Monophyly and Phylogenetic Diagnosis of the Family Cetopsidae, with Synonymization of the Helogenidae (Teleostei: Siluriformes)

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ABSTRACT

de Pinna, Mário C.C., and Richard P. Vari. Monophyly and Phylogenetic Diagnosis of the Family Cetopsidae, with Synonymization of the Helogenidae (Teleostei: Siluriformes). *Smithsonian Contributions to Zoology*, number 571, 26 pages, 20 figures, 1995.—The Neotropical catfishes currently recognized as the families Cetopsidae and Helogenidae are hypothesized to be sister groups. The two taxa share numerous synapomorphies, including a lap joint between the opercle and interopercle, a dorsal displacement of the attachment of the interoperculo-mandibular ligament on the interopercle, and a strongly depressed palatine. Some of these derived characters are unique within Siluriformes. On the basis of this hypothesis of relationships, cetopsids and helogenids are united into an expanded Cetopsidae, itself subdivided into the monophyletic subfamilies Cetopsinae and Helogeninae. The Cetopsinae is synapomorphically diagnosable by, among other characters, an expanded and often ramified cartilaginous posterior process of the basipterygium, an anterior curvature of the third epibranchial, and the articulation of the palatine with the neurocranium only by means of its anterior cartilage. Synapomorphies supporting the monophyly of the Helogeninae include a reduction in the degree of ossification between the mesethmoid cornua and the remainder of the neurocranium, a large paired fontanel in frontal and sphenotic, the posterior expansion of the third basibranchial, and the lack of contact of the sphenotic with the supraoccipital. Phylogenetic diagnoses are provided for the redefined Cetopsidae, Cetopsinae, and Helogeninae. The external morphology of juvenile *Helogenes* and a number of unusual juvenile features, possibly unique to the genus, are described for the first time.

Contents

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Introduction

The families Helogenidae and Cetopsidae (sensu Greenwood et al., 1966) are two small groups of Neotropical freshwater catfishes, which are comprised of four and approximately 15 currently recognized species, respectively. The phylogenetic relationships of both families to other siluriforms always have been obscure, in part due to the poor overall knowledge of phylogenetic relationships among familial-level catfish taxa. Although recognized as distinct entities for over eight decades, neither the Cetopsidae nor the Helogenidae have been demonstrated to be monophyletic on the basis of synapomorphic characters, a situation they share, however, with the majority of catfish families.

The Helogenidae, with a single valid genus *Helogenes* Günther, is a group of distinctive small catfishes (maximum size 73 mm SL) with rather uniform morphology and pigmentation (Figure 1). Helogenids inhabit small, clear and blackwater streams of the Guyanas and the Amazon and Orinoco basins, being most often captured in shallow-water microhabitats of blackwater rain forest streams. The little

known about helogenid biology indicates they are free-living generalized predators of allochthonous terrestrial insects (Vari and Ortega, 1986:15) and other small invertebrates. The species- and generic-level taxonomy of helogenids recently was revised by Vari and Ortega (1986).

The Cetopsidae, with about five nominal genera, also form a rather distinctive group of catfishes (Figure 2). Cetopsids display far greater intrafamilial morphological variation than does the Helogenidae and a significantly greater range of maximum size among the included species (30 to 300 mm SL). The limited available information on cetopsid biology indicates that they range from free-living insect eaters (Saul, 1975; Baskin et al., 1980) to semi-predatory scavengers and flesh-eaters (sometimes erroneously termed "parasitic") known in the Brazilian Amazon as "candiru açu." The flesh-eating cetopsids, notorious for their voracious habits (Magalhães, 1931; Goulding, 1980:193–194), are often inappropriately lumped with some semi-parasitic trichomycterids under the common name of "candiru." Cetopsids have a wider distribution than helogenids, occurring in the Amazon, Essequibo, Orinoco, São Francisco, and Paraná-Paraguay basins, the rivers of the Pacific slope of Ecuador and Colombia, and drainages of the Caribbean versant of Colombia and northwestern Venezuela. Their known habitats range from small rain forest creeks, similar to those inhabited by helogenids, to large rivers. In the absence of a thorough revision of cetopsids, the taxonomy of the group remains unsettled both at the species and generic levels (Ferraris and Brown, 1991). Although two revisionary studies of cetopsids have been completed in recent

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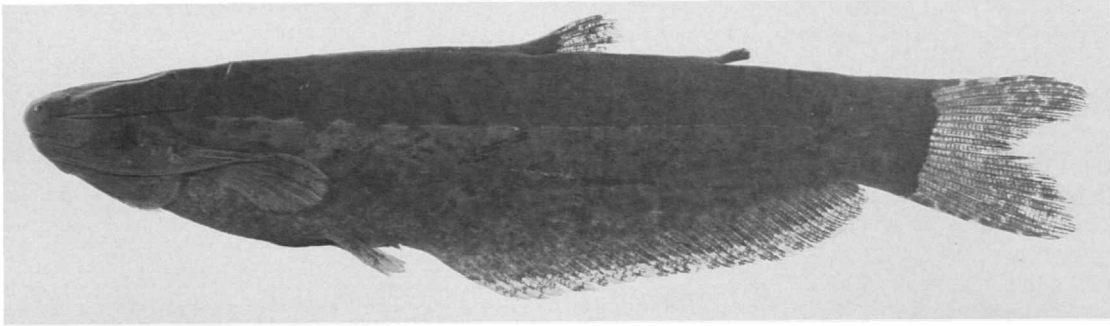
FIGURE 1.—Representative example of the Cetopsidae, subfamily Helogeninae, *Helogenes marmoratus*, USNM 273057, Guyana, Potaro River.
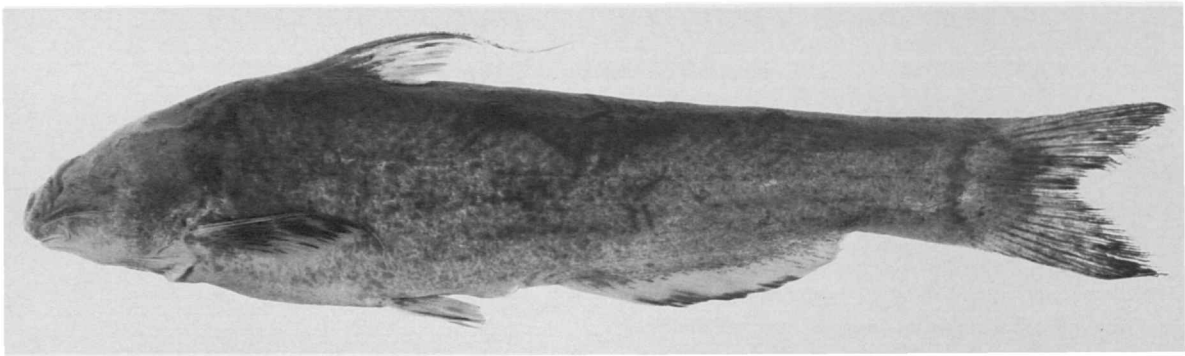
FIGURE 2.—Representative example of the Cetopsidae, subfamily Cetopsinae, *Pseudocetopsis amphiloxa*, USNM 305348, Colombia, Choco, Río Truando system.

years (de Oliveira, 1988; Milani de Arnal, 1991), neither has been published.

The autapomorphic modifications of helogenids and cetopsids, coupled with a lack of detailed morphological analysis, have long made these groups puzzles in siluriform systematics (see "Comparisons with Previous Hypotheses and Classifications" below). In this paper, we offer morphological evidence, most of it new, for a hypothesis of a sister-group relationship between the current Cetopsidae and Helogenidae. As a corollary we unite the two taxa in a redefined Cetopsidae, subdivided into the subfamilies Cetopsinae and Helogeninae. Each of those subfamilies is explicitly hypothesized as monophyletic for the first time. The new data and hypotheses are summarized in a rediagnosis of the family Cetopsidae, and the subfamilies Cetopsinae and Helogeninae. The definition of this well-corroborated clade will greatly facilitate future efforts toward a resolution of the phylogenetic position of the expanded Cetopsidae within Siluriformes, a question that lies beyond the limits of this study.

In the course of this study, we located specimens that are apparently the first juveniles of *Helogenes* identified to date. Noteworthy differences between adult and juvenile helogenid morphology prompted us to provide a brief description of the external anatomy of these specimens. This both highlights various unusual juvenile features in the genus and facilitates the location of additional juvenile material for studies of internal anatomy.

