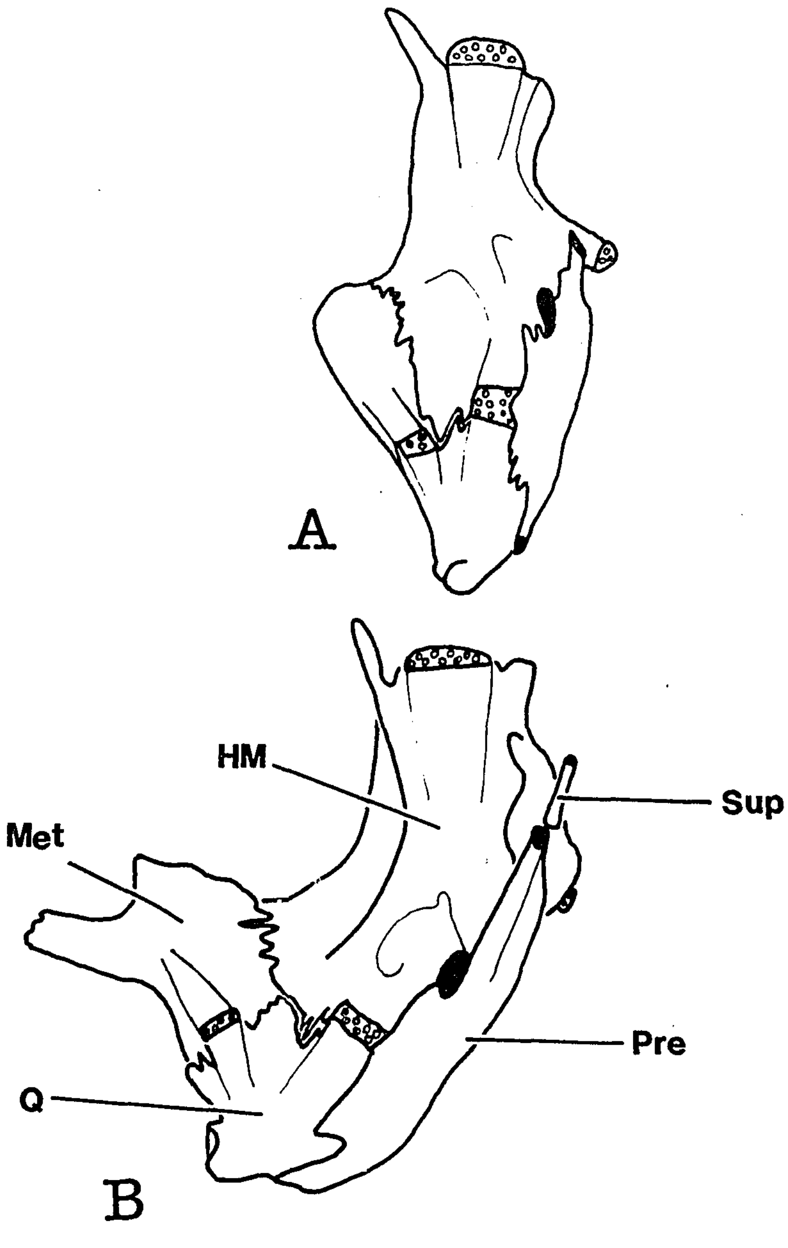
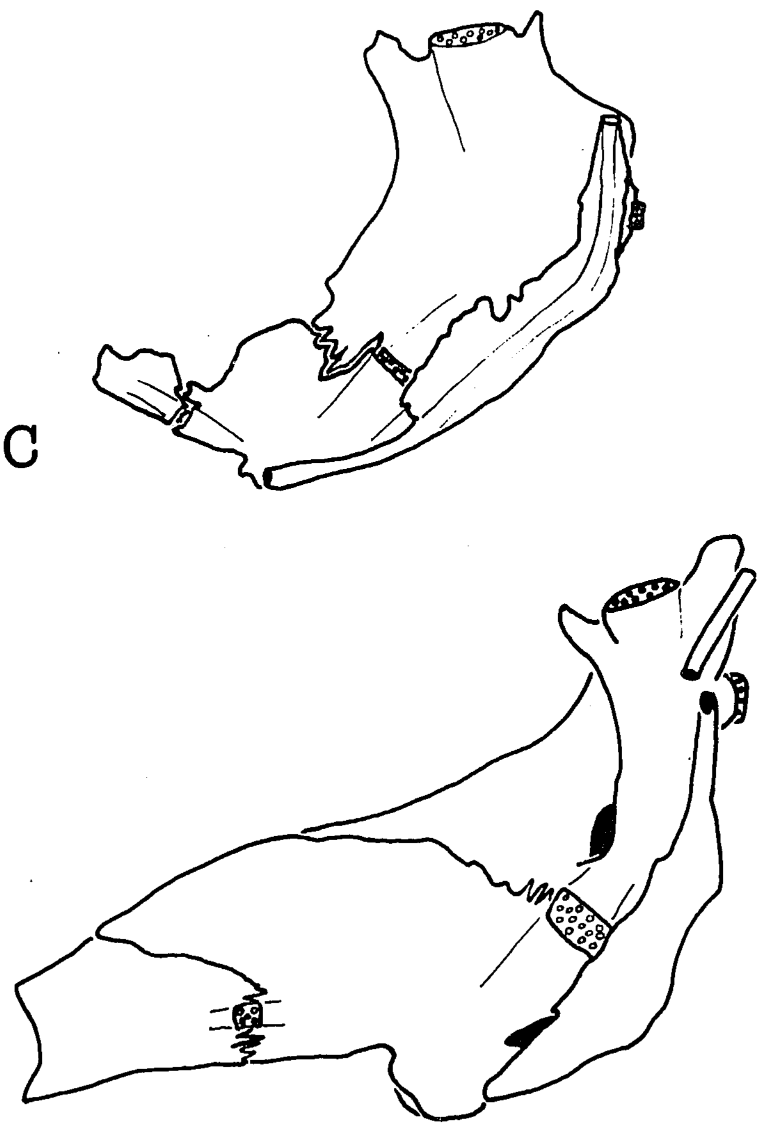



Fig. 7. Left lateral view of the suspensorium elements (palatine and entopterygoid omitted) of
A) Asterophysus batrachus, ANSP 158294,
B) Trachycorystes sp. USNM 273044,
C) Centromochlus heckelii AMNH 55406, and
D) Ageneiosus ucayalensis, AMNH 3844.



C

D

Fig. 7. Continued.

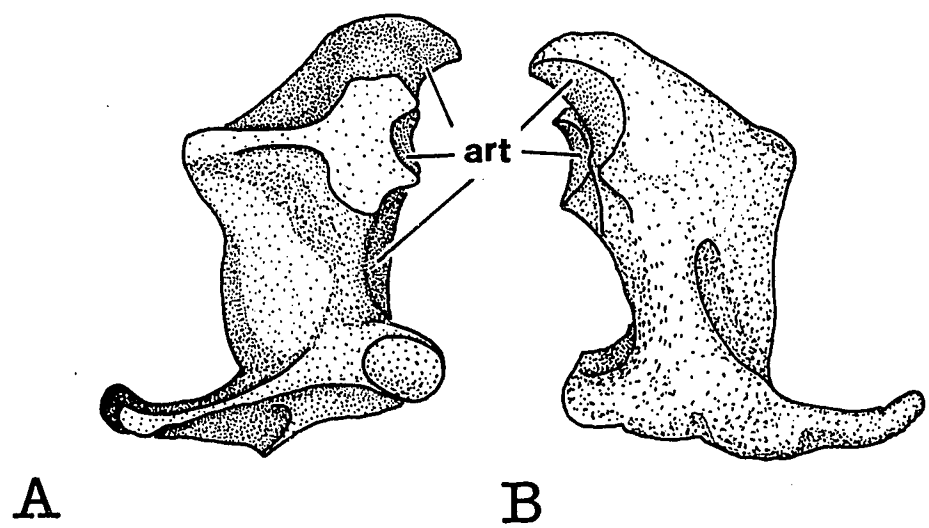



Fig. 8. Left palatine of an adult male specimen of Auchenipterus nuchalis AMNH 3866, A) dorsal view, B) ventral view.

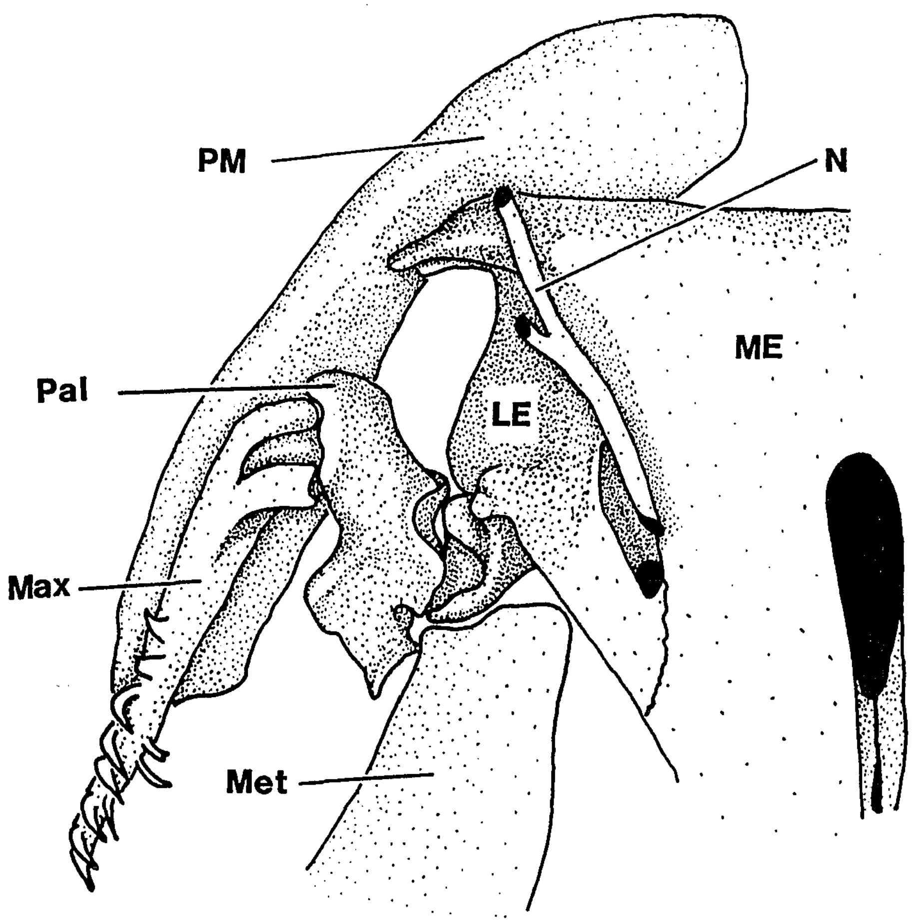



Fig. 9. Ethmoid region of an adult male specimen of _Ageneiosus brevifilis_, AMNH 56229 SD, in dorsal view.

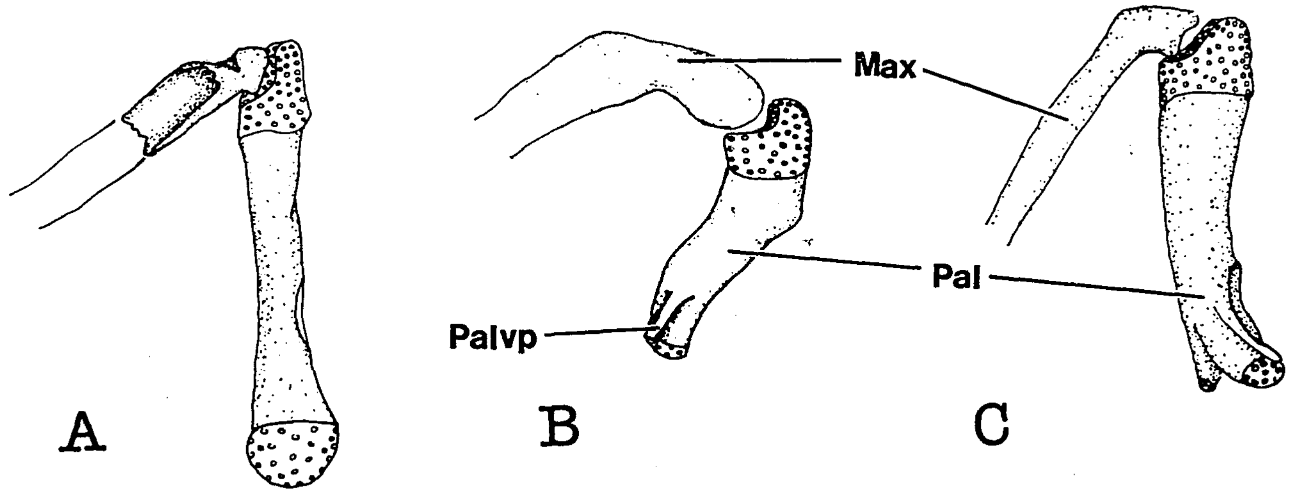



Fig. 10. Left palatine and maxilla, in ventral view, of A) *Asterophysus batrachus*, ANSP 158294, B) *Entomacorus gameroi*, AMNH 55404, C) *Epapterusblohmi*, USNM 260638.

A

B

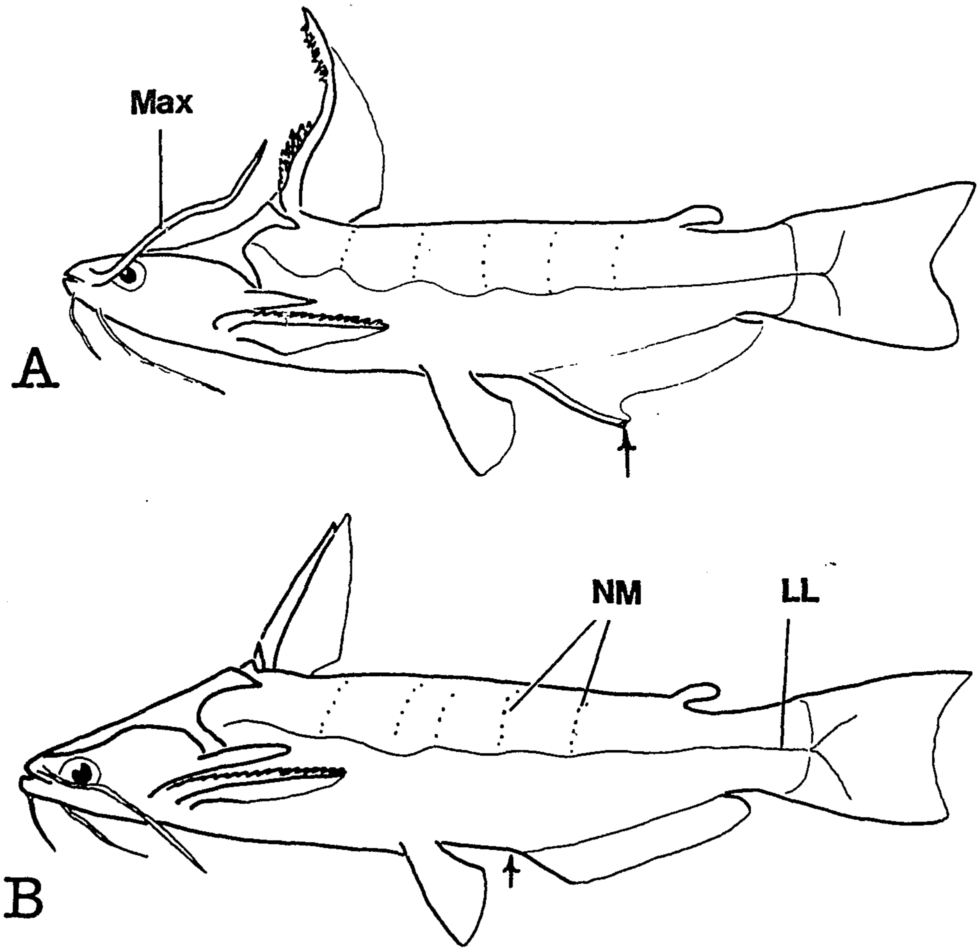



Fig. 11. Left lateral view of <u>Trachelyopterus insignis</u>, A) mature male, B) female, showing sexual dimorphism of the nuchal region, maxillary barbel, dorsal-fin spine, and placement of urogenital pore (indicated by arrow). Drawn from Steindachner, 1878.