Joaquim Maia (MZUSP), Scott A. Schaefer (ANSP), and Stanley H. Weitzman (NMNH) and the careful copy editing and composition of the final paper by Craig Warren, Smithsonian Institution Press. This study was completed during the tenure of the senior author as a Smithsonian Postdoctoral Fellow in the Department of Vertebrate Zoology, National Museum of Natural History.

MATERIAL AND METHODS.—Henceforth the name Cetopsidae is used in its revised meaning, including the former Cetopsidae and Helogenidae (see "New Classificatory Scheme" below), both now recognized as subfamilies. Skeletal material of about 120 valid genera, representing all extant catfish families, was examined for comparative purposes. The complete list is excessive for inclusion herein, but a copy is deposited in the Library, Division of Fishes, National Museum of Natural History, Smithsonian Institution. Examined specimens of the Cetopsinae and Helogeninae are listed below, identified as AL (alcohol-preserved), B (cleared and stained for bone only), BC (cleared and counterstained for bone and cartilage), or RD (radiographed). The number preceding these abbreviations refers to the number of specimens examined.

CETOPSINAE

Bathycetopsis oliveirai Lundberg and Rapp Py-Daniel, DU F1170, 1 BC, paratype.
Cetopsis coecutiens (Lichtenstein), ANSP 137558, 2 BC; USNM 265707, 1 AL, juvenile; AMNH 58168, 1 BC, juvenile.
Hemicetopsis candiru (Spix), AMNH 78109, 2 BC; USNM 167854, 5 AL.
Paracetopsis bleekeri Guichenot, USNM 76971, 4 AL, 1 B; AMNH 5353, 1 BC; AMNH 97234, 1 BC.
Pseudocetopsis amphiloxa (Eigenmann), USNM 305348, 9 AL.
Pseudocetopsis macilentus (Eigenmann), AMNH 55332, 2 BC.
Pseudocetopsis minutus (Eigenmann), FMNH 45708, 2 AL, 1 BC.
Pseudocetopsis morenoi (Fernández-Yépez), MBUCV V-15891, 1 B.
Pseudocetopsis othonops (Eigenmann), USNM 76972, 6 AL, paratypes.
Pseudocetopsis plumbeus (Steindachner), AMNH 99069, 1 BC.
Pseudocetopsis praecox Ferraris and Brown, AMNH 74449, 1 BC, paratype.
Pseudocetopsis sp., USNM 226147, 2 BC, juveniles.

HELOGENINAE

Helogenes gouldingi Vari and Ortega, USNM 269446, 3 AL, 1 BC (specimen uncalcified, poorly stained), paratypes.
Helogenes marmoratus Günther, AMNH 91372, 1 BC; AMNH 13332, 1B; AMNH 7113, 1 B; AMNH uncat., 5 BC; MUSM 2717, 2 AL, juveniles; MUSM 3346, 2 AL; ZSM 28285, 1 AL, juvenile; USNM 269975, 15 AL, including 1 juvenile;

IRSNB 545 (holotype of *Helogenes amazonae* Delsman), 1 RD; FMNH 80463 (holotype of *Helogenes unidorsalis* Glodek and Carter), 1 RD; FMNH 80464 (paratypes of *Helogenes unidorsalis* Glodek and Carter), 4 RD.
Helogenes uruyensis Fernández-Yépez, USNM 219598, 1 AL, paratype.

Specimens prepared for this study were cleared and counterstained for bone and cartilage according to the method of Taylor and Van Dyke (1985). Some previously prepared specimens were stained only for bone. Specimens were dissected according to the procedure of Weitzman (1974), with additional incisions to expose details of branchial arches and jaws. Myological observations were conducted by simple dissection of alcohol-preserved specimens, removing the overlying integument and any nontarget musculature. In some cases it also was necessary to remove the epimysium, in order to delimit muscles. Myological terminology follows Winterbottom (1974). The groups termed the suborders Siluroidei and Gymnotoidei in Fink and Fink (1981) are ranked at ordinal level, as Siluriformes and Gymnotiformes, as suggested by Grande (1987) and de Pinna (1993). Presented familial and subfamilial synonymies are restricted to historically important or synoptic recent publications dealing with higher-level catfish taxonomy.

The systematic methodology employed was phylogenetic, or cladistic, today the standard method for studying organismic relationships. Outgroups used for polarizing character states were practically all other Siluriformes with particular reference to the Diplomystidae, widely accepted as the sister group of all other catfishes living and fossil (Lundberg and Baskin, 1969; Fink and Fink, 1981; Grande, 1987; Arratia, 1987). When necessary, Gymnotiforms and Characiforms were hypothesized as successive sister groups to Siluriformes (Fink and Fink, 1981).

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations are used in the text.

AMNH	American Museum of Natural History, New York, New York
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania
CAS	California Academy of Sciences, San Francisco, California
DU	Vertebrate Collection, Department of Zoology, Duke University, Durham, North Carolina
FMNH	Field Museum of Natural History, Chicago, Illinois
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MBUCV	Museo de Biología, Instituto de Zoologia Tropical, Universidad Central de Venezuela, Caracas, Venezuela
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru

MZUSP   Museu de Zoologia da Universidade de São
         Paulo, São Paulo, Brazil
NMNH   National Museum of Natural History, Smith-
         sonian Institution, Washington, D.C.
UMMZ   Museum of Zoology, The University of
         Michigan, Ann Arbor, Michigan
USNM   Former United States National Museum,
         collections in National Museum of Natural
         History, Smithsonian Institution, Washing-
         ton, D.C.
ZSM   Zoologisches Staatssammlung, Munich, Ger-
         many

ANATOMICAL ABBREVIATIONS.—The following abbrevia-
tions are used in the figures.

AA   angulo-articular
ACP   anterior palatine cartilage
AF   anal fin
AM   adductor mandibulae muscle
AO   anal opening
BB_{2-4} basibranchials 2 to 4
BP   basipterygium
CPP   cartilaginous posterior process of basi-
             pterygium
DEN   dentary
E_{1-4} epibranchials 1 to 4
EC   mesethmoid cornua
ECT   ectopterygoid
F   frontal
FF   fin fold
FO   fontanel
H_{1-3} hypobranchials 1 to 3
HY   hyomandibula
INT   interopercle
IOL   interoperculo-mandibular ligament
LAC   lateral ethmoid cartilage
LJ   lower jaw
LAP   levator arcus palatini muscle
LAT   lateral ethmoid
MAX   maxilla
ME   mesethmoid
MET   metapterygoid
OP   opercle
PAL   palatine
P_{3-4} pharyngobranchials 3 and 4
PF   pelvic fin
POP   preopercle
QUA   quadrate
SPH   sphenotic
SPO   suprapreopercle
TP   tooth plate
UO   urogenital opening
UP   upper pharyngeal tooth plate
V   vomer

Character Evidence

In this section the discovered characters are described and discussed with respect to their implications for the proposed phylogenetic hypotheses. Each character is numbered and arranged sequentially within the component of relationships it is hypothesized to support.

CETOPSIDAE CLADE

1. *Maxilla with a single proximal head.* Most cat-fishes have the maxilla proximally divided into two processes that partly surround and attach to the anterior portion of the palatine by means of a double condyle. This condition is a synapomorphy for Siluriformes and, thus, is considered primitive within the order (Lundberg, 1970). In the Cetopsidae, the maxilla is instead undivided proximally and articulates with the palatine by means of a single condyle. This less complex condition of the maxilla, although similar to that seen in ostariophysan outgroups to siluriforms, must be interpreted as apomorphic within the context of available evidence about catfish monophyly and relationships. The only other siluriforms with a proximally undivided maxilla are the members of the Neotropical family Astroblepidae. In view of well-corroborated phylogenetic hypotheses joining astroblepids more closely with other loricarioids in which the maxilla is proximally divided (Baskin, 1973; Howes, 1983; Schaefer, 1987), the condition in the Cetopsidae must be interpreted as independent of that in the Astroblepidae and therefore autapomorphic for cetopsids.

2. *Posterior portion of palatine depressed, expanded lateromesially.* The posterior portion of the palatine of most catfishes is rod-like and approximately round or oval in cross-section. In the Cetopsidae, the palatine is highly modified with its posterior portion dorsoventrally depressed and horizontally expanded into a shelf bordered distally by a proportionally enlarged cartilage (Figure 3A,B). This condition, absent in examined catfish outgroups, is hypothesized as derived.