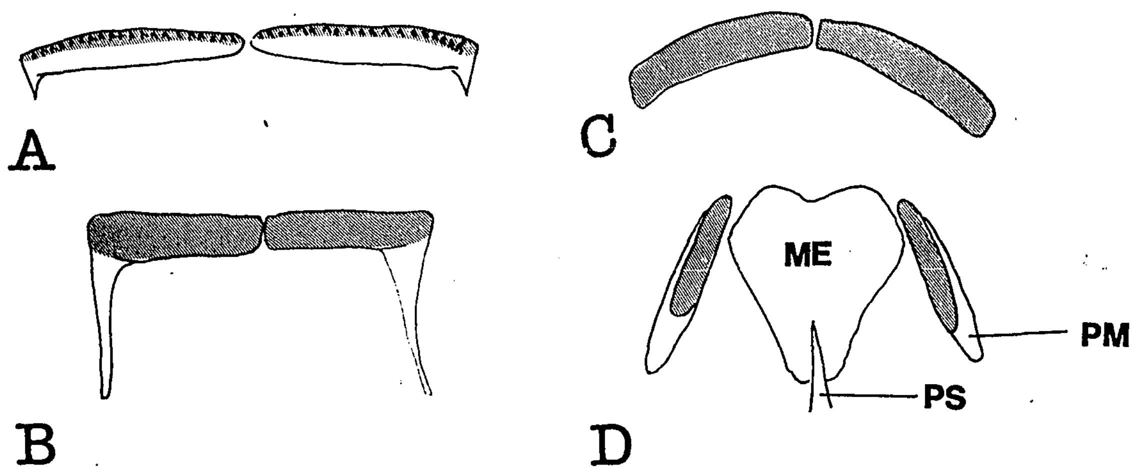



Fig. 12. Ventral view of the premaxillae of A) Entomacorus gameroi, AMNH 55404, B) Auchenipterus nuchalis AMNH 3866, C) Trachycorystes sp. USNM 273044, and D) Gelanoglanis stroudi ANSP 142941. Hatched area indicated tooth-bearing portion of bone.

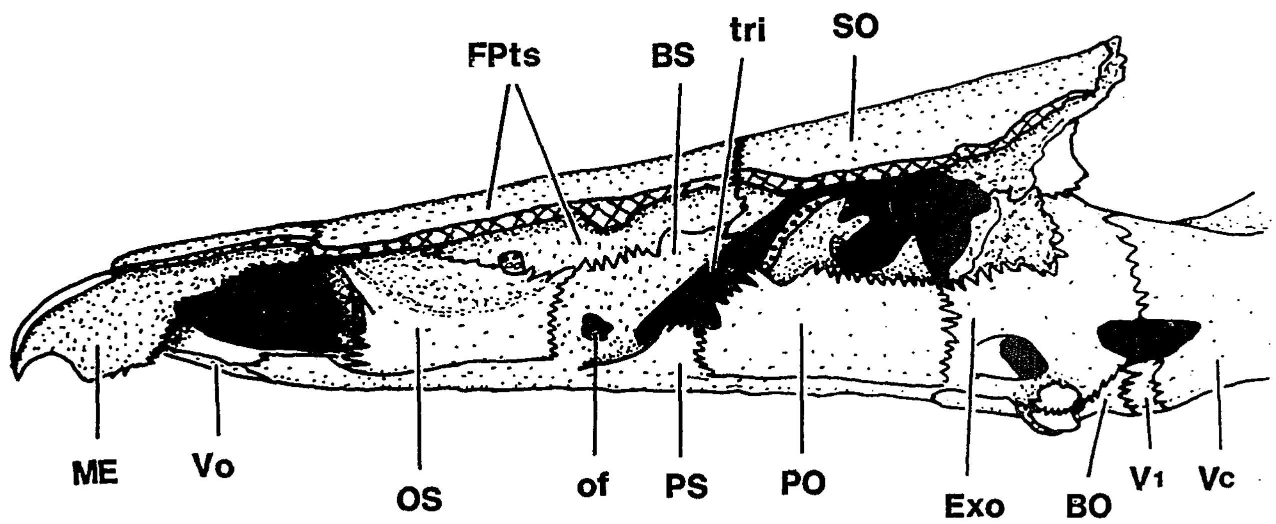



Fig. 13. Left lateral view of neurocranium of <u>Trachelyopterus</u> <u>galeatus</u>, UMMZ 207075. Lateral ethmoid, sphenotic, pterotic, epioccipital, and posttemporal removed to show position of optic and trigeminofascialis foramina.

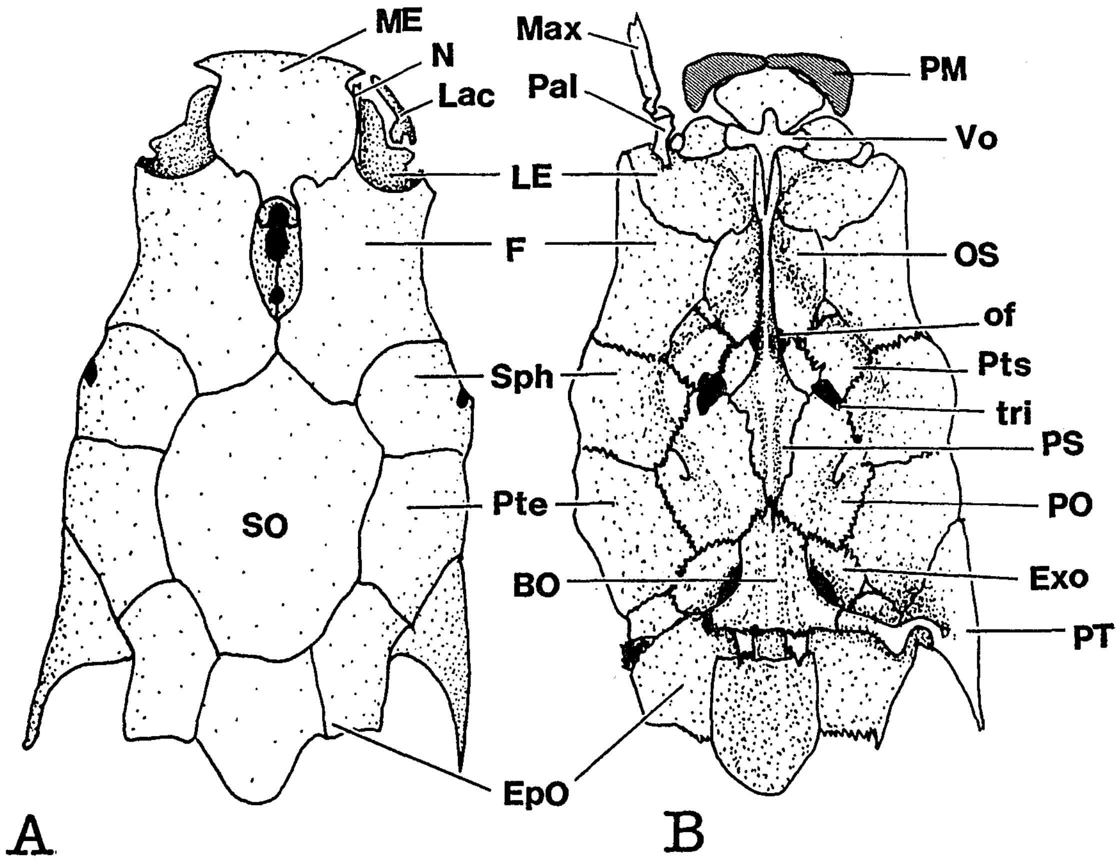



Fig. 14. Neurocranium and expanded first pterygiophore of Centromochlus heckelii, AMNH 55406. A) dorsal view, B) ventral view. Left lacrimal and nasal removed from dorsal view. Right posttemporal removed from ventral view.

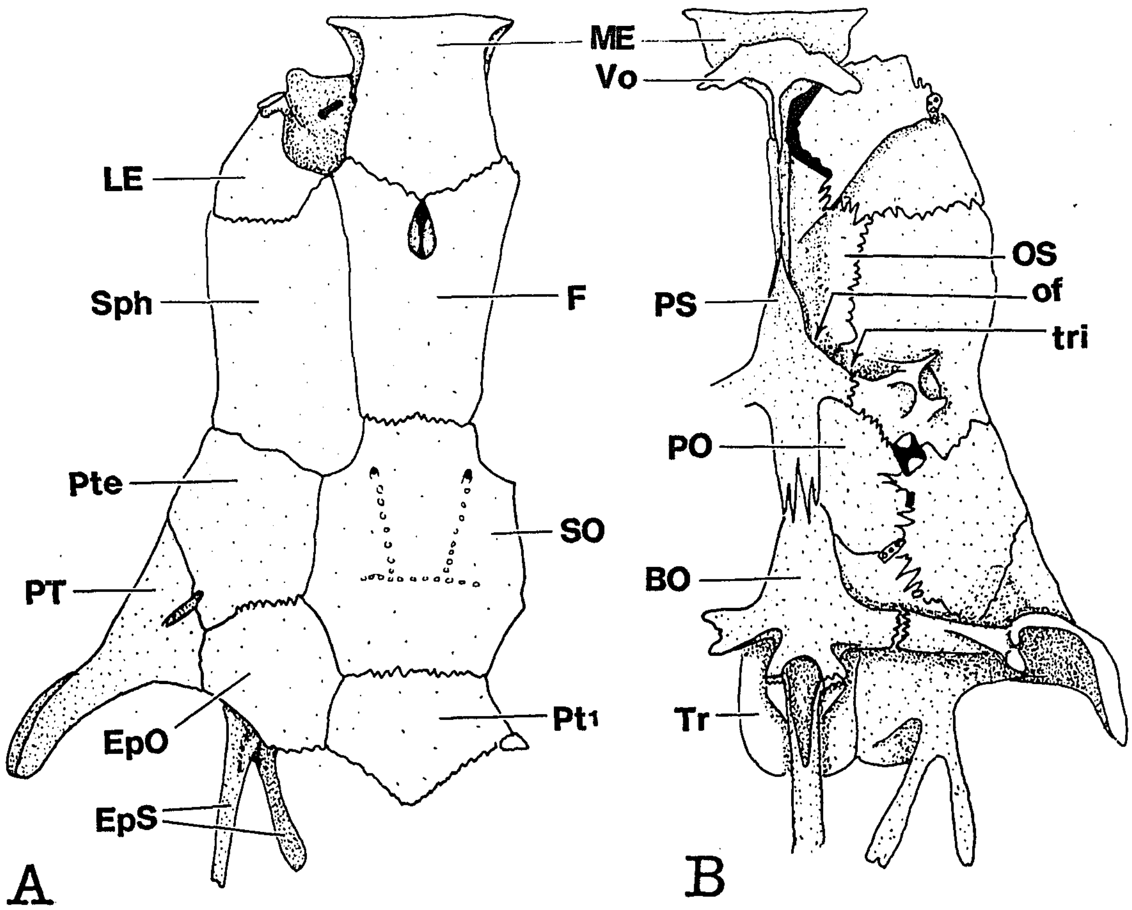



Fig. 15. Neurocranium and expanded first pterygiophore of <u>Trachelyopterus galeatus</u>, UMMZ 207075. A) dorsal view, B) ventral view. Right member of paired bones not illustrated. Note that frontals are not typically fused in this species. approximate position of optic and trigeminofascialis foramina are indicated by arrows.

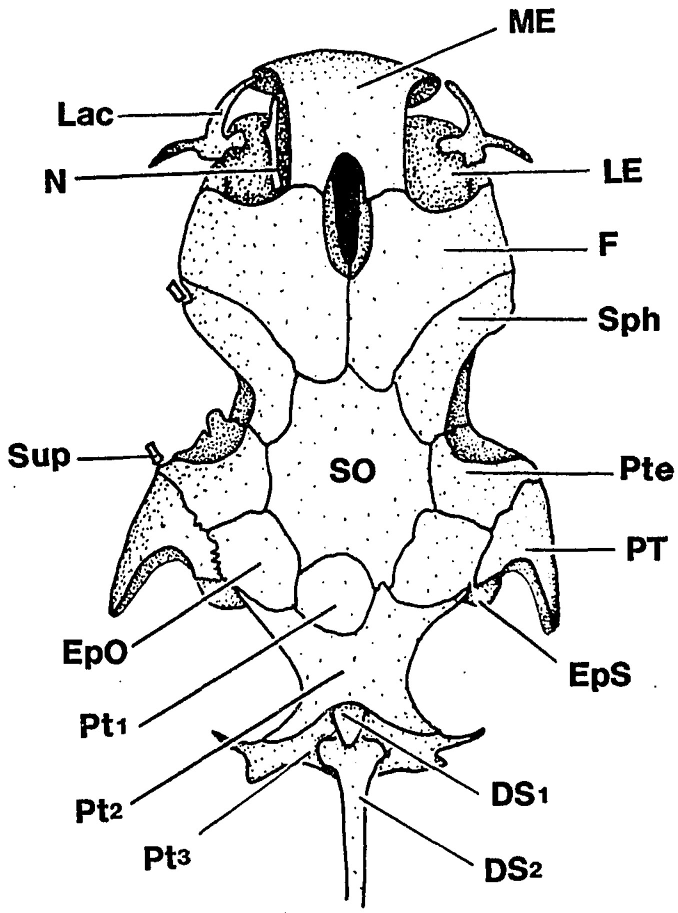



Fig. 16. Neurocranium, expanded pterygiophores, and dorsal spines of Glanidium leopardus, RMNH 28576, in dorsal view.

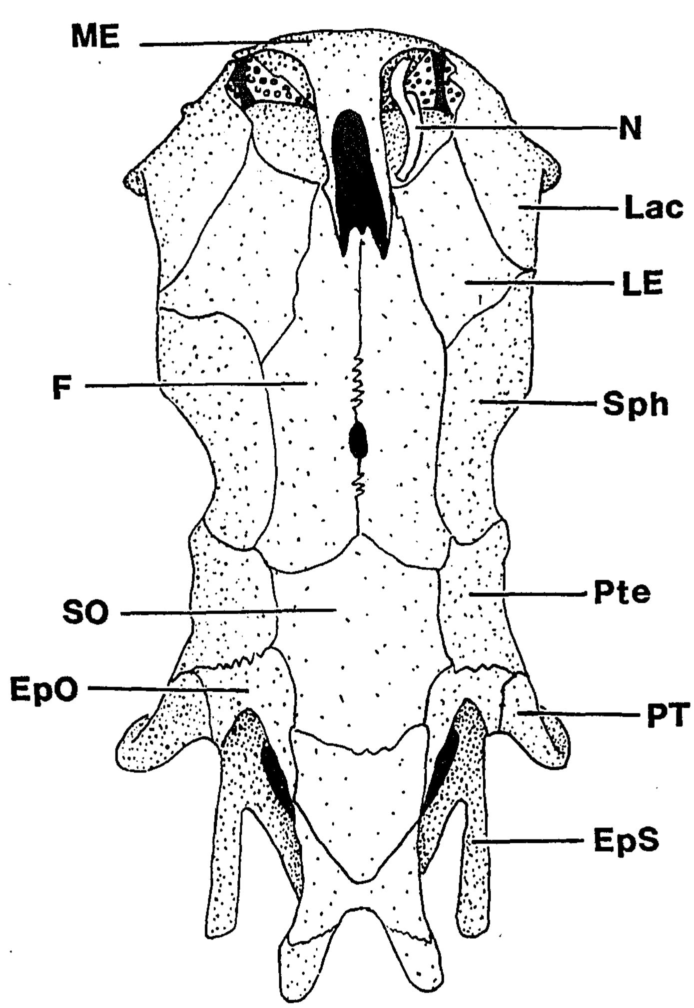



Fig. 17. Neurocranium and expanded pterygiophores of <u>Auchenipterus nigripinnis</u>, BMNH unregistered, in dorsal view.

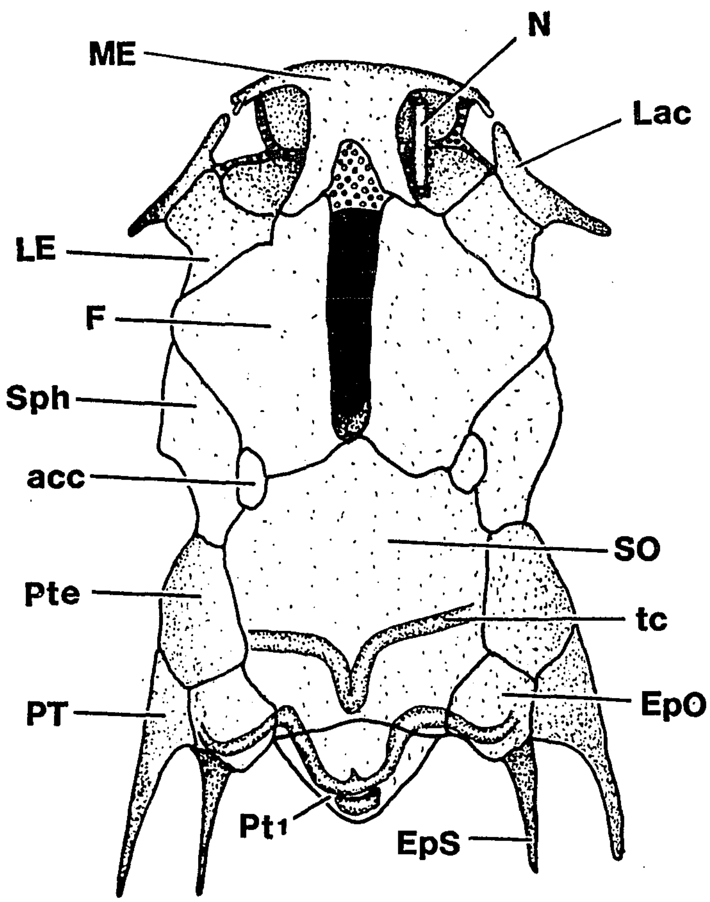



Fig. 18. Neurocranium and expanded first pterygiophore of <u>Entomacorus gameroi</u>, AMNH 55404, in dorsal view.

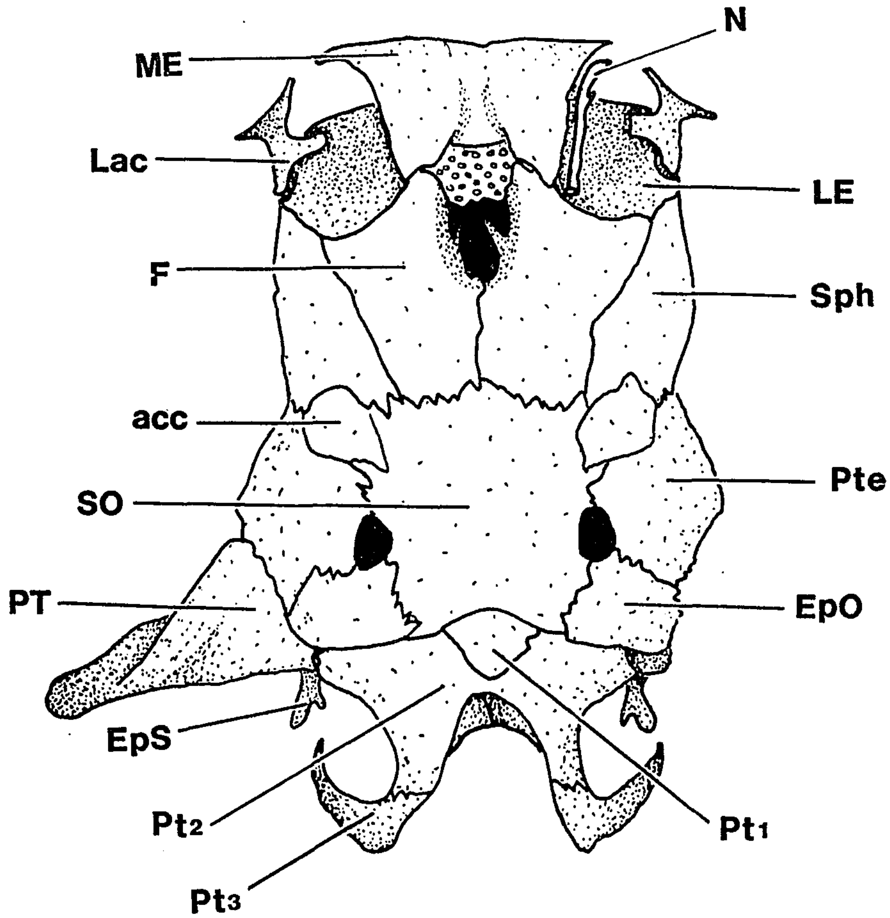



Fig. 19. Neurocranium and expanded pterygiophores of <u>Asterophysus</u> <u>batrachus</u>, ANSP 158294, in dorsal view.

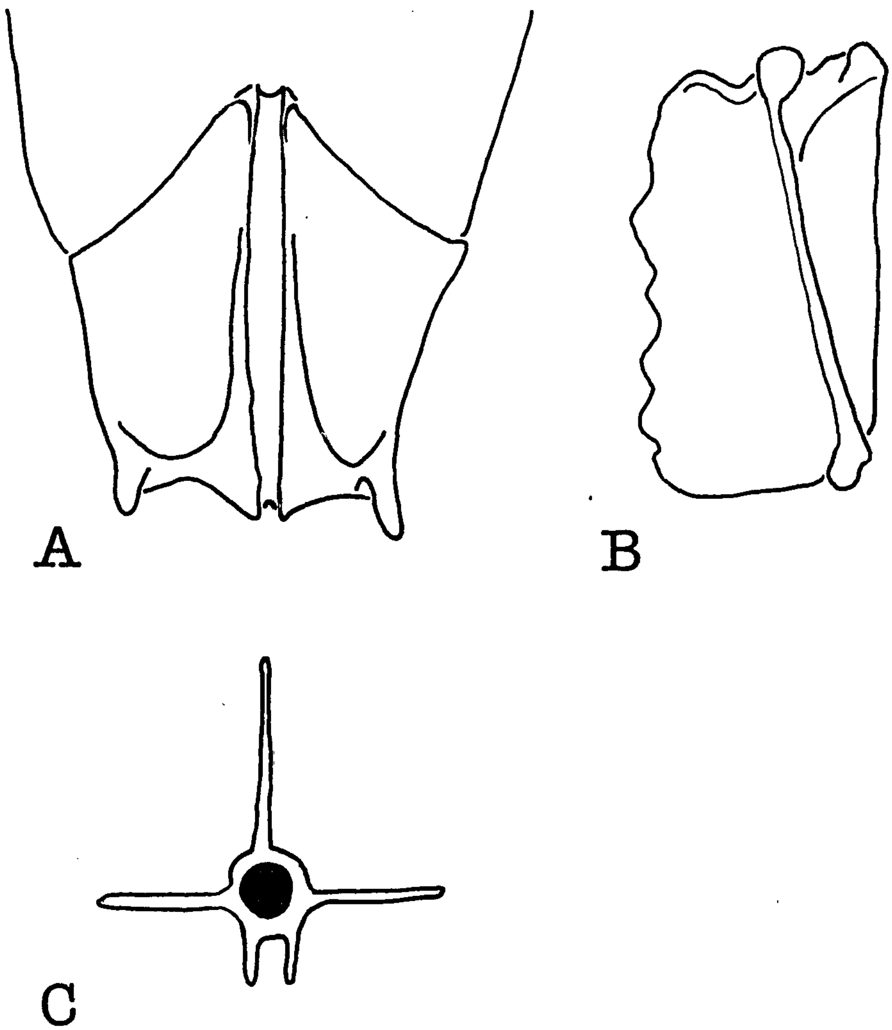



Fig. 20. Orbitosphenoid of an adult male Auchenipterus nuchalis, AMNH 3866, in ventral view (A), left lateral view (B), and posterior view (C).

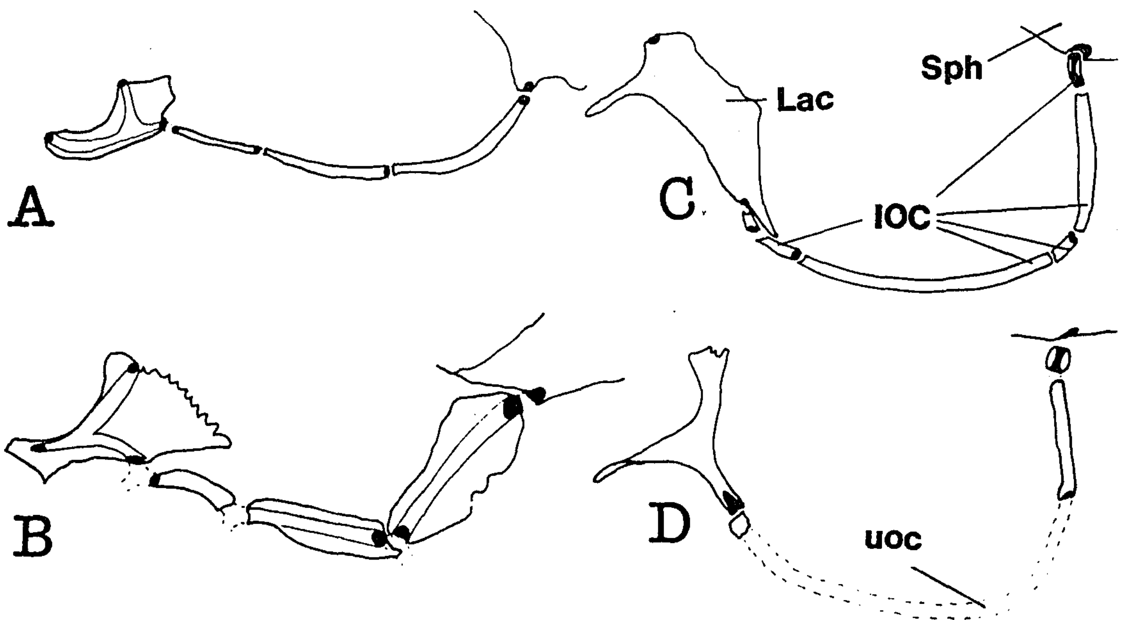



Fig. 21. Infraorbital canal ossifications, in left lateral view, of A) Anduzedoras microstomus AMNH 74491, B) Pterodoras angeli, AMNH 78915, C) Centromochlus heckelii, AMNH 55406, D) Tatia galaxias, AMNH 78898, E) Ageneiosus nigricollis, AMNH 78911, F) Ageneiosus ucayalensis, AMNH 3844, G) Auchenipterus demararae, AMNH 55352, H) Entomacorus gameroi, AMNH 55404, I) Trachelyopterichthys taeniatus, AMNH 78901, J) Pseudauchenipterus nodosus, AMNH 78903, K) Asterophysus batrachus, ANSP 158294, and L) Auchenipterichthys sp., AMNH 78902. Dashed lined indicate unossified portions of canal.

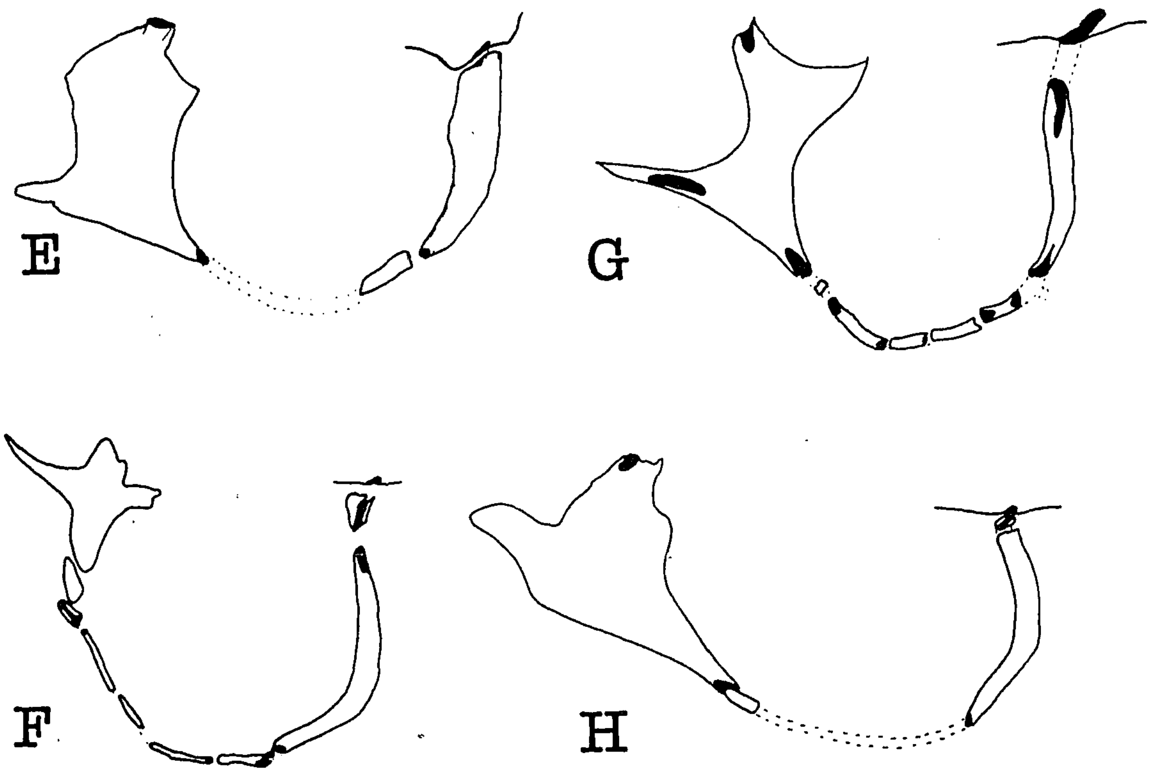
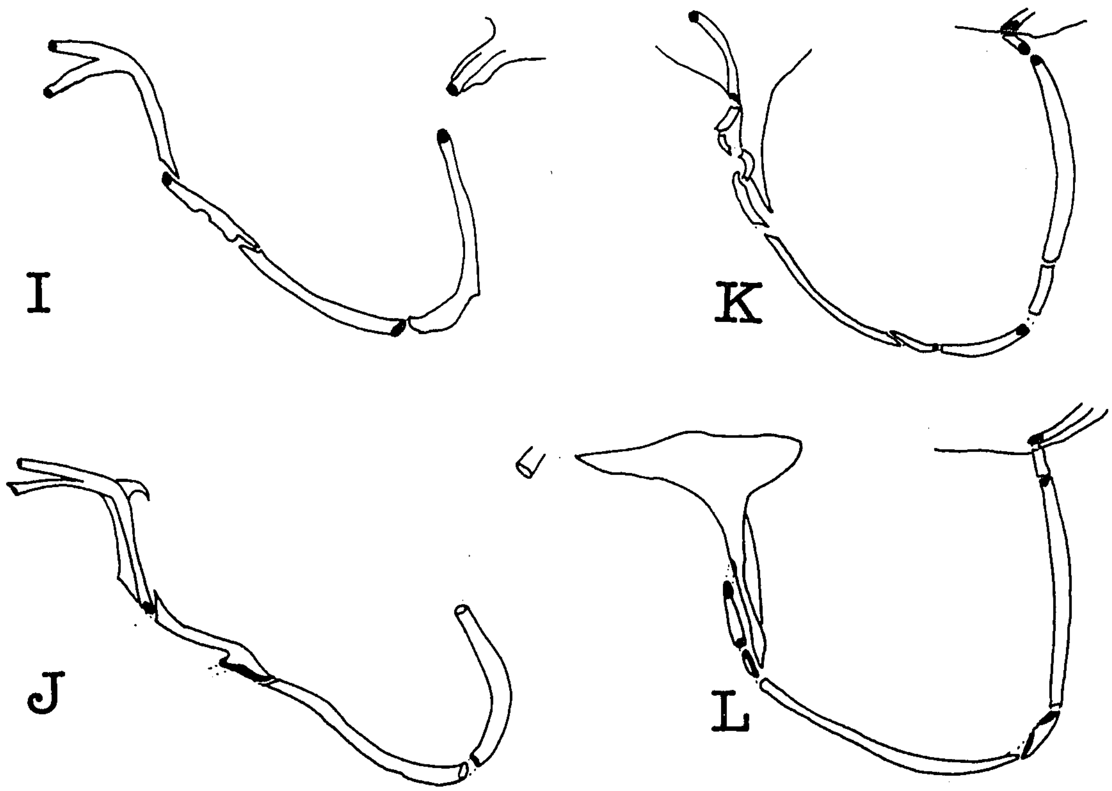



Fig. 21, continued.

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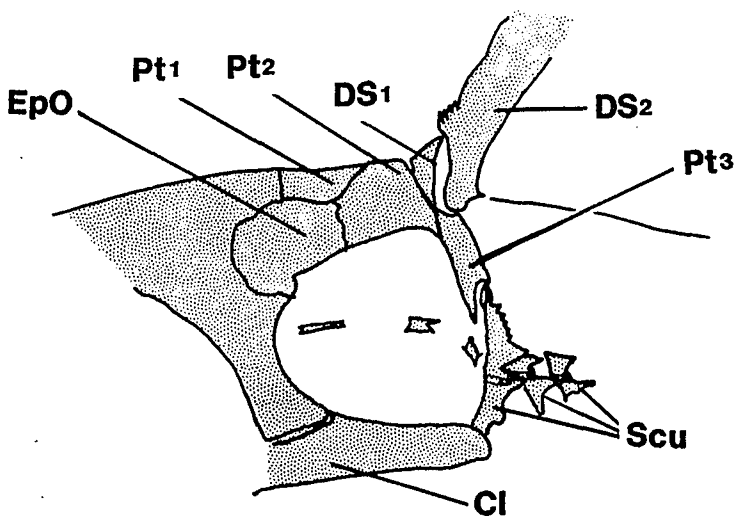



Fig. 22. Left lateral view of nuchal region of <u>Anduzedoras</u> <u>microstomus</u>, AMNH 74491, to showing first three of the lateral scute series characteristic of the Doradidae.