An apparently similar, but in fact nonhomologous condition, is seen in the Asiatic sisorid subfamily Glyptosterninae. The glyptosternine palatine is rather compressed laterally and subsequently partially rotated into the horizontal plane, resulting in a condition superficially similar to that in cetopsids. The fact that the glyptosternine condition is a consequence of a partially rotated, laterally compressed posterior portion of the palatine (as opposed to a depression of the primitive dorsal surface of the bone) is evident by its shift from the horizontal plane and in the obvious torsion of that portion of the bone relative to the anterior part of the palatine.
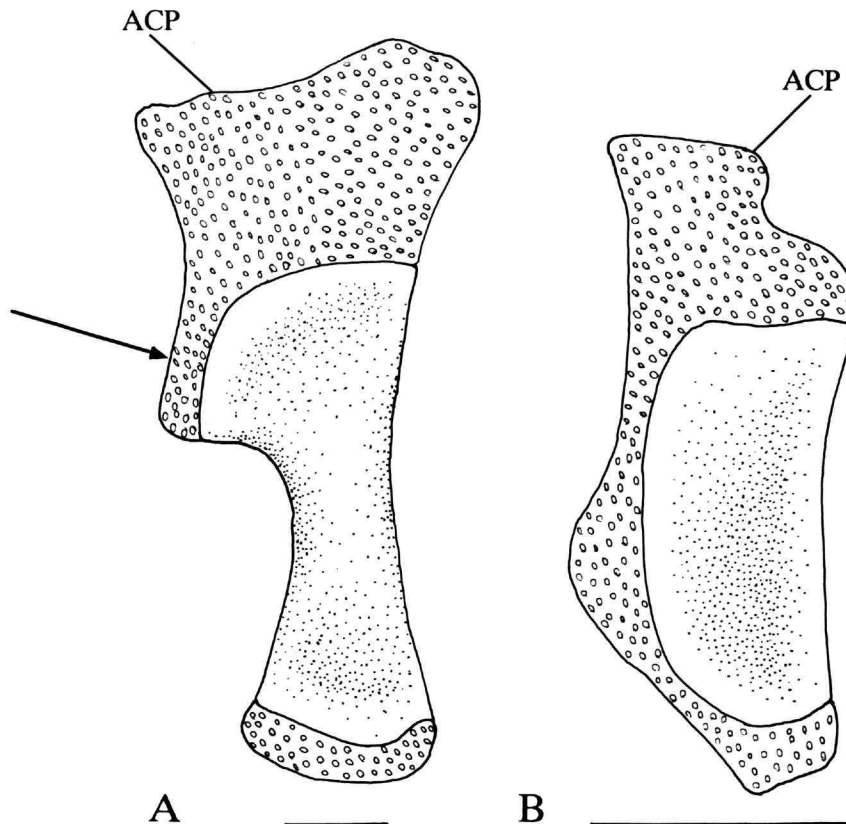
FIGURE 3.—Palatine, dorsal view of right side, anterior at top of A, *Pseudocetopsis plumbeus* AMNH 99069 and B, *Helogenes marmoratus* AMNH 91372. Arrow indicates posterior extension of anterior cartilage of palatine. Stippling represents bone, open circles represent cartilage. (Scale bars = 1 mm.)

The conditions in glyptosternines and cetopsids, therefore, are considered nonhomologous.

3. *Anterior distal cartilage of palatine extending onto mesial surface of bone.* The anterior cartilage of the palatine in siluriforms is primitively restricted to, and forms a rim along, the anterior margin of the bone. In the derived state found in cetopsids the cartilage is markedly extended mesially to additionally border the mesial margin of the palatine (Figure 3A,B). In cetopsines the cartilage extends mesially for about one-third or one-fourth of the longest axis of the ossified portion of the palatine (Figure 3A). Helogenines demonstrate some intraspecific variation in the development of the cartilage, with some specimens of *Helogenes marmoratus* having the anterior cartilage so enlarged as to be continuous with the cartilage on the posterior part of the palatine. In such individuals the resultant cartilage is continuous along the anterior, mesial, and posterior margins of the bone (Figure 3B).

Among catfishes, a situation similar to that in cetopsids is found elsewhere only in the Old World family Claroteidae (Mo, 1991:60, described this condition as a laminar sheet of the palatine). However, current hypotheses on the relationships of claroteids within siluriforms (Mo, 1991) indicate that the occurrences of the character in Claroteidae and Cetopsidae are homoplastic.

4. *Anterior cartilage of palatine expanded anteriorly.* The plesiomorphic condition of the anterior cartilage of the palatine in catfishes is a dorsoventrally relatively short layer extending slightly beyond the anterior margin of the bone. In many cases the anterior cartilage is limited to a cartilaginous cap continuous with the cylindrical bony portion of the palatine. In cetopsids, in contrast, the cartilage is expanded anteriorly into a large, dorsoventrally flattened, plate-like process along the anterior margin of the palatine, with its longest antero-posterior measurement nearly one-half the length of the longest axis of the bony portion of the palatine (Figure 3A,B), a derived condition.
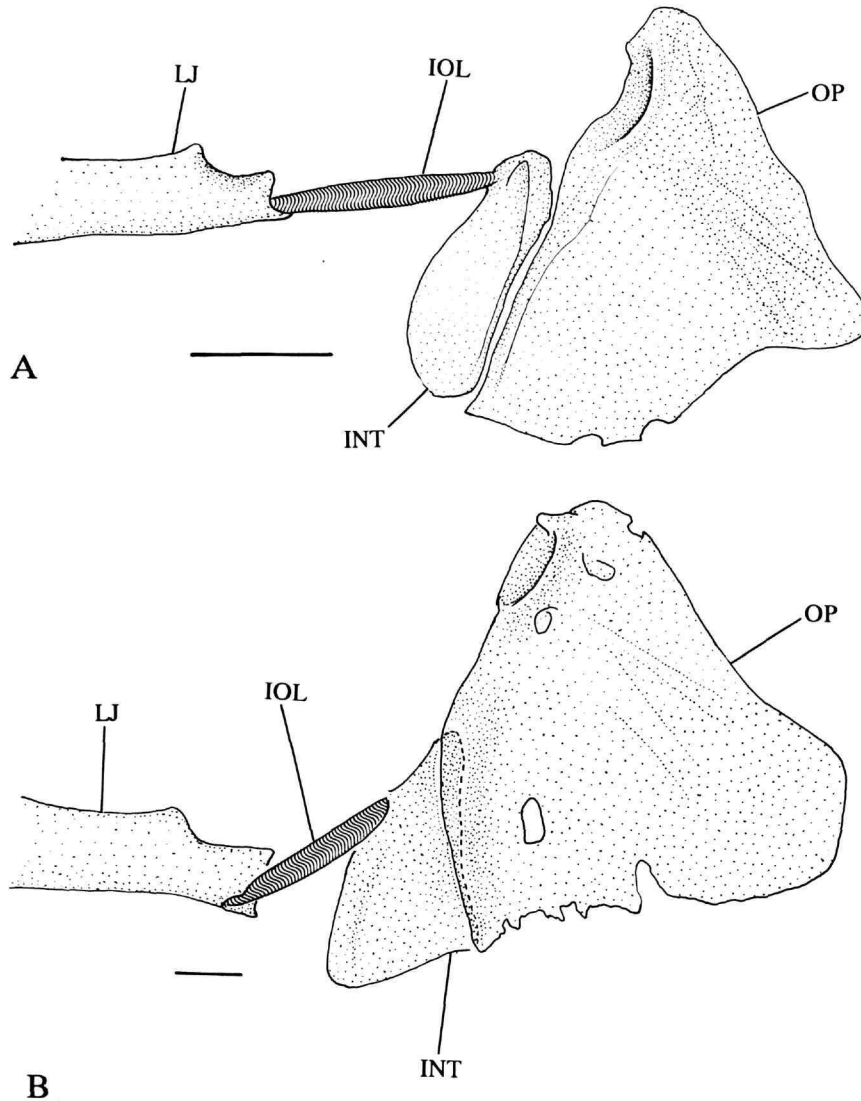
FIGURE 4.—Opercular apparatus and related structures, mesial view of right side, anterior to left of A, *Helogenes marmoratus*, AMNH 91372 and B, *Paracetopsis bleekeri*, AMNH 97234. (Scale bars = 1 mm.)