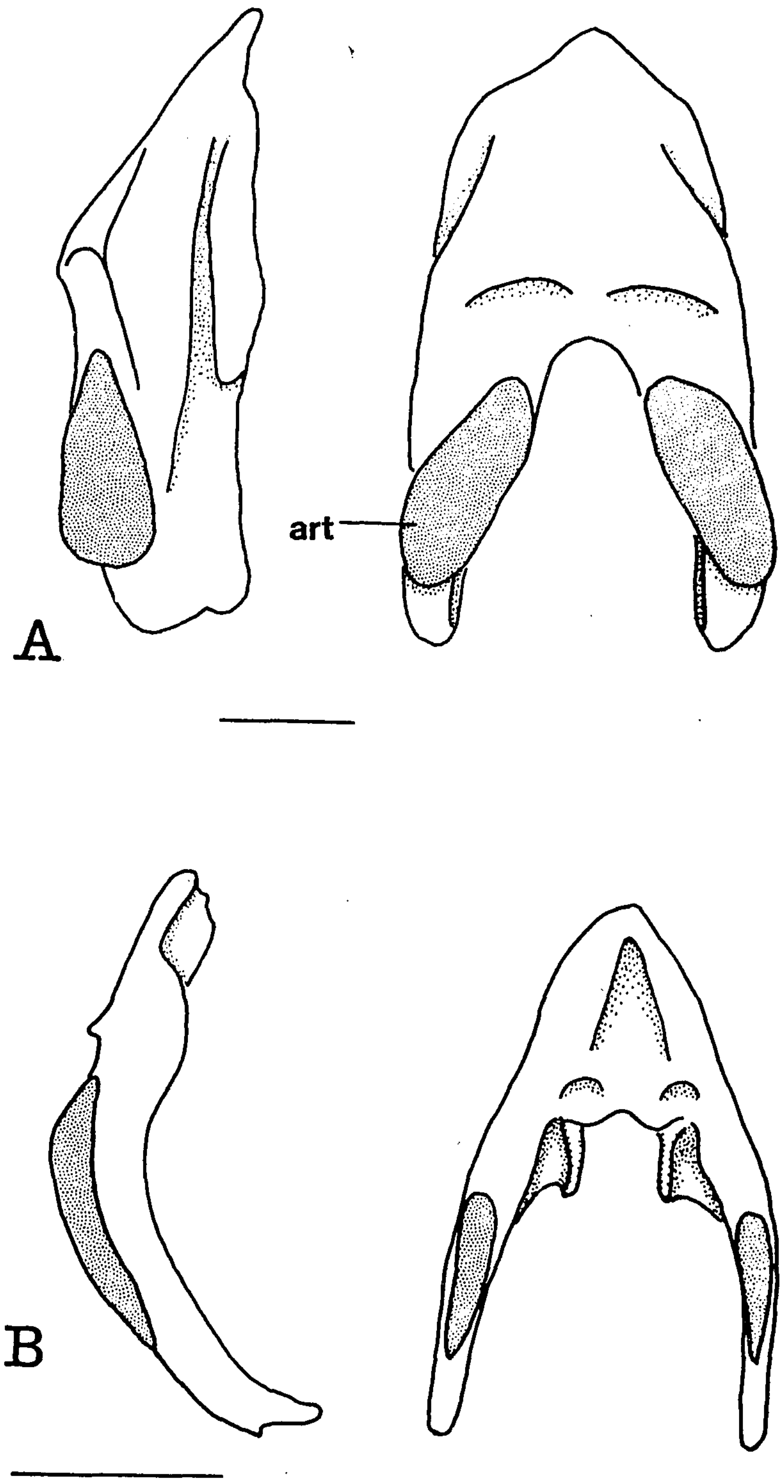
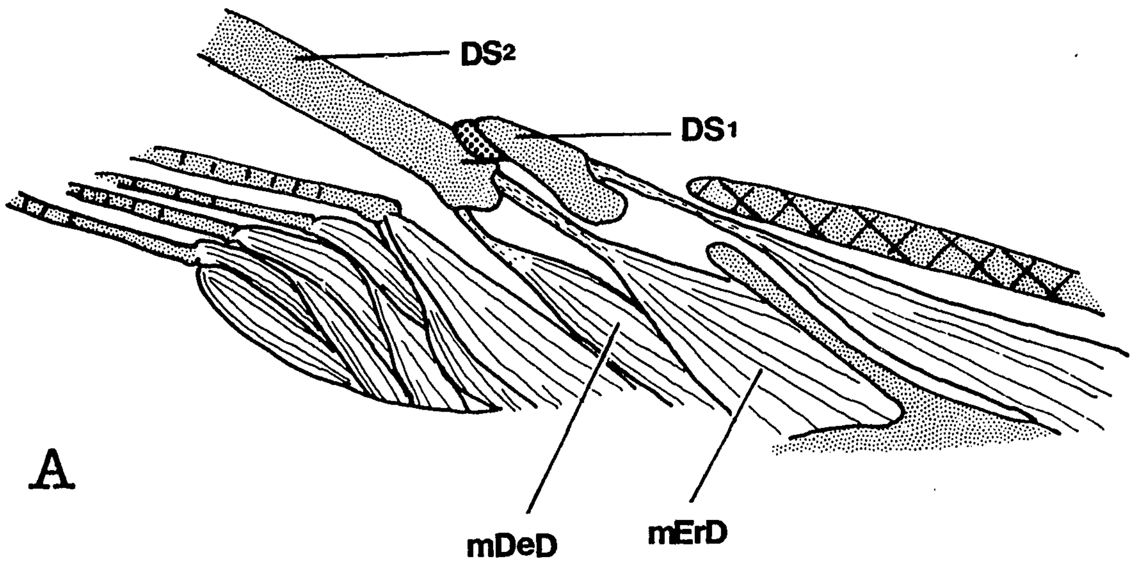



Fig. 23. First dorsal fin spine, in left lateral view (on left) and anterior view, (on right) of A) Ictalurus punctatus, AMNH 55927, and B) Doras lipophthalmus, AMNH 74489.




A

Fig. 24. Right lateral view of dorsal spines and attached muscles of A) Arius felis AMNH 52054, B) Synodontis njassae, AMNH 55409, C) Doras lipophthalmus AMNH 74489, and D) Centromochlus heckelii, AMNH 55406. Epaxial musculature and parts of some bones removed to facilitate viewing. Bones indicated by fine stipple, cut bones indicated by crosshatching, ligaments indicated by bold stipple.

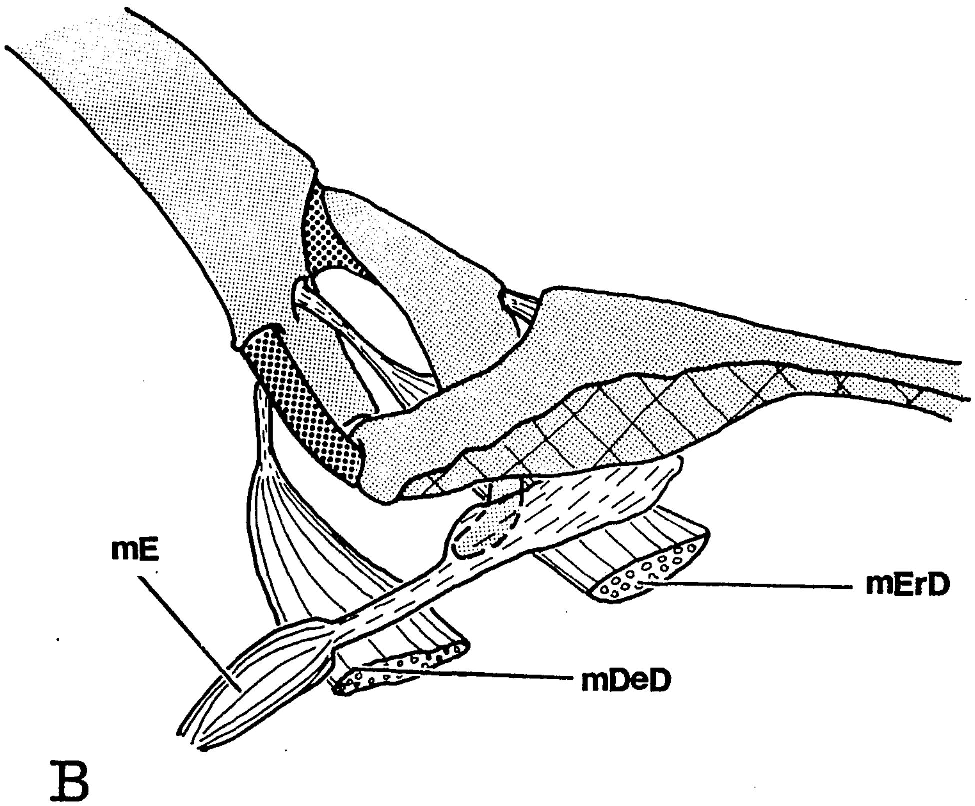



Fig. 24, continued.

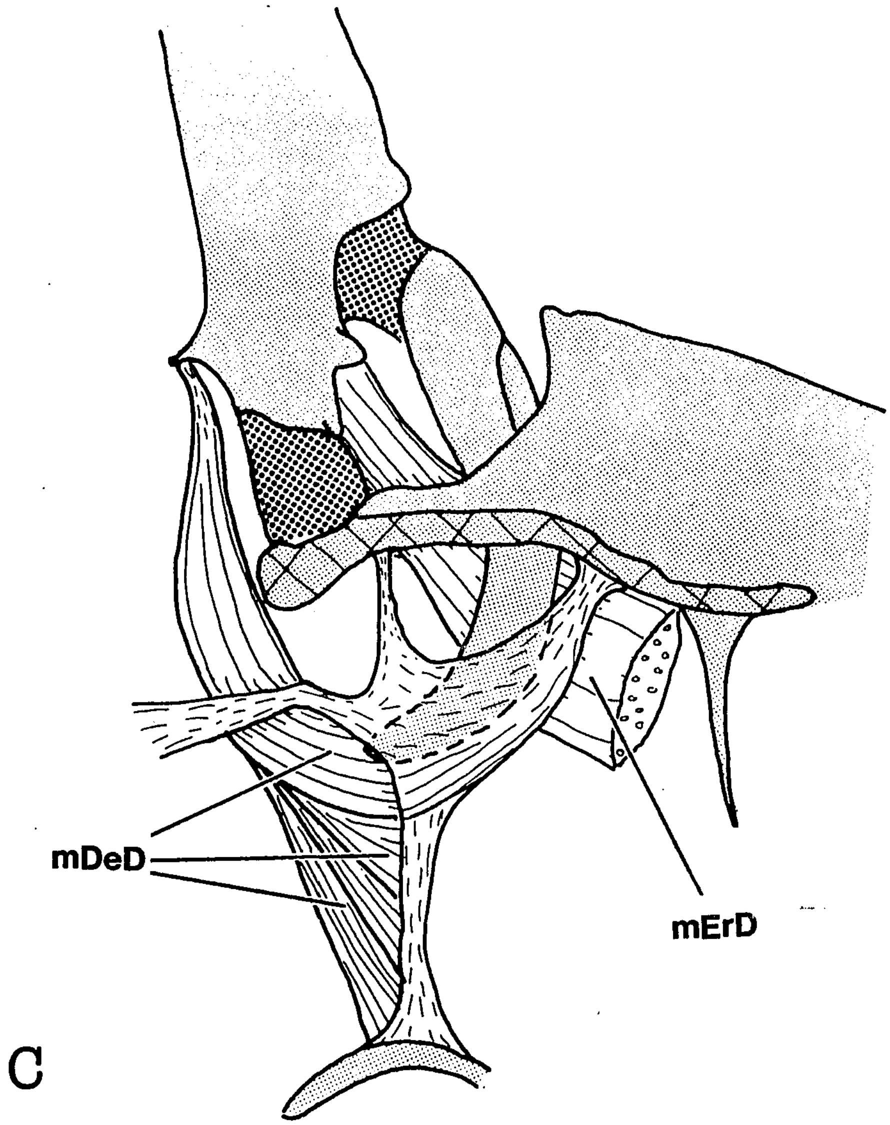



Fig. 24, continued.

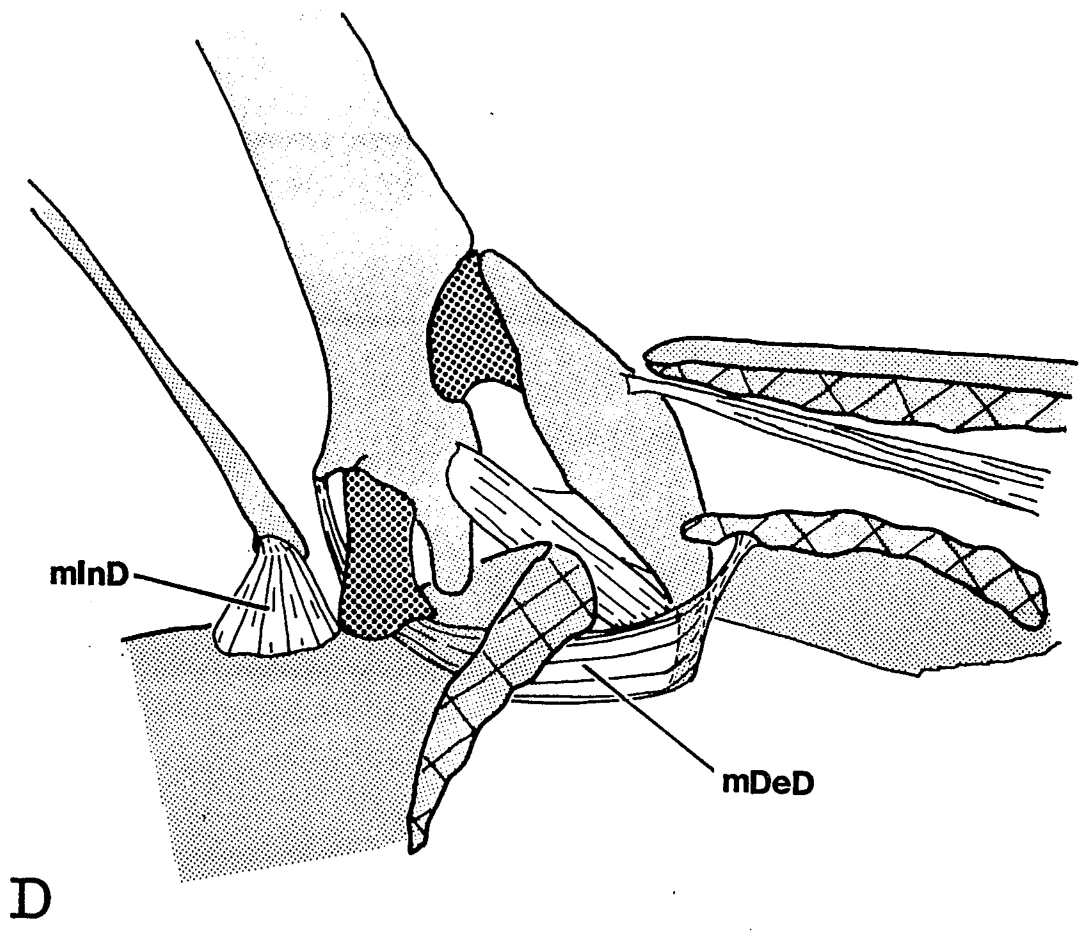



Fig. 24, continued.

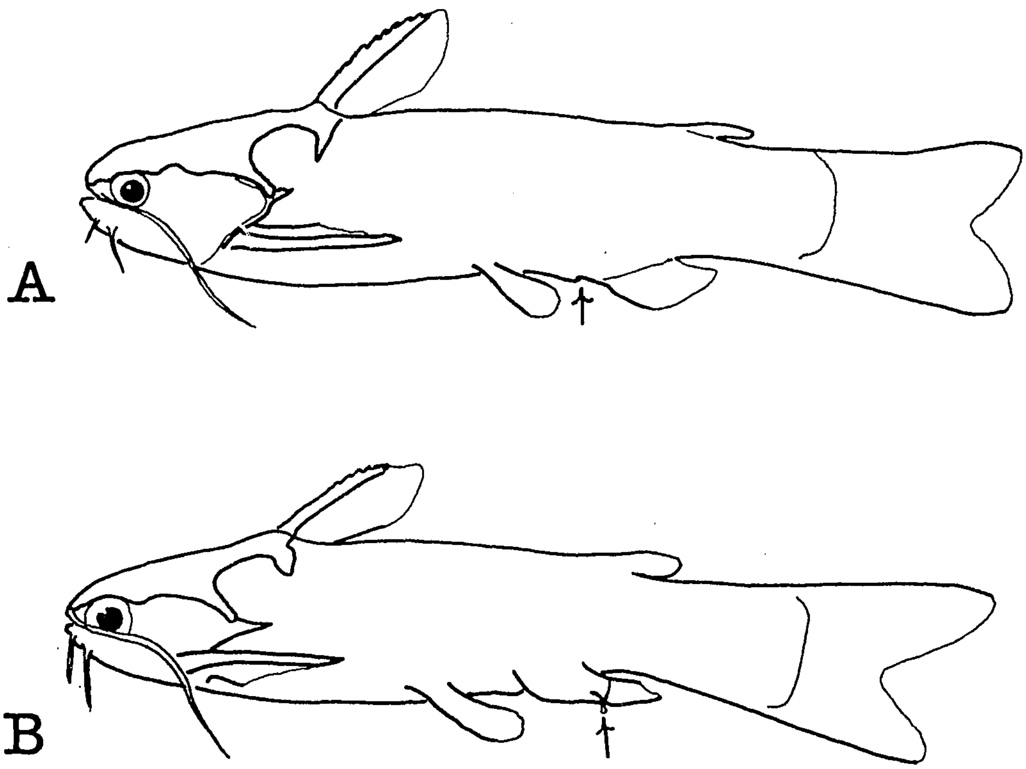



Fig. 25. Left lateral view of <u>Tatia</u> <u>intermedia</u> ZMA 105.791, Position of urogenital pore indicated by an arrow, A) female, B) male.