5. *Lap joint present between opercle and interopercle.* In most siluriforms and outgroup ostariophysans, the proximate margins of the opercle and interopercle are linked by a thin sheet of connective tissue and their laminar surfaces, although in the same plane, do not overlap. The proximate margins of the opercle and interopercle of all cetopsids, in contrast, partly overlap each other along modified laminar surfaces (Figure 4). In addition, both the opercle and interopercle in cetopsids are notably thickened in the region of overlap, a modification that disrupts their otherwise smooth lateral surfaces. The degree of thickening is greater on the

opercle, which has a well-defined groove accommodating the posterior margin of the interopercle. These modifications result in the opercle and interopercle in cetopsids forming a lap joint uniquely derived within catfishes.

In helogenines the area of overlap is reoriented into a plane almost perpendicular to that of the main lamina of the opercle (Figure 4A), making the degree of overlap less obvious in lateral view. Nonetheless, the arrangement in helogenines, although distinct in some details from the simpler condition in cetopsines (Figure 4B), shares the overall basic morphology of the joint with the latter

subfamily. Thus the modifications are considered homologous in, and a synapomorphy for, the two subfamilies.

6. *Attachment of interoperculo-mandibular ligament on dorsal portion of interopercle.* An attachment of the interoperculo-mandibular ligament on the anterior tip of the interopercle is primitive in catfishes and most other teleosts. Cetopsids display a unique dorsal shift of the posterior attachment of the ligament away from the anterior tip of the interopercle to a position at or near the dorsal margin of the bone. In helogenines the attachment is displaced dorsally to the dorsal tip of the interopercle (Figure 4A), whereas in cetopsines the attachment site is slightly ventral to the dorsal tip (Figure 4B).

7. *Interopercle expanded along dorsoventral axis, deeper than long.* The interopercle in catfishes and most other ostariophysans plesiomorphically has its anteroposterior axis longer than the dorsoventral axis. In the derived condition found in cetopsines and helogenines, the interopercle is expanded along its dorsoventral axis, resulting in an interopercle that is distinctly higher than long (Figure 4A,B).

8. *Shaft of second basibranchial expanded laterally, with strongly convex lateral margins.* The second basibranchial in siluriformes (the anteriormost element in the series, because the first basibranchial is absent as an independent ossification in catfishes) is primitively a cylinder of bone restricted to the center of ossification of its cartilage precursor. In cetopsids, the second basibranchial has flat lateral shelves of bone extending laterally beyond the margin of the cylindrical center of ossification (Figure 5). These expansions are more developed along the anterior portion of the basibranchial, resulting in an overall convex lateral profile of the bone when observed from a dorsal view. The shelves are clearly present in all large specimens of helogenines examined and also occur in most cetopsines. They are absent, however, in miniature cetopsines including *Pseudocetopsis macilentus* (placed in an undescribed genus by both de Oliveira, 1988, and Milani de Arnal, 1991). We interpret the absence of the shelves in these diminutive species as reversals associated with miniaturization, a phenomenon that frequently results in reductions in the degree of overall ossification (Weitzman and Vari, 1988:445).

9. *Metapterygoid elongate, roughly rectangular in shape.* The metapterygoid in most siluriforms is a plate-like bone consisting of a cylindrical center of ossification at its articulation ventrally with the quadrate and a larger laminar portion expanding posterodorsally from that ossification center. The margins of the metapterygoid are usually quite irregular, and the shape of the ossification consequently varies widely among
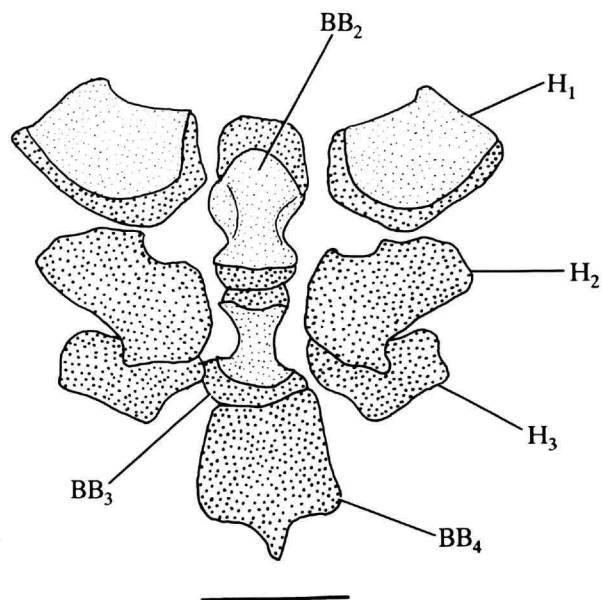
FIGURE 5.—*Helogenes marmoratus*, AMNH 91372, ventral elements of gill arches, dorsal view, anterior at top. Larger stippling represents cartilage. (Scale bar = 1 mm.)

catfish taxa. In general, however, the metapterygoid is roughly square, circular, or triangular, or if it has an irregular margin, then the bone is not significantly longer in any particular axis. In cetopsids, the metapterygoid is anterodorsally lengthened into an irregular rectangle extending between the antero-dorsal margin of the quadrate and the ectopterygoid. The portion of the posterior surface of the metapterygoid that contacts the hyomandibula is also proportionally increased (Figures 6, 7). These modifications, not encountered in other catfishes, are hypothesized as apomorphic for the family.