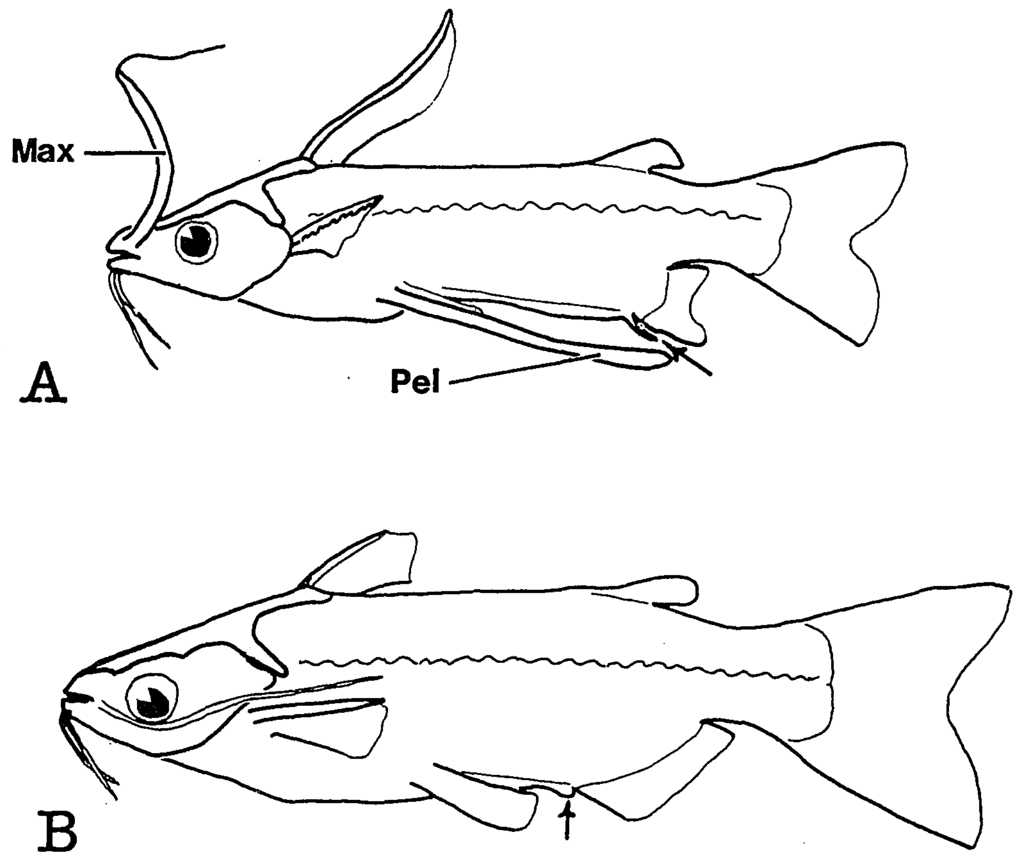



Fig. 26. Left lateral view of <u>Entomacorus gameroi</u>, ANSP 158849, A) male, B) female, showing sexual dimorphism of the maxillary barbel, dorsal-fin spine, size of first pelvic-fin ray,and placement of orientation of anal-fin base.

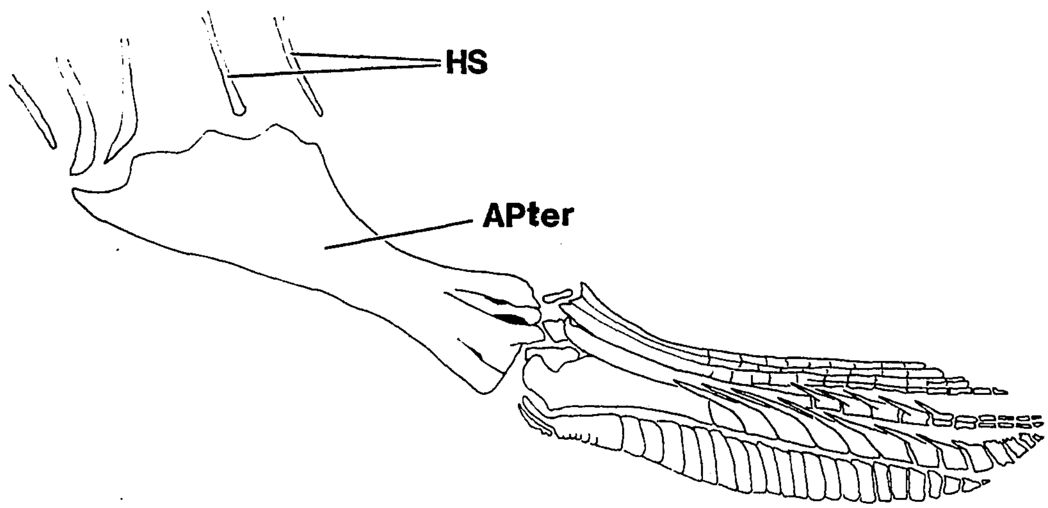



Fig. 27. Anal-fin rays and pterygiophores of an adult male Centromochlus heckelii, AMNH 55406, in left lateral view. All basal radial elements are fused into a single element which does not penetrate between the hemal spines.

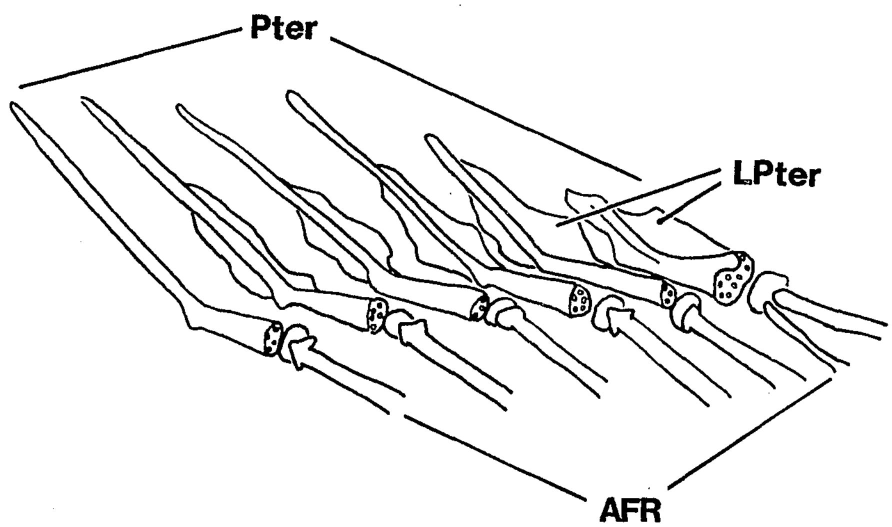



Fig. 28. Posterior four anal-fin pterygiophores in _Auchenipterus_ _nuchalis_, AMNH 3866, showing median lamina characteristic of _Auchenipterus_ and _Epapterus_.

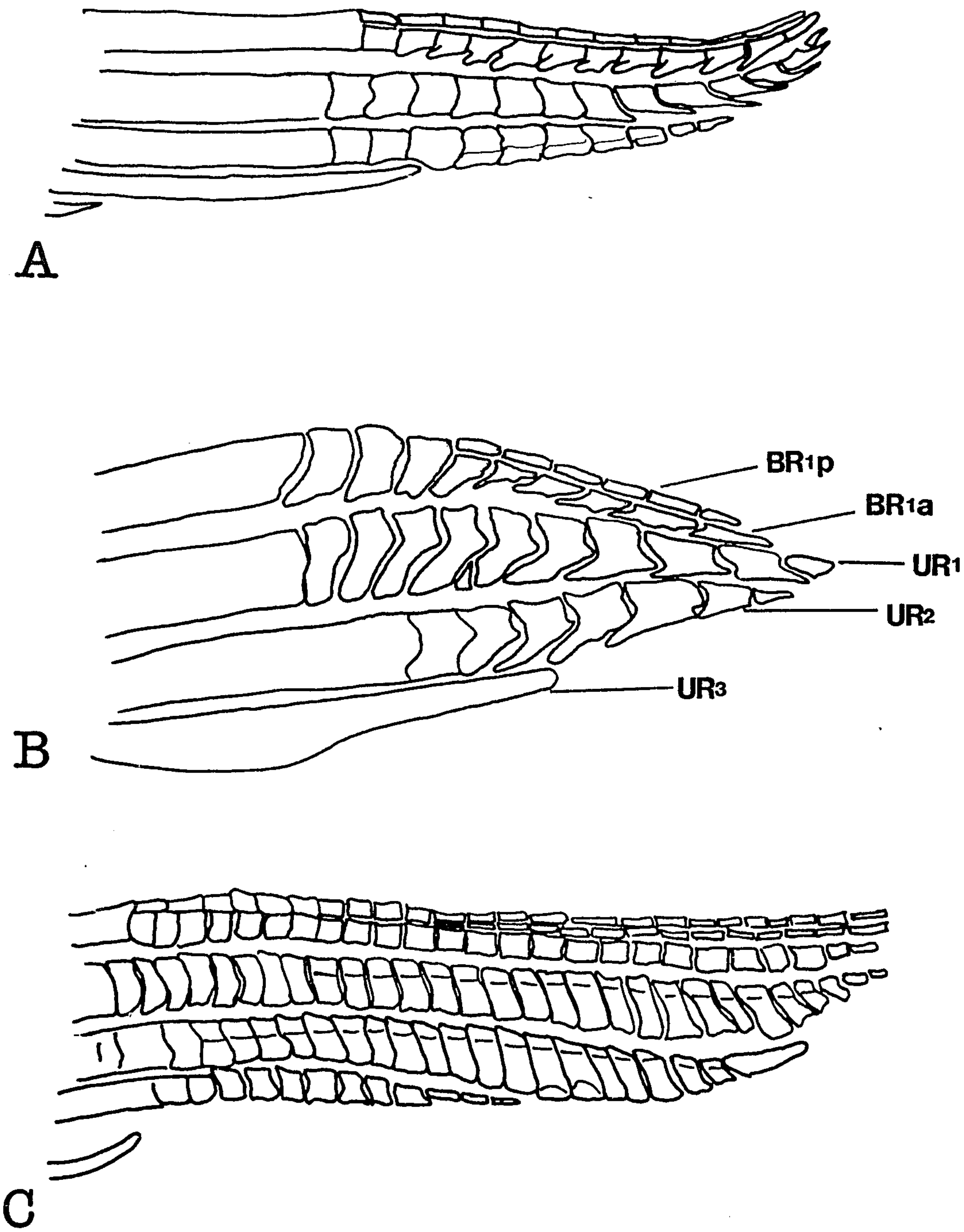



Fig. 29. Anterior anal-fin rays, in left lateral view, of mature males of A) Tatia galaxias, AMNH 78898, B) Genus b sp. AMNH 74441, and C) Glanidium leopardus ZMA 105.854.

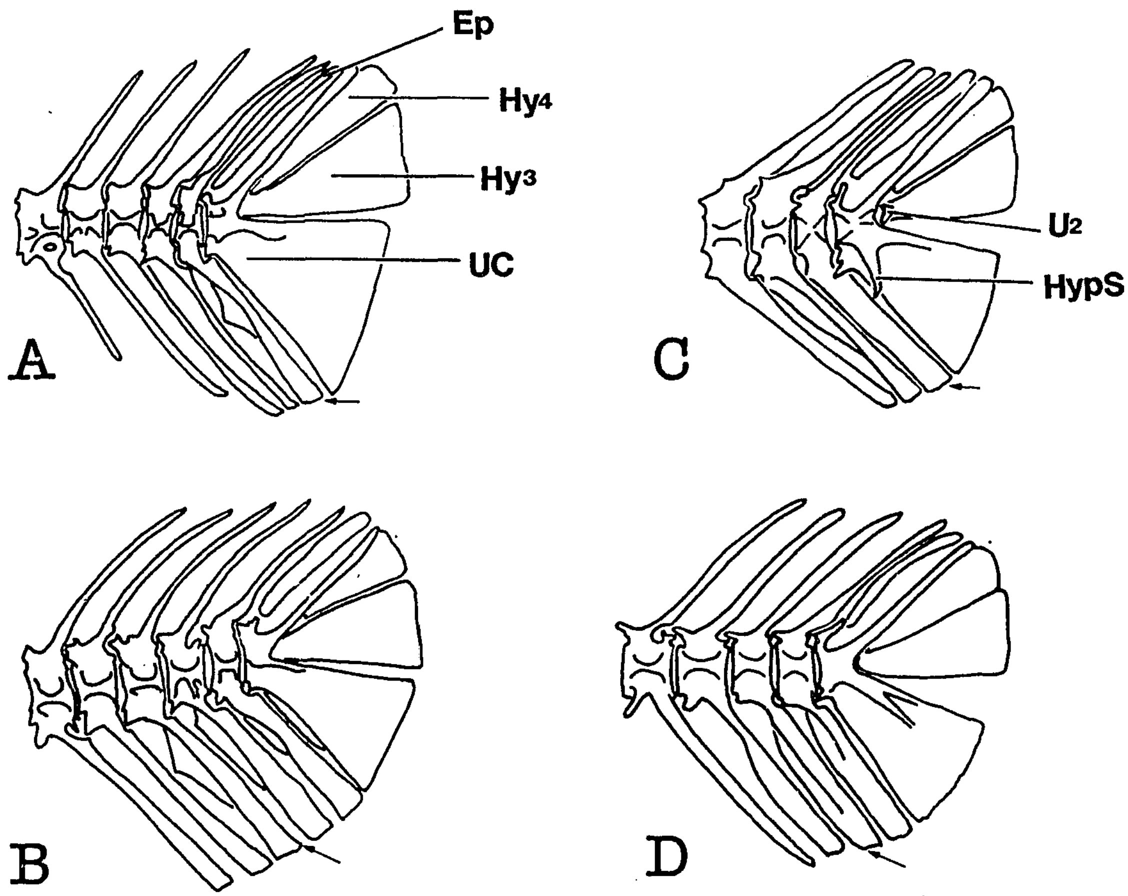



Fig. 30. Caudal fin skeletons, in left lateral view, of A) Tatia sp. AMNH 74443, B) Trachelyopterus striatulus, AMNH 8675, C) Entomacorus gameroi, AMNH 55404, and Auchenipterichthys thoracatus, AMNH 12700. Point of attachment of first unbranched ray of lower lobe of caudal fin is indicated by an arrow.

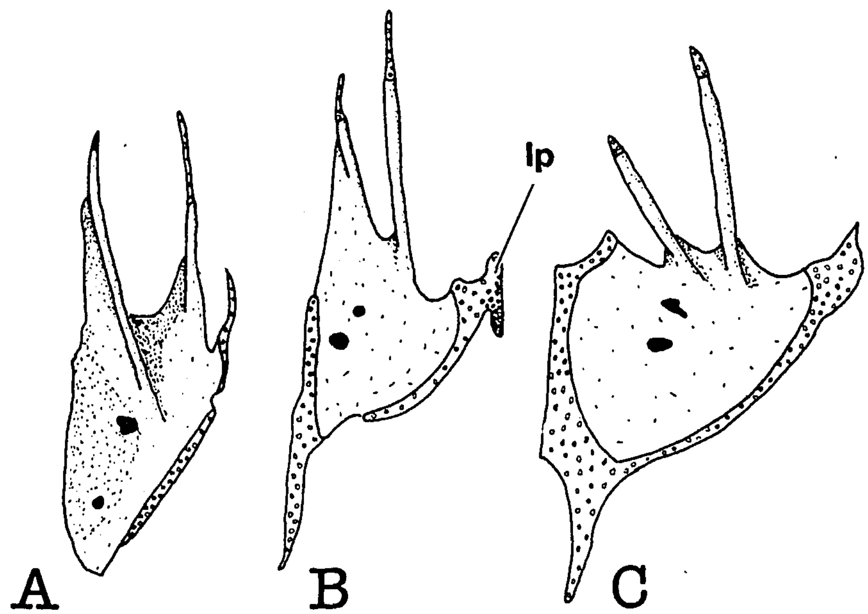



Fig. 31. Left half of basipterygium, in ventral view, of A) Auchenipterus demerarae, AMNH 55352, Centromochlus heckelii AMNH 55406, and Trachycorystes sp. USNM 273044.

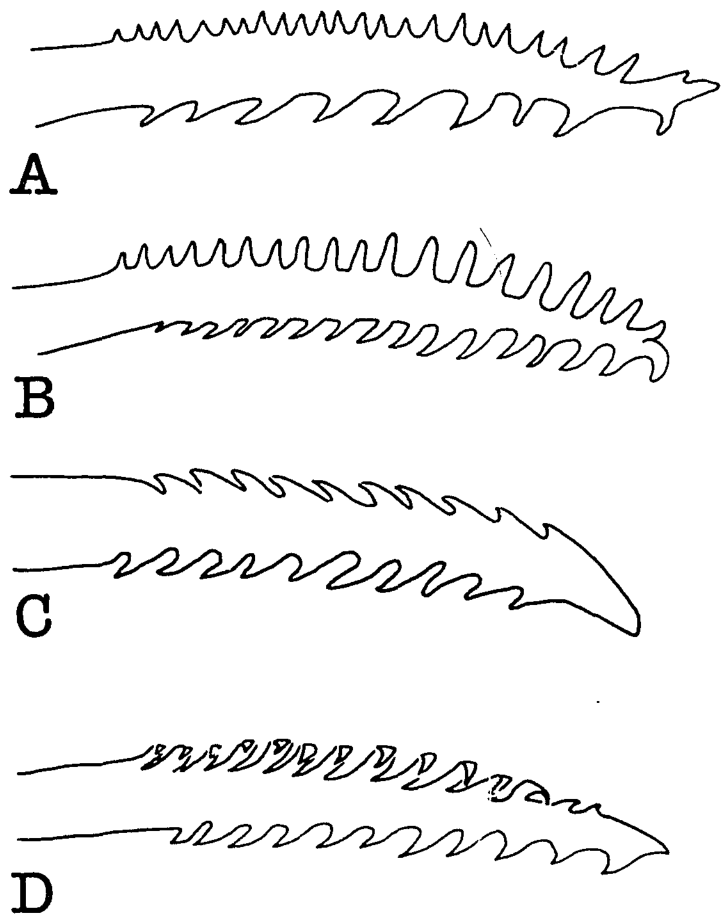



Fig. 32. Left pectoral spine, in ventral view, of A) Genus a sp.(Colombia) ANSP 134872, B) Tatia intermedia, ZMA 105.791, C) Tocantinsia depressa, 13398, and D) Entomacorus gameroi, ANSP 158849, spine base not illustrated.