CETOPSINAE CLADE

1. *Posterior cartilaginous process of basipterygium expanded and distally ramified.* The cartilaginous elements of the catfish basipterygium show a large degree of morphological variation, which although potentially informative phylogenetically, has yet to be rigorously analyzed. In the plesiomorphic condition for siluriforms, the cartilage bordering the posterior process of the basipterygium (Shelden, 1937) is relatively simple and proportionally small, not extending posteriorly much beyond the bony portion of the bone. In the Cetopsinae, this posterior cartilage is markedly enlarged, and ramified distally into a root-shaped structure (Figure 8). The ramifications are restricted to the horizontal plane, with the entire posterior portion of the cartilage dorsoventrally
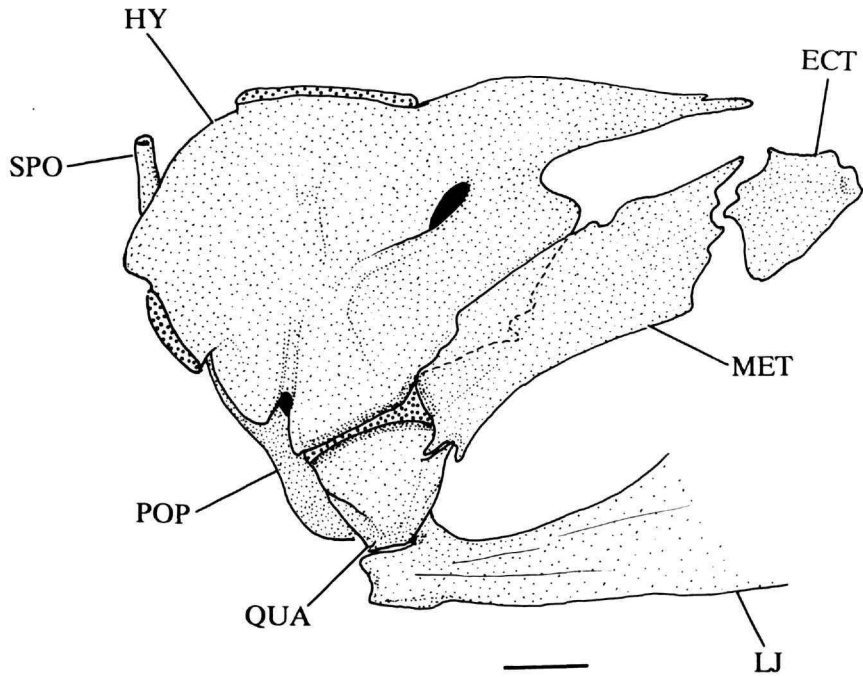
FIGURE 6.—*Pseudocetopsis plumbeus*, USNM 257763, suspensorium and selected associated structures, mesial view of left side, anterior to right. Larger stippling represents cartilage. (Scale bar = 1 mm.)
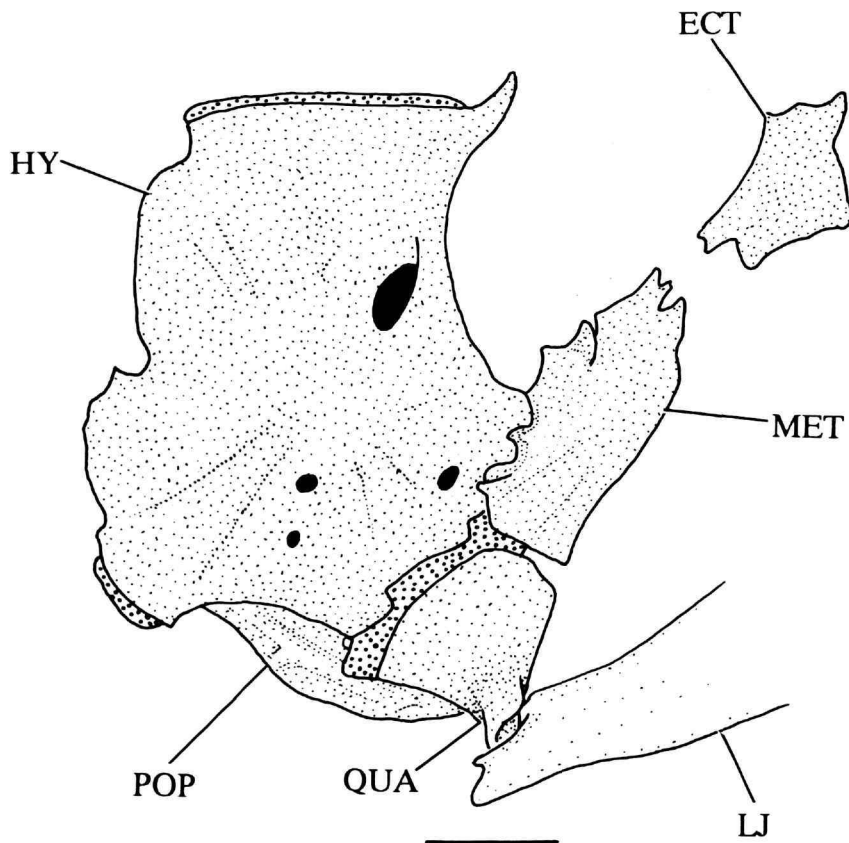
FIGURE 7.—*Helogenes marmoratus*, AMNH 91372, suspensorium and selected associated structures, mesial view of left side, anterior to right. Larger stippling represents cartilage. (Scale bar = 1 mm.)
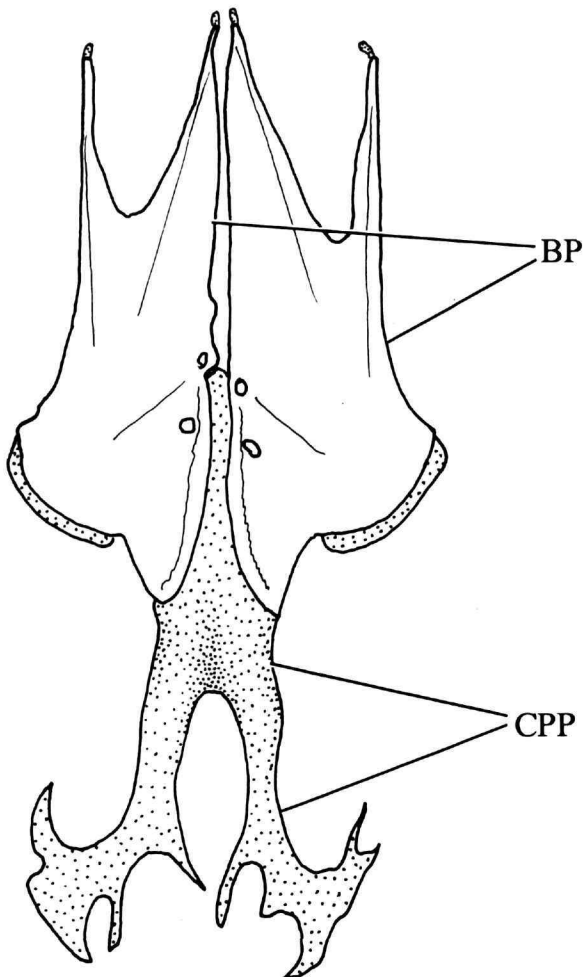
FIGURE 8.—*Pseudocetopsis plumbeus*, AMNH 99069, ventral view of pelvic girdle, anterior at top. Stippling represents cartilage.

FIGURE 9.—*Bathycetopsis oliveirai*, DU F1170, ventral view of pelvic girdle, anterior at top. Larger stippling represents cartilage. (Scale bar = 1 mm.)

flattened. In the miniature cetopsine *Bathycetopsis oliveirai* the posterior basipterygial cartilage retains the apomorphic enlarged condition, although lacking the posterior ramifications (Figure 9), apparently as a result of the paedomorphic condition of the species. A hypothesis of the connection between the absence of ramifications and paedomorphosis is supported by the observation that a young cleared and stained specimen of *Cetopsis coecutiens* (AMNH 58168) has the ramifications of the basipterygial cartilage less developed than in adults of that species. It is noteworthy, however, that another possibly paedomorphic species, *Pseudocetopsis minutus*, has the basipterygial ramifications as well developed as that in larger cetopsine species.

The enlargement of the posterior basipterygial cartilage occurs in a few other siluriforms. In the Asiatic families Pangasiidae and Schilbidae this cartilage is proportionally as long as or longer than that in cetopsines, but it differs from the cetopsine condition in being neither ramified nor dorsoventrally flattened. Also, available evidence (de Pinna, 1993) indicates that pangasiids and schilbids are more closely related to siluriform lineages lacking the enlarged basipterygial cartilage than to the Cetopsidae. The expansion of the cartilage in those Asiatic families is therefore considered nonhomologous with that of cetopsines. In the sisorid *Bagarius*, the posterior basipterygial cartilage is somewhat similar to that in cetopsines; however, the whole process is far less elongate, and the posterior ramifications are very short. These morphological differences, plus the fact that *Bagarius* probably is more closely related to remaining members of the Sisoridae and other Asiatic catfish families, which retain the primitive condition for the posterior basipterygial cartilage (de

Pinna, 1993), indicates that the expansions of the cartilage in cetopsines and *Bagarius* are independent.

2. *Anterior tip of the third epibranchial curved anteriorly and articulating directly with the third pharyngobranchial.* The third epibranchial in siluriforms primitively articulates mesially with the anterodorsal margin of the third or fourth pharyngobranchial. Regardless of the pharyngobranchial with which it articulates, the shaft of the third epibranchial is relatively straight, without any pronounced curvature along its mesial portion (Figure 10). Uniquely in the Cetopsinae among siluriforms, the anterior portion of the third epibranchial is markedly curved anteriorly to contact the posterior margin of the third pharyngobranchial (curvature indicated by arrow in Figure 11). This modification is best observed when the dorsal gill arches are viewed from slightly anterior of a completely dorsal view.

3. *Palatine articulating with the lateral ethmoid only through its anterior cartilage.* The palatine in catfishes primitively articulates with the lateral ethmoid by means of a facet located on the mesial face of its bony shaft (Gosline, 1975). In cetopsines uniquely among catfishes, the articulation between these elements is displaced anteriorly on the palatine and is restricted to the anterior cartilage of the palatine (Figure 12). This restriction of the attachment of the palatine to the lateral ethmoid may be the result of a posterior displacement of the palatine relative to the neurocranium.

4. *Adductor mandibulae muscle hypertrophied, extending dorsally to the midline of neurocranium.* Siluriforms often have the adductor mandibulae muscles massively developed, with this hypertrophy reflected in the expansion of the musculature onto portions of the skull roof. A certain degree of skull-roof envelopment by these muscles occurs in the primitive catfish family Diplomystidae and several other generalized siluriforms, such as ictalurids and certain pimelodids (e.g., *Brachyglanis, Myoglanis,* and *Leptorhamdia*). At present it is impossible to unambiguously assess whether the primitive siluriform condition is a limited amount of skull-roof envelopment by the adductor mandibulae or none at all. Regardless of which alternative is correct, the Cetopsinae have an extreme condition of skull-roof invasion by the muscle, which is certainly apomorphic and almost unparalleled within the order. The cetopsine adductor mandibulae envelops the skull roof all the way to the dorsal midline. As a consequence, practically no section of the dorsal surface of the braincase remains exposed (Figure 13). Although the adductor mandibulae covers the entire dorsal surface of the braincase and extends posteriorly to abut the anterior limit of the anterodorsal portion of the epaxial musculature, the attachment of the adductor mandibulae on the skull is actually restricted to a narrow area proximate to the midline.

Elsewhere within siluriforms such an extreme hypertrophy of the adductor mandibulae muscle is rare, occurring only in a few specialized taxa such as *Brachyglanis* and *Leptorhamdia* of the Neotropical family Pimelodidae. The absence of the extreme development of the adductor mandibulae muscle in the other members of the monophyletic subfamily Rhamdiinae (Lundberg et al., 1991) of the Pimelodidae indicates that the development of the enlarged muscle in the cited pimelodid genera is independent of that in cetopsines. The only other siluriform with the adductor mandibulae clearly more highly developed than that of cetopsines is the subterranean Asiatic clariid *Horaglanis*. Because *Horaglanis* apparently is more closely related to other members of the Clariidae (Menon, 1951), which otherwise lack an extreme development of the adductor mandibulae, the condition in *Horaglanis* is hypothesized to be independent of that in the Cetopsinae.

Note Added in Proof: Our observations of *Bathycetopsis oliveirai* were restricted to a single cleared and stained specimen. In a publication that appeared after this paper was in press, Lundberg and Rapp Py-Daniel (1994:382) observed that the "jaw adductor muscle" in *B. oliveirai* is restricted to the cheek and does not extend onto the skull roof. Whether this condition represents a primitive state or a secondary reduction is a question that must await a phylogenetic analysis of cetopsines. If the nonspecialized musculature actually presents a primitive condition, then the derived state (Cetopsinae Character 4) is diagnostic for a more restricted group comprised of non-*Bathycetopsis* cetopsines rather than for the entire subfamily.

5. *Levator arcus palatini muscle enlarged and prominent in dorsal view.* The levator arcus palatini muscle in catfishes primitively is restricted mainly to the vertical plane and is attached to the ventrolateral portion of the skull posterior to the orbit. As a consequence, this muscle can be seen clearly only in a lateral view of the head. In cetopsines, the levator arcus palatini is more massively developed and extends over the dorsum of the anterior portion of the skull; thus it is clearly visible in dorsal aspect (Figure 13). Posteriorly, the levator is closely adpressed to the anterior margin of the adductor mandibulae, and the two muscles together form a continuous block of muscle covering practically the entire skull roof. In the cetopsine genus *Hemicetopsis,* the derived condition of the levator arcus palatini is not readily apparent. This apparently different condition is the result of the massive development of the adductor mandibulae in *Hemicetopsis,* so as to nearly completely cover the dorsal surface of the levator. Removal of the anterior part of the adductor reveals, however, that the form of the underlying levator arcus palatini in *Hemicetopsis* is comparable to that in other cetopsines.

FIGURE 10.—*Helogenes marmoratus*, AMNH 91372, dorsal elements of branchial arches, dorsal view of left side, anterior at top. Larger stippling represents cartilage. (Scale bar = 1 mm.)

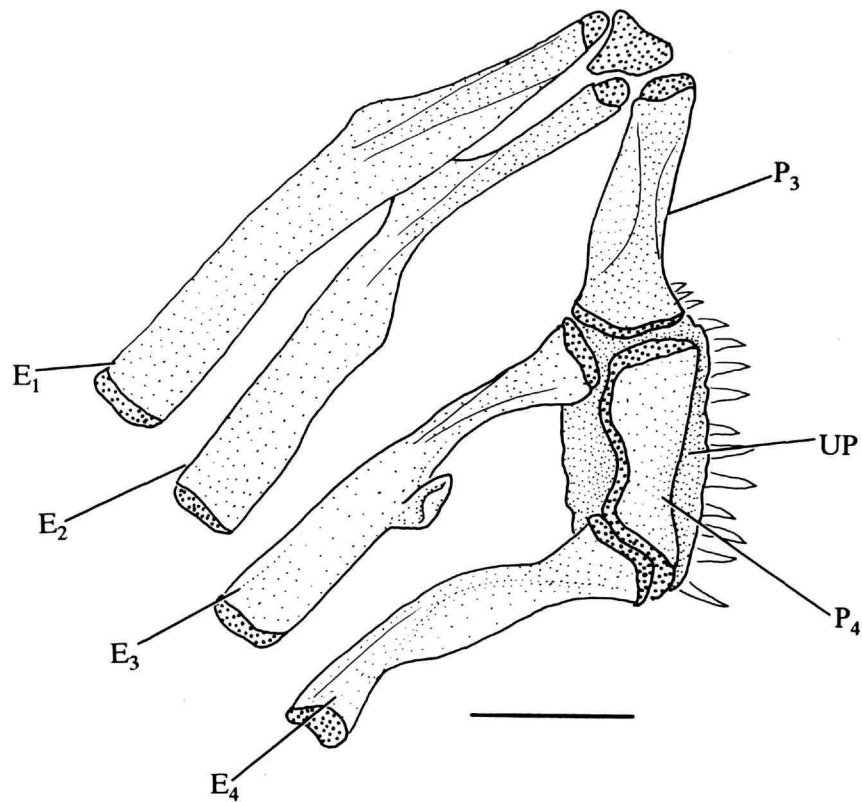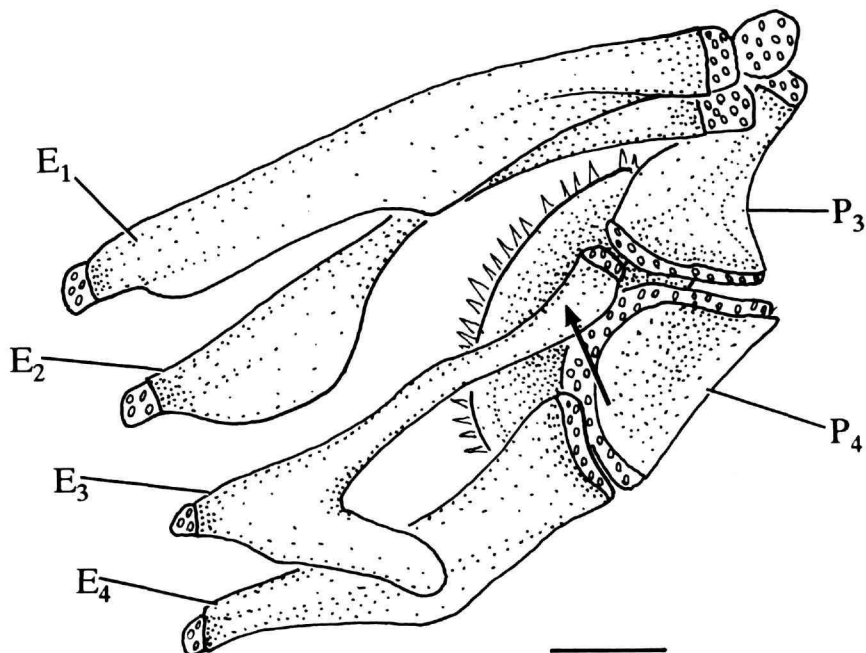FIGURE 11.—*Paracetopsis bleekeri*, AMNH 97234, dorsal elements of branchial arches, dorsal view of left side, anterior at top. Larger stippling represents cartilage. (Scale bar = 1 mm.)
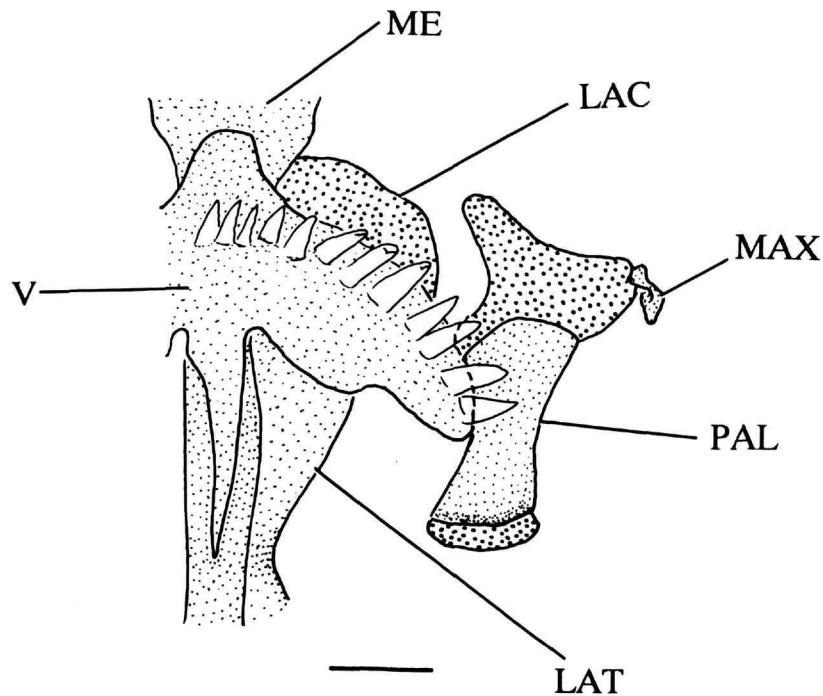
FIGURE 12.—*Pseudocetopsis plumbeus*, USNM 257763, palatine and part of ethmoid region, ventral view of left side, anterior at top. Larger stippling represents cartilage. (Scale bar = 1 mm.)