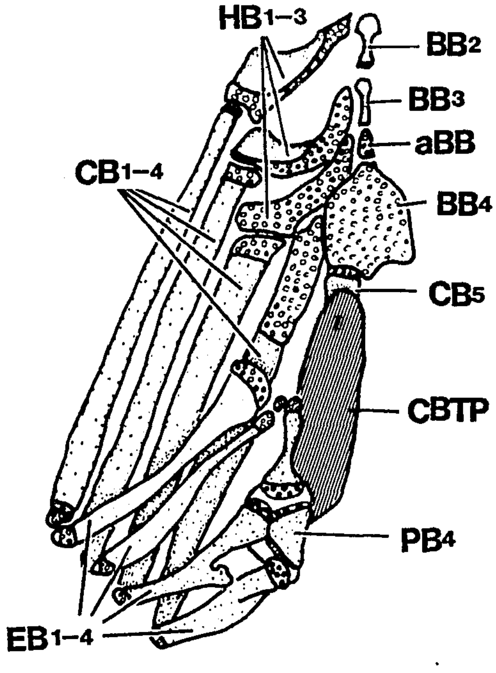



Fig. 33. Gill arch elements, in dorsal view, of Ageneiosus guianensis, AMNH 55349. Right elements not drawn.

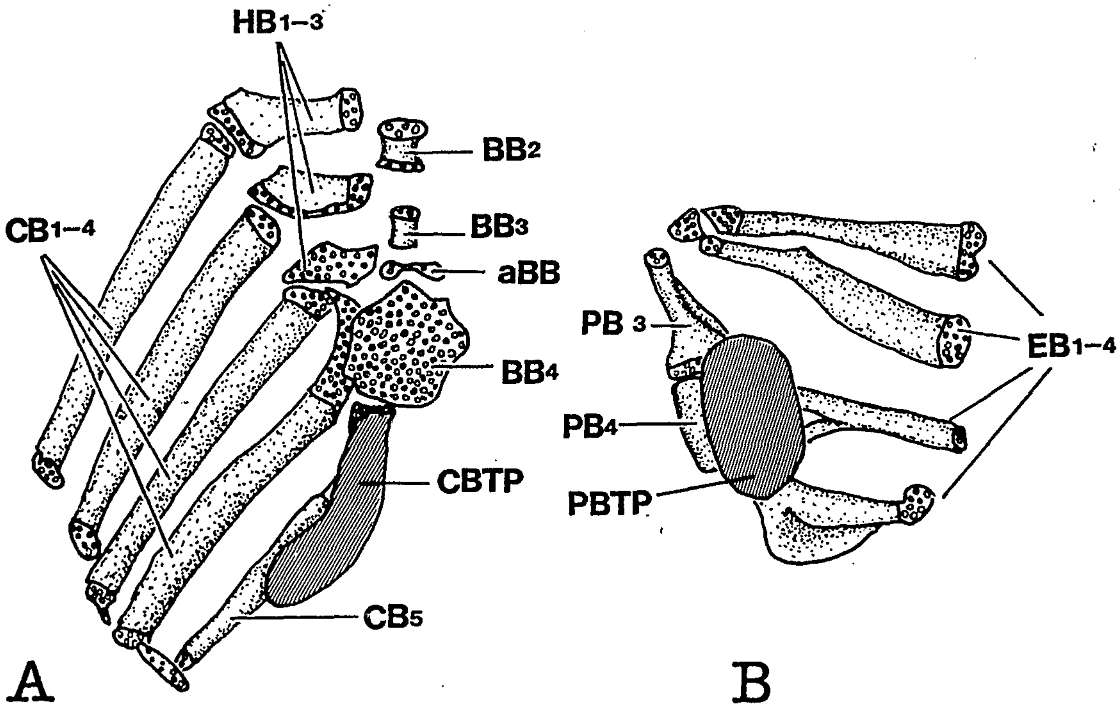



Fig. 34. Gill arch elements of Trachycorystes sp., USNM 273044, A) lower elements, in dorsal view, B) upper elements, in ventral view. Tooth plates are indicated in hatching.

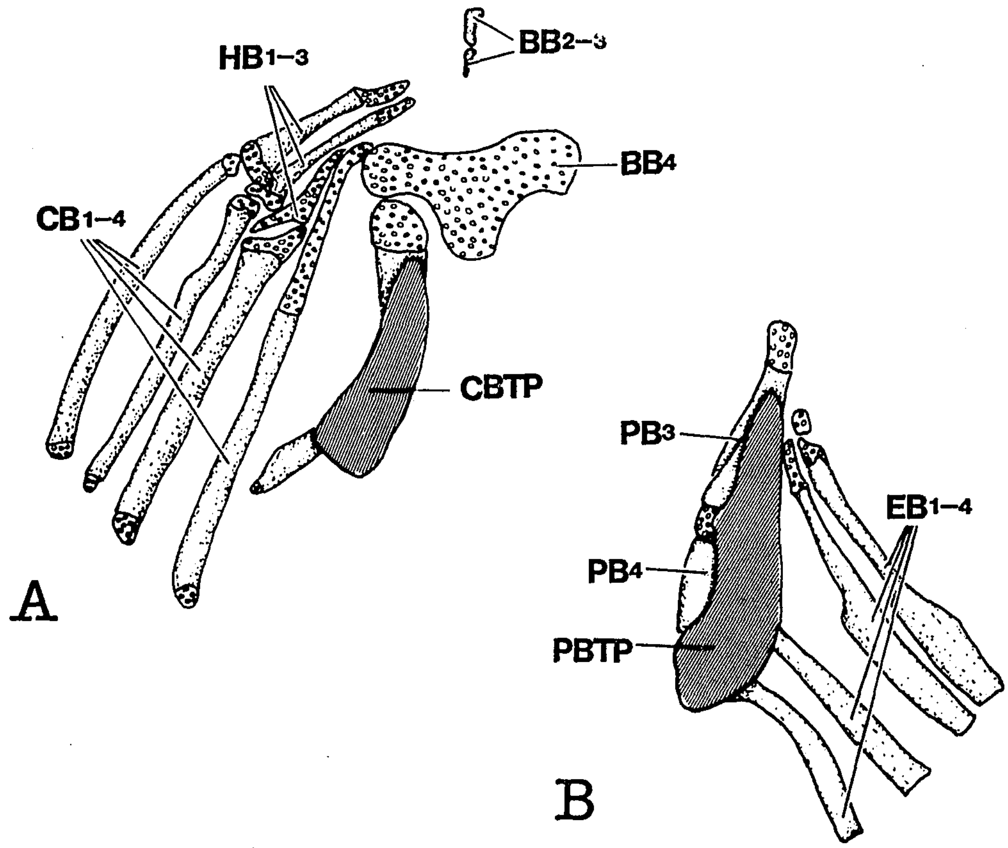



Fig. 35. Gill arch elements of Asterophysus batrachus, ANSP 158294, A) lower elements, in dorsal view, B) upper elements, in ventral view. Tooth plates are indicated in hatching.

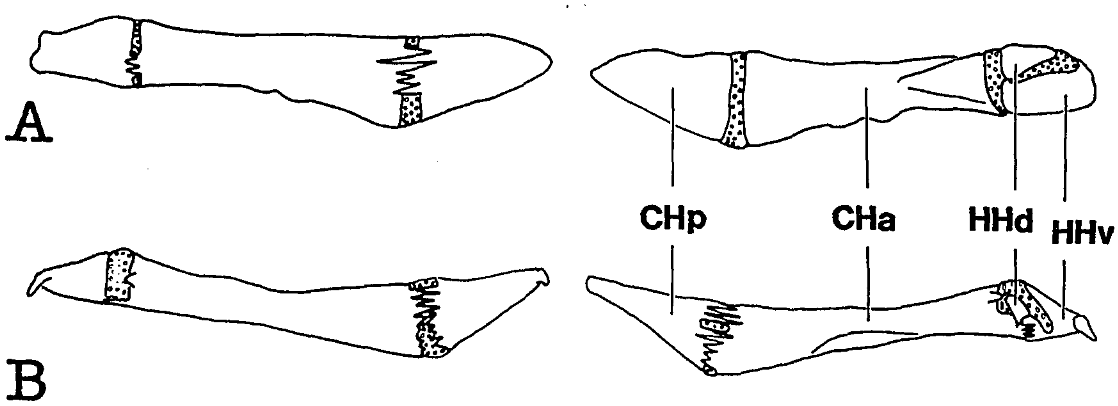



Fig. 36. Left hyoid bar of A) Trachycorystes sp., USNM 273044, and B) Ageneiosus guianensis, AMNH 55349. Lateral view on left and medial view on right.

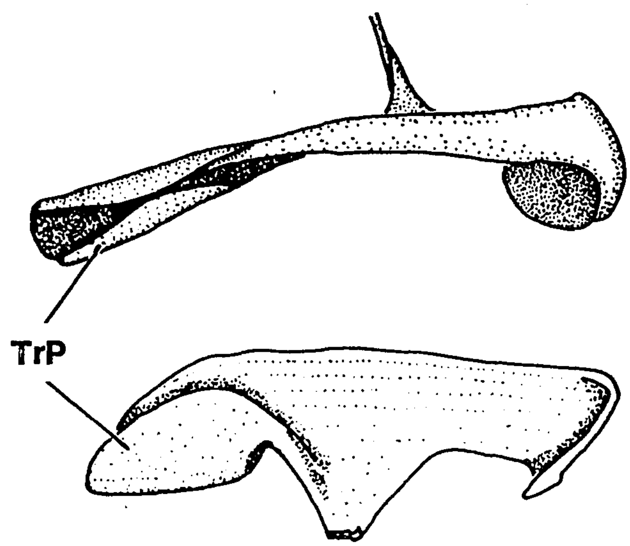



Fig. 37. Right tripus of Auchenipterus nuchalis, AMNH 3866, in lateral view (above) and ventral view (below).

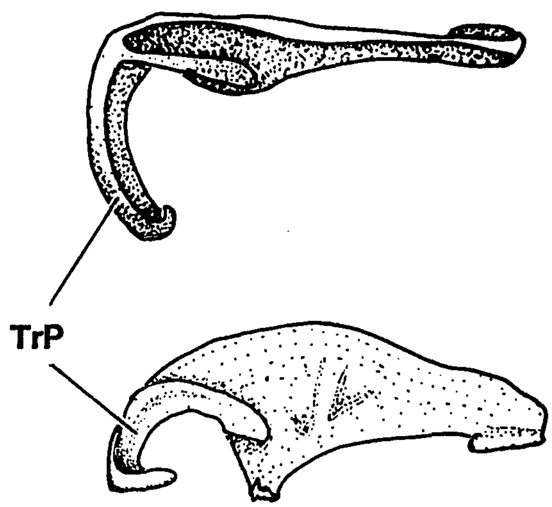



Fig. 38. Right tripus of Synodontis decorus, AMNH 55626, in lateral view (above) and ventral view (below).

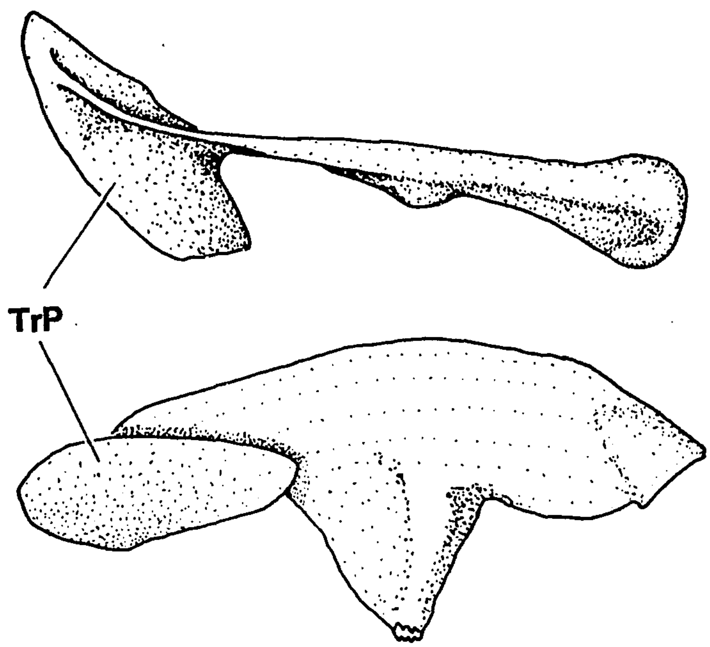



Fig. 39. Right tripus of Ageneiosus brevifilis, AMNH 56229 SD, in lateral view (above) and ventral view (below).

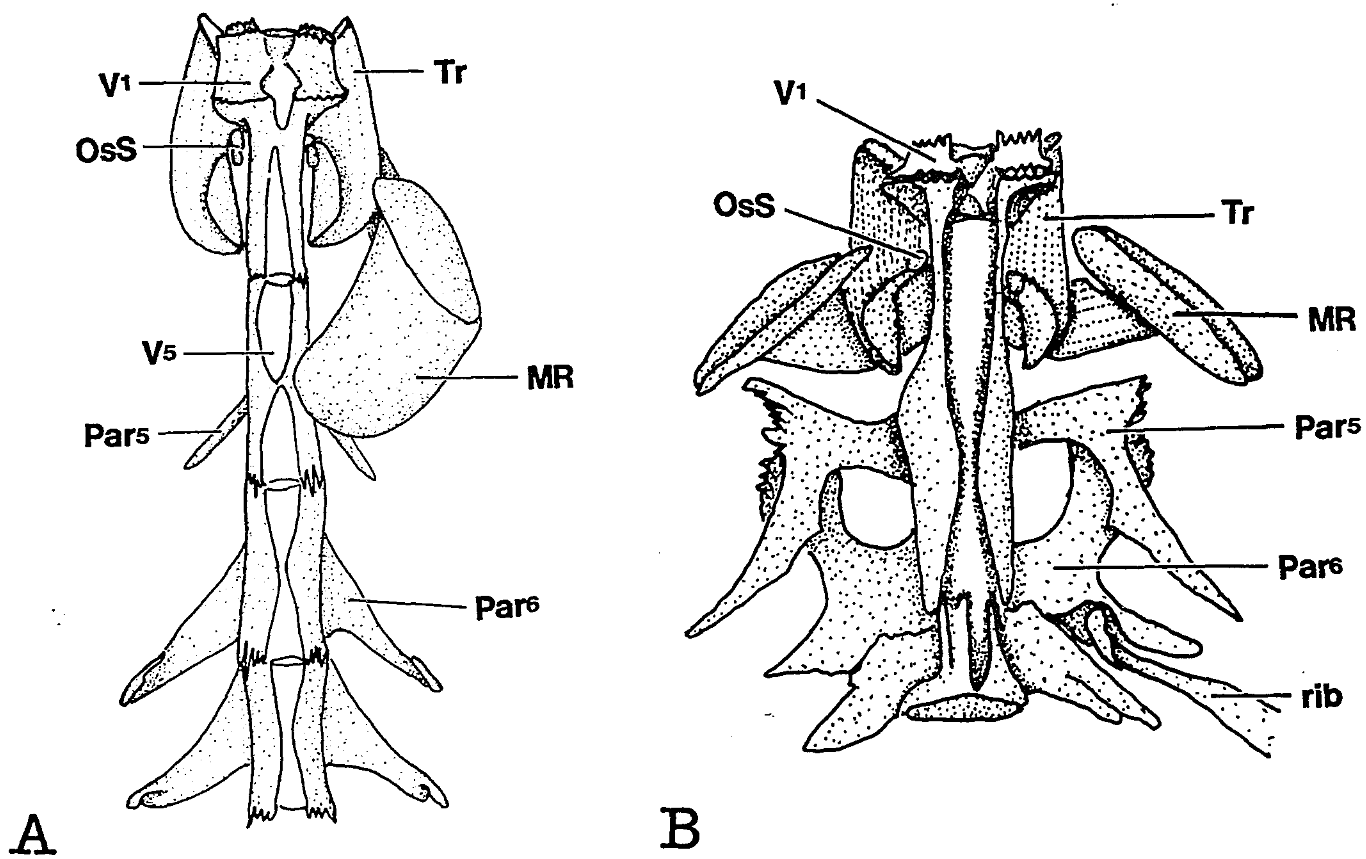



Fig. 40. Anterior vertebrae and associated bones, in ventral view, of A) Centromochlus heckelii, AMNH 55406, and B) Auchenipterus nuchalis, AMNH 3866. Left Müllerian ramus removed from Centromochlus illustration.

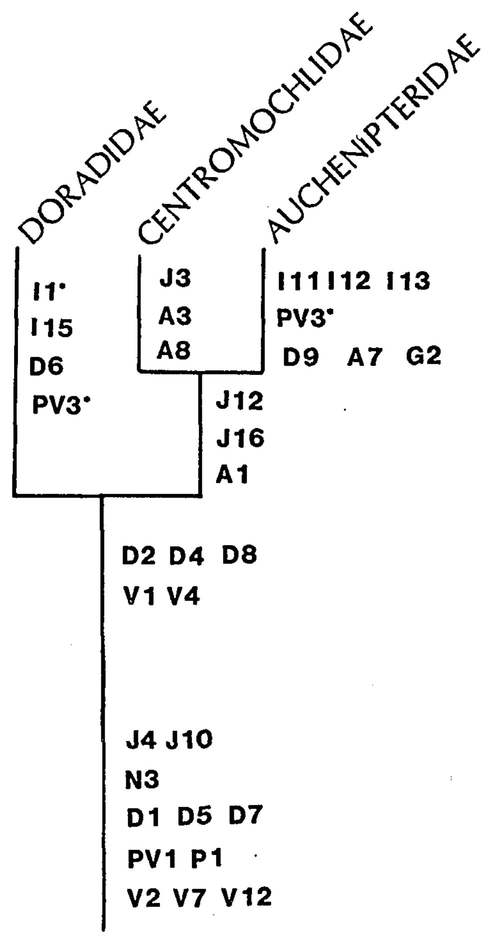



Fig. 41. Summary of derived characters of the superfamily Doradoidea and each of the included families. Numbers correspond to characters discussed in the text. Starred numbers indicate that the character is found elsewhere within the Doradoidea. Characters at the base of the branching diagram are in two clusters. The upper cluster includes characters known to occur only in the Doradoidea, those of the lower cluster have been found elsewhere in siluriform fishes, but may still be defining for the Doradoidea.

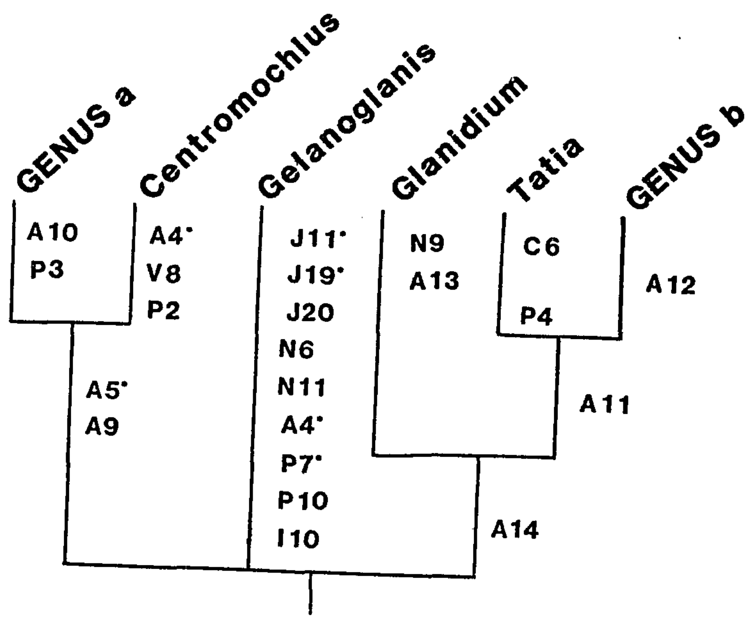



Fig. 42. Summary of derived characters of the family Centromochlidae. Numbers correspond to characters discussed in the text. Starred numbers indicate that the character is found elsewhere within the Doradoidea.

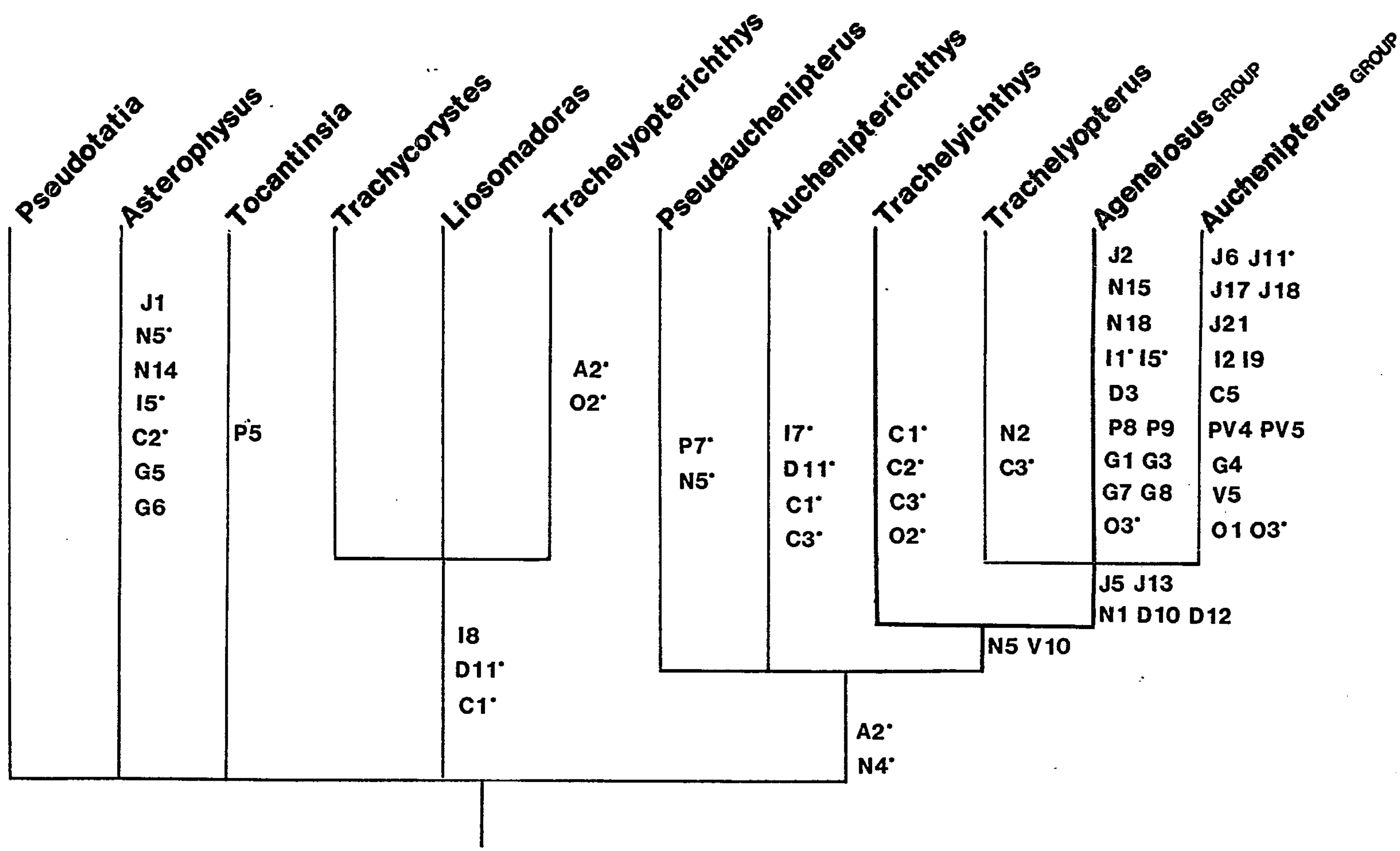



Fig. 43. Summary of derived characters of the family Auchenipteridae. Numbers correspond to characters discussed in the text. Starred numbers indicate that the character is found elsewhere within the Doradoidea.

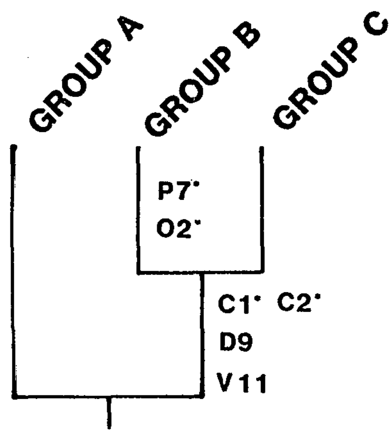



Fig. 44. Summary of derived characters of the genus <u>Trachelyopterus</u>. Numbers correspond to characters discussed in the text. Starred numbers indicate that the character is found elsewhere within the Doradoidea.

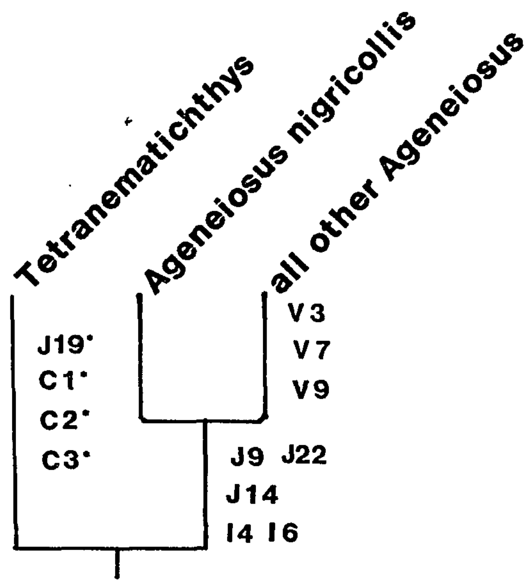



Fig. 45. Summary of derived characters of the Ageneiosus group. Numbers correspond to characters discussed in the text. Starred numbers indicate that the character is found elsewhere within the Doradoidea.

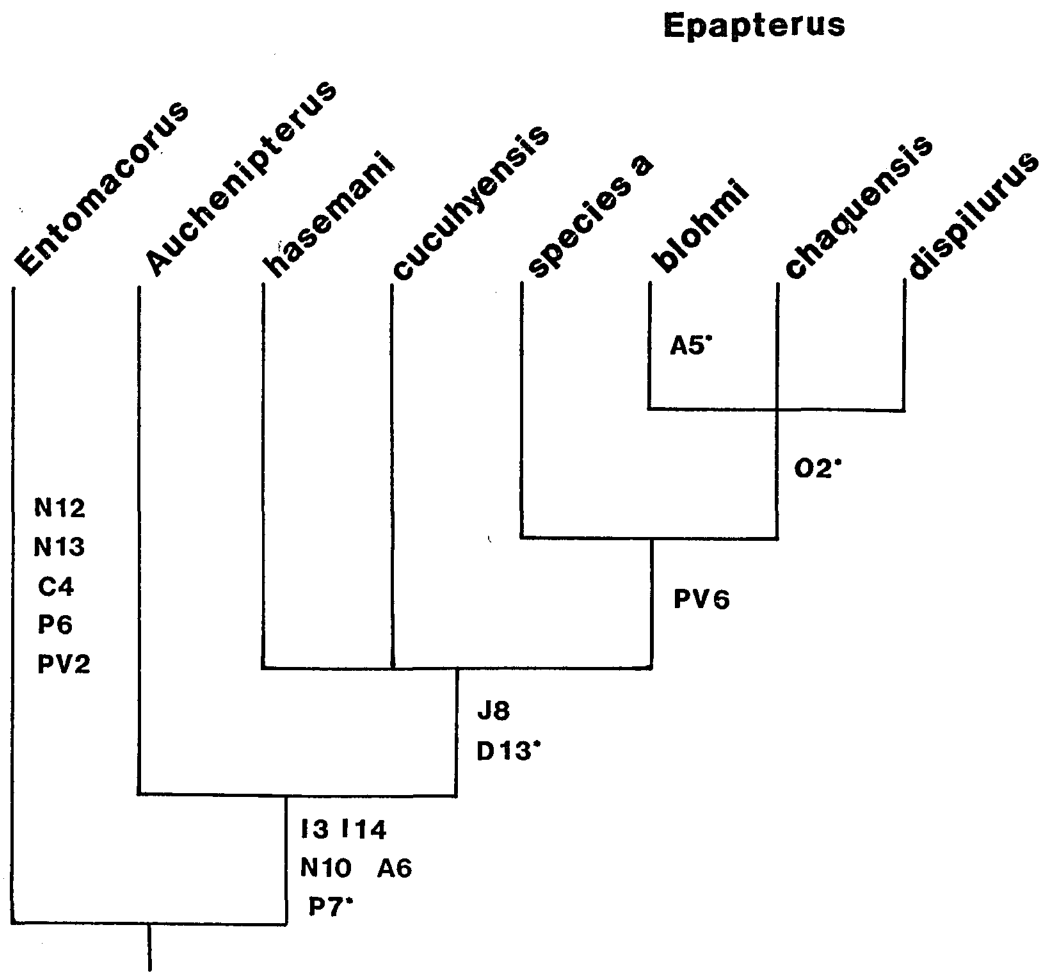



Fig. 46. Summary of derived characters of the *Auchenipterus* group. Numbers correspond to characters discussed in the text. Starred numbers indicate that the character is found elsewhere within the Doradoidea.

# References Cited

Alexander, R. McN.

1965. Structure and function in the catfish. J. Zool., 148:88-152.

Baskin, J.

1972. Structure and relationships of the Trichomycteridae. Unpublished doctoral dissertation, The City University of New York. 217 pp., 86 figs.

Berg, C.

1901. Comunicaciones ictiologicas. Com. Mus. Nac. Buenas Aires, 1:293-311.

Bleeker, P.

1858. Ichthyologiae archipelagi indici, Prodromus, 1(Siluri), Batavia, 357 pp.

1862a. Atlas Ichthyologique, 2:1-112, pls. 69-101.

1862b. Notice sur les genres Trachelyopterichthys, Hemicetopsis et Pseudocetopsis. Comptes-rendus de l'Acad. R. des Sci., Section Sciences exactes., 14:400-403.

1863. Systema silurorum revisum. Neder. Tijdschr. Dierk., 1:87-218.

1864. Description des espêces de silures de Suriname conservées aux Musées de Leide et D'Amsterdam. Nat. Verh. Hall. Maatsch. Wetensch. (2) 20:1-104, 16 pls.

Bloch, M. E.

1794. Naturgeschichte der ausländischen Fische. Berlin., pt. 8, 174 pp., pls.

Boeseman, M.

1953. Scientific results of the Surinam expedition 1948-1949. Part II. Zoology. No. 2. The fishes(1). Zool. Meded., 32(1):1-24.

Böhlke, J. E.

1951. Description of a new auchenipterid catfish of the genus Pseudepapterus from the Amazon basin. Stanford Ichthyol. Bull., 4(1):38-40.

1980. Gelanoglanis stroudi; a new catfish fron the Rio Meta system in Colombia (Siluriformes, Dordadidae, Auchenipterinae), Proc. Acad. Nat. Sci. Philadelphia, 132:150-155.

Borodin, N. A.

1927. Some new catfishes from Brazil. Am. Mus. Novitates, (266):1-7.

Boulenger, G.

1895. Abstract of a report on a large collection of fishes formed by Dr. C. Ternetz at various localities in Matto Grasso and Paraguay, with descriptions of new species. Proc. Zool. Soc. London, (1895):523-529.

Britski, H. A.

1972. Sistemática e evolução dos Auchenipteridae e Ageneiosidae (Teleostei, Siluriformes). Unpublished doctoral dissertation, Universidade de São Paulo, Brazil, 146 pp., 60 fig., 6 maps.

Brown, B. A., and C. J. Ferraris, Jr.

IN PRESS Comparative osteology of the Asian catfish family Chacidae, with the description of a new species from Burma. Amer. Mus. Novitates, 16 pp.

Burgess, W. E.

1982. First aquarium spawning of the woodcat, <u>Trachycorystes insignis</u>. Tropical Fish Hobbyist, 30(12):84-89.

Castelnau, F. de

1855. Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para. Poissons. P. Bertrand, Paris. i-xii, 112 pp, 50 pls.

Chardon, M.

1968. Anatomie compareé de l'appareil de Weber et des structures connexes ches les Siluriformes. Mus. Roy. de l'Afr. Cent., Ann. (Serie 8, Zoologie), 169:1-277.

Cope, E. D.

1869. Descriptions of new species of American and African fishes. Trans. Amer. Philos. Soc., 13:400-407.

1878. Synopsis of the fishes of the Peruvian Amazon, obtained by Professor Orton during his expeditions of 1873 and 1877. Proc. Amer. Philos. Soc., 17:673-701.

Cuvier, G., and A. Valenciennes

1840. Histoire Naturelle des Poissons. A. Asher, Co., reprint (1969) of Strasbourg edition. 15:1-540, pls. 421-455.

Dahl, G.

1955. An ichthyological reconnaissance of the Sinu River. Revista Linnaena, 1:11-19. Sincelejo.

Devincenzi, G. J.