6. *Dorsal portion of hyomandibula extended anteriorly along ventrolateral margin of neurocranium.* In the plesiomorphic condition for siluriforms, the anterodorsal portion of the hyomandibula does not extend significantly beyond the anterior limit of its synchondral articulation with the neurocranium (Figure 7). The Cetopsinae display an apomorphic modification of the hyomandibula where the anterodorsal portion of the bone continues anteriorly beyond the region of synchondral articulation with the neurocranium, and is adpressed to the ventrolateral margin of the neurocranium (Figure 6). The tight, direct bone-to-bone contact between the anterior portion of the hyomandibula and neurocranium is considerably longer than their synchondral articulation. This anterior extension increases the attachment area between the hyomandibula and the neurocranium, thus apparently providing a firmer support for the hyomandibula. A somewhat similar condition occurs in the Diplomystidae, although the anterior extension of the anterodorsal portion of the hyomandibula in this family is far less marked than in cetopsines. Even though the occurrence of a similar anterodorsal expansion of the hyomandibula in diplomystids casts some doubt on the polarity of the presence of the modification per se, the more extreme unique condition in cetopsines can be considered derived for the subfamily.

7. *Olfactory capsule partly protected by layer of cartilage-like tissue.* The prominent snout seen in all cetopsines accommodates a pair of markedly enlarged olfactory organs and associated nasal cavities. Although the enlargement of the olfactory organ is difficult to quantify precisely, a number of qualitative apomorphic modifications are seen in connection with its relative enlargement. Usually in siluriforms, the nasal capsule lies posterior to the mesethmoid cornua with the anterodorsal surface of the capsule bordered by the posterior face of the cornua. Cetopsines, in contrast, have the nasal organ and capsule displaced dorsally and anteriorly. The organ and capsule as a result lie completely dorsal to the mesethmoid cornua, which now borders the anteroventral rather than anterodorsal surface of the capsule.

Also apparently associated with the enlargement of the olfactory organs is the presence of shelves formed by rigid connective tissue that borders the olfactory capsule anteriorly and usually also mesially. These shelves are transparent in cleared and stained preparations and attach to the surface of the mesethmoid. They extend laterally from the dorsal margin of the mesethmoid shaft and dorsoposteriorly from the posterior margin of the cornua. The tissues forming the shelves have a cartilage-like gross appearance, but they do not demonstrate as much
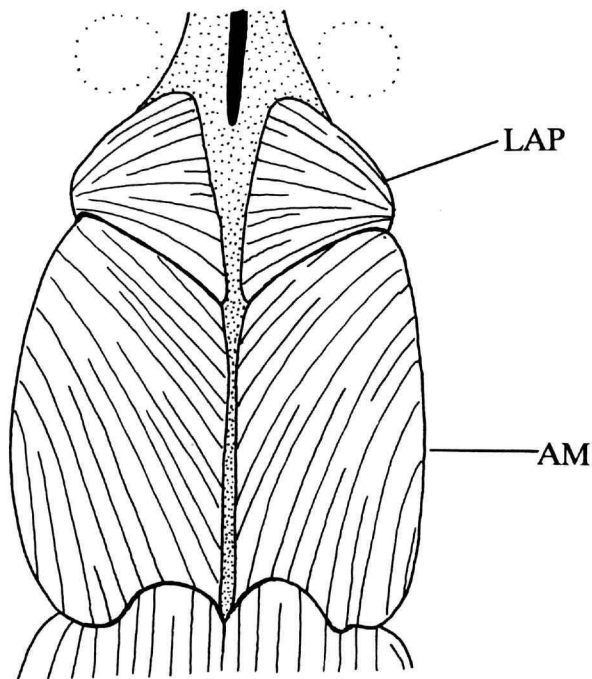
FIGURE 13.—*Paracetopsis occidentalis*, USNM 76971, head musculature, dorsal view, anterior at top. Stippling represents bone. Profile of eyes indicated by dots.

affinity for alcian blue as do remaining skull cartilages. Although the type of tissue forming these shelves remains undetermined, the structures evidently serve as support for the integument surrounding the nasal capsule and apparently provide mechanical protection at the borders of the enlarged olfactory organ. In species with small body size, like *Pseudocetopsis minutus*, only the dorsoposteriorly directed shelves on the mesethmoid cornua are well defined.

The modifications in size and position of the olfactory organ on the one hand, and the associated protective shelf on the other, likely serve as independent evidence for cetopsine monophyly. However, in view of the still poor knowledge about the exact nature of the olfactory shelf, the various apomorphic alterations in the olfactory region of cetopsines are conservatively subsumed into a single character.

HELOGENINAE CLADE

1. *Third basibranchial and associated cartilage greatly expanded posteriorly.* The posterior margin of the cylindrical third basibranchial in most Siluriformes and most other otophysans is transversely flat and bordered posteriorly by a small cartilage. In the Helogeninae uniquely, the posterior margin of the third basibranchial

is markedly expanded laterally, with a fan-like profile in a dorsal view (Figure 5). The posterior cartilage of the bone is comparably expanded, forming a semicircular rim around the posterior margin of the third basibranchial.

2. *Second hypobranchial with anterior concavity.* The anterior margin of the second hypobranchial in siluriforms is primitively straight or slightly convex. In helogenines, the second hypobranchial, which is totally cartilaginous in this subfamily, has a well-defined concavity along its anterior margin when seen from a dorsal view (Figure 5).

3. *Distal cartilage of fifth ceratobranchial with an ossification at its posterior tip.* The posterior tip of the fifth ceratobranchial in siluriforms primitively terminates in a rod-like cartilage without any included independent ossifications. Helogenines are the only catfishes with an additional ossification on the distal portion of the posterior cartilage of the fifth ceratobranchial (Figure 14), a condition hypothesized as derived. This ossification is evident only in large specimens of *Helogenes*.

4. *Outer row of teeth on dentary enlarged and widely spaced.* The plesiomorphic condition for the dentary teeth of siluriforms is one in which the individual teeth slightly increase in size gradually towards the outer margin of the bone. In addition, the distance between individual teeth is approximately uniform among the different tooth rows. In *Helogenes,* in contrast, the lateral teeth of the anterior portion of the dentary are markedly larger than all other teeth on the bone (Figure 15). Furthermore, the distance between the individual teeth on the anterior portion of the dentary is greater than that between teeth of other rows. This condition is hypothesized as uniquely derived for the subfamily.

Elsewhere within Siluriformes, modifications of dentary teeth reminiscent of those in the Helogeninae are known to occur only in the predatory genus *Bagarius* of the Asiatic family Sisoridae. In *Bagarius,* however, the enlarged widely separated teeth are on the innermost tooth row, the reverse of the condition in helogenines and thus not homologous.