1933. Peces del Uruguay, Notas complementarias, II. Ann. Mus. Historia Nat. Montevideo, Ser. 2, 4(3,4): 11 pp., 1 pl.

Devincenzi, G. J., and G. W. Teague

1942. Ictiofauna del Río Uruguay medio. Ann. Mus. Historia Nat. Montevideo, ser. 2, 5(4): 103 pp., 6 pl., 8pp. glossary.

Dingerkus, G., and L. D. Uhler

1977. Enzyme clearing of alcian blue stained whole vertebrates for demonstration of cartilage. Stain Technol., 52(4):229-232.

Eigenmann, C. H.

1912. The freshwater fishes of British Guiana, including a study of the ecological groupings of species and the relation of the fauna of the plateau to that of the lowlands. Mem. Carnegie Mus.,(9): 1-346, pls. 1-103.

1916. VI. New and rare fishes from South American rivers. Ann. Carnegie Mus., 10(1-2):77-86, pl. 13-16.

1917. New and rare species of South American Siluridae in the Carnegie Museum. Ann. Carnegie Mus., 11(3-4):398-404, + 2 Pl.

1925. A review of the Doradidae, a family of South American Nematognathi, or catfishes. Trans. Am. Philos. Soc., new series, 22(5):280-365, 27 pls.

Eigenmann, C. H., and W. R. Allen

1942. Fishes of western South America, I. The intercordilleran and Amazonian lowlands of Peru. II. The high Pampas of Peru, Bolivia, and Northern Chile with a revision of the Peruvian Gymnotidae and of the genus Orestias. Univ. Kentucky, xv + 494 pp.

Eigenmann, C. H., and R. S. Eigenmann

1888. Preliminary notes on South American Nematognathi. I. Proc. California Acad. Sci., Ser. 2, 1:119-172.

1890. A revision of the South American Nematognathi or catfishes. Occas. Pap. Calif. Acad. Sci., 1:1-508.

Fernández-Yépez. A.

1973. Contribucion al conocimiento de Auchenipteridae. Evencias, (29), 5 unnumbered pp.

Ferraris, C. J., Jr., and J. Fernandez

1987. Trachelyopterichthys anduzei, a new species of auchenipterid catfish from the upper Rio Orinoco of Venezuela with notes on T.taeniatus (Kner). Proc. Biol. Soc. Wash., 100(2):257-261.

Filippi, P. de

1853. Nouvelle especies de poissons. Rev. Magasin Zool., (4):1-8.

Fink, S. V., and W. Fink

1981. Interrelationships of the ostariophysan fishes (Teleostei). Zool. J. Linnean Soc., 72(4):297-353.

Fisher, H. G.

1917. A list of the Hypophthalmidae, the Diplomystidae, and of some unrecorded species of Siluridae in the collections of the Carnegie Museum. Ann. Carnegie Mus., 11(3-4):405-427.

Fowler, H. W.

1911. Some fishes from Venezuela. Proc. Acad. Nat. Sci. Philadelphia, 43:419-437.

1914. Fishes from the Rupununi River, British Guiana. Proc. Acad. Nat. Sci. Philadelphia, 46(2):229-284.

1915. Notes on nematognathous fishes. Proc. Acad. Nat. Sci. Philadelphia, 47(2):203-243.

1940. A collection of fishes obtained by Mr. William C. Morrow in the Ucayali River basin, Peru. Proc. Acad. Nat. Sci. Philadelphia, 91:219-289.

Fowler, H. W. (continued)

1945. Colombian zoological survey. Part I. The freshwater fishes obtained in 1945. Proc. Acad. Nat. Sci. Philadelphia, 97:93-135.

1951. Os peixes de água-doce do Brasil. Arq. Zool. Sao Paulo, 6:405-628.

Gill, T.

1870. On some new species of fishes obtained by Prof. Orton from the Maranon River, upper Amazon and Napo rivers. Proc. Acad. Nat. Sci. Philadelphia, 22:92-96.

Gosline, W. A.

1942. Notes on South American catfishes (Nematognathi). Copeia, 1942(1):39-41.

1945. Catálogo dos Nematognatos de água-doce da América do Sul e Central. Bol. do Mus. nac., nova Sér., zool., (3 3):1-138.

1975. The palatine-maxillary mechanism in catfishes, with comments on the evolution and zoogeography of modern siluroids. Occas. Pap. California Acad. Sci., (120):31pp.

Grande, L.

1987 Redescription of +<u>Hypsodoris farsonensis</u> (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. J. Vert. Paleo., 7(1):24-54.

Greenfield, D. W., and G. S. Glodek

1977 Trachelyichthys exilis, a new species of catfish (Pisces: Auchenipteridae) from Peru. Fieldiana: Zool., 72(3):47-58

Günther, A.

1864. Catalogue of the fishes in the British Museum.Vol. 5, Catalog of the Physostomi, containing the families Siluridae, Characidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiatidae, in the collection of the British Museum. London, 455 pp.

Hennig, W.

1966. Phylogenetic Systematics. University of Illinois Press, Urbana, 263 pp.

Hoedeman, J. J.

1961. Notes on the Ichthyology of Surinam and other Guianas. 8. Additional records of siluriform fishes (2). Bull. Aquatic Biol., 2:129-139

Howes, G.

1983. Problems in catfish anatomy and phylogney exemplified by the Neotropical Hypophthalmidae (Teleostei: Siluroidei). Bull. British Mus. Nat. Hist. (Zool.), 45(1):1-39.

Ihering, R. von

1928. _Glanidium cesarpintoi_ sp. nov. de peixe de couro (fam. Siluridae sub fam. Auchenipterinae). Bol. Biol. de Lab. Parasit. de Fac. med. Sao Paulo, (12):46-48.

1930. Notas ecologicas referentes a peixes d'agua doce do Estado de Sao Paulo e descripcao de 4 especies novas. Arch. do Inst. Biol., Sao Paulo, 3:93-104, pl. 13.

1937. Oviducal fertilization in the South American catfish _Trachycorystes_. Copeia, 1937(4):201-205

International Commission on Zoological Nomenclature

1985. International Code of Zoological Nomenclature, 3rd ed. Berkeley: University of California Press

Jordan, D.S.

1917. The genera of fishes from Linnaeus to Cuvier, 1758-1833, seventy-five years, with the accepted type of each. Stanford Univ., 160 pp.

1923. A classification of fishes including families and genera as far as known. Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3(2):77-243.

Kner, R.

1858. Ichthyologische Beiträge. II. Sitzb. Akad. Wiss. Wien, Math.-Naturwiss. klasse., 26:373-448

Köpke, H. J.

1986. Erste Beobachtungen über das Fortflanznngsverhalten von Ageneiosus spec. Die Aquarien- und Terrerien-Zeitschrift, 39(9):393-395.

LaCépède

1803. Histoire naturelle des poissons. in G. L., compte de Buffon, Histoire naturelle générale et particuliere, Paris. Inter Documentation Company, AG, Switzerland, Micro-Edition (5436-14+):535-549.

Linnaeus, C.

1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata.

1766. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio duodecima, reformata., I: 532 pp.

Lundberg, J. G.

1970. The evolutionary history of North American catfishes, family Ictaluridae. Unpublished doctoral dissertation, The University of Michigan

Lundberg, J. G., and J. N. Baskin

1969. The caudal skeleton of the catfishes, order Siluriformes. Am. Mus. Novitates,(2398):49 pp.

Lütken, C. F.

1874. Siluridae novae Brasiliae centralis.... Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger og dets Medlemmers Arbejder i Aaret 1874., Meddeelelser:29-36 [offprint pp. 1-8].

1875. Ichthyographiske Bidrag. II. Nye eller mindre vel kjendte Mallerformer fra forskjellige Verdensdele. Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn., Ser. 3, 5[1874](12-16):190-240.

Mago-Leccia, F.

1984. Entomocorus gameroi una nueva especie de bagre auquenipterido (Teleostei, Siluriformes) de Venezuela, incluyendo la descripción de su dimorfismo sexual secundario. Acta Biol. Venezuelica, (1983)(4):215-236.

Mayden, R. L., B. M. Burr, and S. L. Dewey

1980. Aspects of the life history of the Ozark madtom, Noturus alabater, in Southeastern Missouri (Pisces: Ictaluridae). Am. Midland Nat., 104(2):335-340.

Meek, S. E., and S. F. Hildebrand

1913. New species of fishes from Panama. Field Mus. Nat. Hist., Zool. ser., Publ. 166, 10(8):77-91.

Mees, G. F.

1974. The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi). Zool. Verhand., (132):1-256, pl. 1-15.

1978. On the identity of Arius oncinus R. H. Schomburgk (Pisces, Nematognathi, Auchenipteridae). Zool. Meded., 52(23):267-276.

Mees, G. F. (continued)

1984. A note on the genus Tocantinsia (Pisces, Nematognathi, Auchenipteridae). Amazoniana, 9(1):31-34.

Miranda Ribeiro, A. de

1911. Fauna Brasiliense. Peixes IV (A): Eleutherobranchios Aspirophoros. Arch. Mus. Nac. Rio de Janeiro, 16:1-504, pls. 22-54.

1914. Pimelodidae, Trachycorystidae, Cetopsidae, Bunocephalidae, Auchenipteridae, e Hypophthalmidae. Annexo no. 5, Historia natural, Zoologia. Commissao de Linhas Telegraphicas Estrategicas de Matto-Grosso ao Amazonas, Rio de Janeiro, 13 pp., 2 pls.

1917. De Scleracanthis. Fluvio "Solimões" anno MCMVIII a cl. F. Machado da Silva duce brasiliense inventis et in Museo Urbis "Rio de Janeiro" servatis. Revista Sociedade brasileira de Sciencias, 1:49-52.

1918. Tres generos e dezesete especies novas de peixes brasileiros. Determinados nas collecções do Museu Paulista. Revista Mus. Paulista, 10:629-646. 1 pl.

1920. Peixes (excl. Characinidae). Annexo no. 5, Historia natural, Zoologia. Commissao de Linhas Telegraphicas Estrategicas de Matto-Grosso ao Amazonas, 58: 16 pp., 17 pl.

Miranda Ribeiro, A. de (continued)

1937. Sôbre uma collecção de vertebrados do nordeste brasileiro, primeira parte: peixes e batrachios. O Campo, :54-56.

Miranda Ribeiro, P. de

1962. Apontamentos Ictiológicos I. Bol. Mus. Nac. (Nova sér.), Zool., (240): 6 pp.

1968a. Sôbre o dimorphismo sexual no gênero Auchenipterus Valenciennes, 1840 (Pisces - Auchenipteridae). Bol. Mus. Nac. (Nova sér.), Zool., (261): 11 pp.

1968b. Apontamentos ictiológicos III. Bol. Mus. Nac., (Nova sér.), Zool., (263): 14 pp.

Müller, J.

1842. Über die Schwimmblase der Fische, mit Bezug auf einige neue Fischgattungen. II. Ueber einen Springfeder-Apparat zur Verdünnung und Verdichtung der Luft der Schwimmblase bei einigen Gattungen der Siluroiden, und ähnliche Structuren dei anderen Fischen. Archiv für Anatomie, Physiologie und Wiss. Medicin, in Verbindung mit mehreren gelehrten Jahr 1842, :307-329

Myers, G. S.

1928. New fresh-water fishes from Peru, Venezuela, and Brazil. Ann. Mag. Nat. Hist., ser. 10, 2:83-90.

Nelson, G. J.

1968. Infraorbital bones and their bearing on the phylogeny and geography of osteoglossomorph fishes. Amer. Mus. Novitates, (2394): 37 pp.

Nelson, G., and N. Platnick

1981. Systematics and biogeography: cladistics and vicariance. Columbia Univ. Press, New York.

Nelson, J. S.

1984. Fishes of the world. Second edition. John Wiley & Sons, Inc, New York, 523 pp.

Posada, A.

1909. Los peces, contribución al estudio de la fauna Colombiana, pp. 285- 322, in Molina, C., (ed.) Estudios cientificos del doctor Andres Posada con algunos otros escritos suyos sobre diversos temas y con ilustraciones ó grabados, Medellin, Colombia, 432 pp.

Regan, C. T.

1906. On the freshwater fishes of the island of Trinidad, based on the collection, notes, and sketches of Mr. Lechmere Guppy, Jnr. Proc. Zool. Soc. London, (1) 378-393, 5 pls.

———

1911. The classification of teleostean fishes of the order Ostariophysi. 2. Siluroidea. Ann. Mag. Nat. Hist., ser. 8, 8(47):553-577.

Risso, F. J. J., and E. N. P. de Risso

1962. Epapterus chaquensis, nueva especie de Auchenipteridae (Pisces, Nematognathi). Notas Biol. Fac. Cien. Exactas, Fisicas Y Naturales Corrientes, Zool., (3):4-8.

1964. Los Siluriformes conocidos como "Manduré" y otras especies afines (Pisces: Auchenipteridae, Ageneiosidae, Hypophthalmidae y Pimelodidae). Not. Mus. Cien. Nat. Chaco Resistencia, 1(1):1-31.

Rössel, F.

1962. Centromochlus schultzi, ein neuer wels aus Brasilien (Pisces, Teleostei, Auchenipteridae). Senck. Biol., 43:27-30.

Schomburgk, R. H.

1841. Fishes of Guiana. I. Fishes of British Guiana, in Jardine, W.,(ed.), The Naturalists Library (Ichthyology, 3), 39:1-263, 31 pl. [1841 copy not seen, undated copy and 1852 reprint examined].

Schultz, L. P.

1944. The catfishes of Venezuela, with descriptions of thirty-eight new forms. Proc. U. S. Natl. Mus., 94(3172):173-338, pls. 1-14.

Shelden, F. F.

1937. Osteology, myology and probable evolution of the nematognath pelvic girdle. Ann. New York Acad. Sci., 37(1):1-96.

Spix, J. B., and L. Agassiz

1829. Selecta genera et species piscium. Monachii. I-II, i-xvi, I-II, 1-138, Tab A-G, 1-75, ant, A-F.

Steindachner, F.

1877. Die Süsswasserfische des südöstlichen Brasilien, (III). Sitzber. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, 74(1):559-694.

1878. Zür Fischfauna des Magdalenenstromes. Anz. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, 15:88-91.

Steindachner, F. (continued)

1880. Zür Fisch-fauna des Cauca und der Flüsse bei Guayaquil. Denks. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, :55-104, pls. 1-9

1882a. Beiträge zur Kenntnis der Flussfische Südamerika's. III. Denken. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, 44(1):1-18, 5 pls.

1882b. Beiträge zur Kenntnis der Flussfische Südamerika's. IV. Anz. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, 19(19):175-180.

1908. Über drei neue Characinen und drei Siluroiden aus dem Stromgebiete des Amazonas innerhalb Brasiliens. Anz. Kaiserliche Akad. Wiss. Wien Math.-Naturwiss. Klasse, 45:61-69.

1909. Über eine Ageneiosus (Pseudageneiosus) Art. Anz. Kaiserliche Akad. Wiss. Wien Math.-Naturwiss. Klasse, 46(20):341-343.

1911. Über einige Ageneiosus- und Farlowella-Arten etc. Ann. K. K. naturhistorischen Hofmuseums, 24:399-408, pl. 8-10.

Steindachner, F. (continued)

1915. Vorläufiger Bericht über einige neue Süsswasserfische aus Südamerika. Anz. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, 52(17):199-202

1917. Beitrage zur kenntnis der flussfische Südamerikas. V. Denks. Kaiserliche Akad. Wiss. Wien, Math.-Naturwiss. Klasse, 93:15-106, pl 1-13.

Stigchel, J. W. B. van der

1947. South American Nematognathi. Zool. Meded., 39:327-330.

Tavolga, W. N.

1962. Mechanisms of sound production in the ariid catfishes Galeichthys and Bagre. Bull. American Mus. Natur. Hist., 124(1):1-30, 28 pls.

Taylor, W. R.

1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus., 122:(2596):1-17.

1969. A revision of the catfish genus Noturus Rafinesque, with an analysis of the higher grous in the Ictaluridae. U. S. Natl. Mus. Bull., 282: 315 pp., 21 pls.

Taylor, W. R. (continued)

1977. Pseudauchenipterus nodosus. FAO Identification sheets, Fishing Area 31 (W. Cent. Atlantic). AUCHEN Pseud 1.

Valenciennes, A.

1847. Poissons. In A. D'Orbigny, Voyage dans l'Amérique Méridionale ..., 5(2)1-11, 16 pls.

Vari, R. P., S. L. Jewett, D. C. Taphorn, and C. R. Gilbert

1984. A new catfish of the genus Epapterus (Siluriformes: Auchenipteridae) from the Orinoco River Basin. Proc. Biol. Sci. Wash., 97(2):462-472.

Vari, R. P., and H. Ortega

1986. The catfishes of the Neotropical family Helogenidae (Ostariophysi: Siluroidei). Smithson. Contrib. Zool., (442):20 pp.

Weitzman, S. H., and R. P. Vari

In Press. Miniaturization in South American freshwater fishes; an overview and discussion. Proc. Biol. Soc. Washington.

Whitley, G.

1940. Nomenclator Zoologicus and some new fish names. Australian Natur., 10:241-243.

Winterbottom, R.

1974. A descriptive synonomy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Philadelphia, 125(12):225-317.