5. *Mesethmoid unossified mesially in adults.* Primitively in siluriforms and ostariophysans, the mesethmoid is well ossified along its dorsal and ventral shelves, and there is extensive ossification mesially that is continuous with the equally ossified mesethmoid cornua. In helogenines, the mesial portion of the mesethmoid is mostly cartilaginous, and only the cornua are ossified (Figure 16). The cornua are attached to the remainder of the neurocranium primarily by cartilage. The only remaining bony connections of the cornua with the rest of the neurocranium are the narrow ossified dorsolateral bridges on each side of the skull. This limited ossification of the mesethmoid, not present in other examined
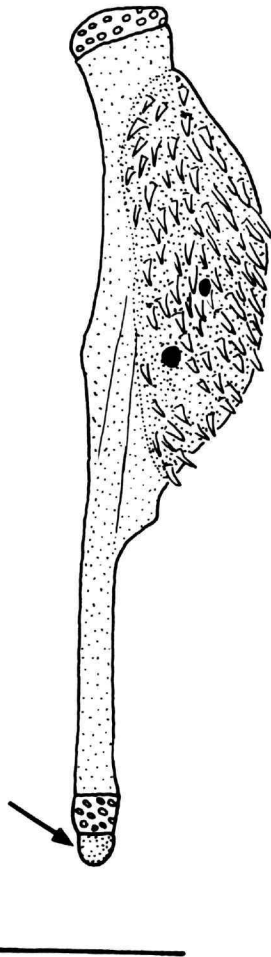
FIGURE 14.—*Helogenes marmoratus*, AMNH 91372, fifth ceratobranchial, dorsal view of left side. Arrow indicates distal ossification. Open circles represent cartilage. (Scale bar = 1 mm.)

catfishes, occurs even in the largest specimens examined of the subfamily, and it is certainly a derived adult condition.

6. *Sphenotic not contacting supraoccipital.* The arrangement of neurocranial bones in the Helogeninae is among the most highly modified of all siluriforms. The most conspicuous of those specializations is the lack of contact between the sphenotic and supraoccipital (Figure 16), a trait first observed by Chardon (1968:153) and later commented on by Lundberg (1975:70). The loss of such contact between the ossifications is the result of a number of associated modifications in surrounding bones. One of them is the reduction in size of the supraoccipital. In most catfishes the supraoccipital is a major element of the posterior part of the skull roof, whereas in *Helogenes* the supraoccipital is reduced to a narrow bone with a maximum width roughly 10% of the total length of the neurocranium when seen in dorsal view. The small size of the supraoccipital resembles the condition in characiforms and other nonsiluriform ostariophysans. In all catfishes with the exception of *Helogenes* the supraoccipital occupies an area topologically corresponding to both the primitive supraoccipital and the parietal of other ostariophysans. Such a topological position is compatible with the ontogenetic fusion observed between those two ossifications in siluriforms (Bamford, 1948). In *Helogenes,* in contrast, a large plate-like bone fills in the space between the supraoccipital and sphenotic occupied by the larger supraoccipital in other catfishes.

The homologies of this plate-like, sensory canal-bearing bone between the supraoccipital and sphenotic in helogenines have been controversial. Lundberg (1975) discussed possible homologies of the ossification with the posttemporal, parietal, intertemporal portion of pterotic, and dermosphenotic, favoring the latter hypotheses. Fink and Fink (1981:332–334) contested Lundberg's views on the homologies of the elements of the catfish shoulder girdle but did not specifically discuss

FIGURE 15.—*Helogenes marmoratus*, AMNH 13332, lower jaw, lateral view of right side. (Scale bar = 1 mm.)
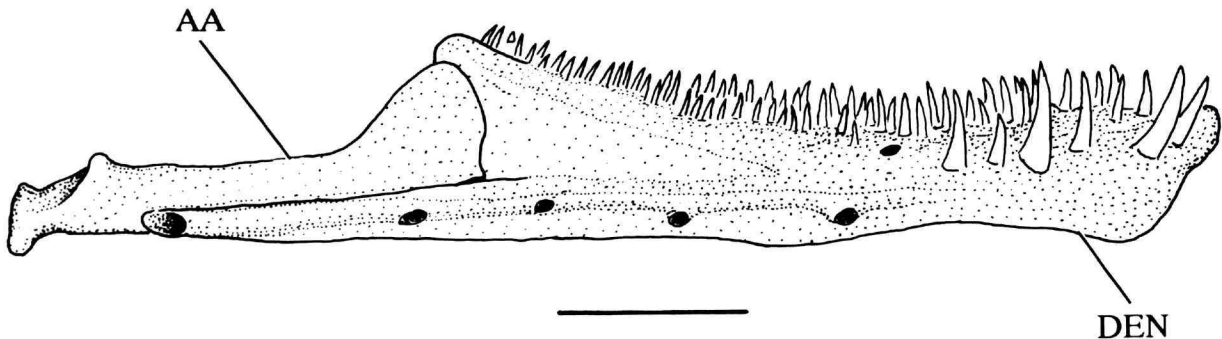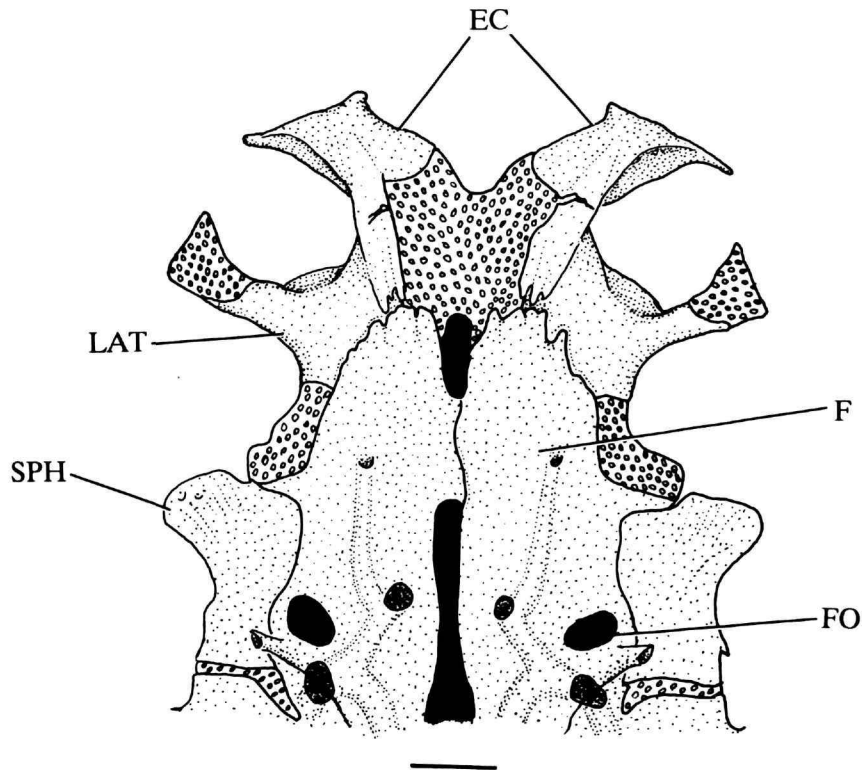
FIGURE 16.—*Helogenes marmoratus*, AMNH 91372, anterior portion of neurocranium, dorsal view, anterior at top. Open circles represent cartilage. (Scale bar = 1 mm.)

the situation in helogenines. Regardless of which hypothesis of transformational homology is favored, the arrangement of the posterior skull-roof bones in helogenines is unique and is certainly synapomorphic for the subfamily. Most likely the array of modifications in the posterior part of the skull in helogenines encompasses several different characters; however, we conservatively consider them as a single apomorphy until such time as the problem can be analyzed in depth.

7. *Large paired fontanel in frontal.* The skull roof of Siluriformes primitively lacks any large openings other than the median cranial fontanels. The Helogeninae has a pair of conspicuous round openings located on the frontal, close to its border laterally with the sphenotic (Figure 16). These paired fontanels, which we name frontal fontanels, have not been mentioned previously in the literature, and they are not represented in the only illustration of a complete dorsal view of a helogenine skull published to date (Lundberg, 1975, fig. 4). The helogenine frontal fontanels are true fontanels, and not simply fossae, as they are actual openings to the inside of the neurocranium, rather than depressions in the bone.

The openings are not passageways for nerves or blood vessels and thus are not foramens. Dissections of cleared and stained and alcohol-preserved specimens did not reveal any associated modifications of nerves, blood vessels, or other soft structures close to the paired fontanels.

8. *Posterior process of vomer reduced or absent.* The vomer in siluriforms primitively consists of an anterior laterally expanded portion that sometimes bears tooth plates, and a narrow posterior median shaft usually ankylosed to the anterior portion of the parasphenoid. The vomer in helogenines shows an apomorphic reduction of the posterior process (Figure 17), which is completely lacking in some individuals. The shape of the whole vomer in the taxon is very irregular and varies markedly intraspecifically.

DISCUSSION

A number of additional characters found in the course of this study could not be precisely assessed as to their exact phylogenetic level. For the most part these apparently are
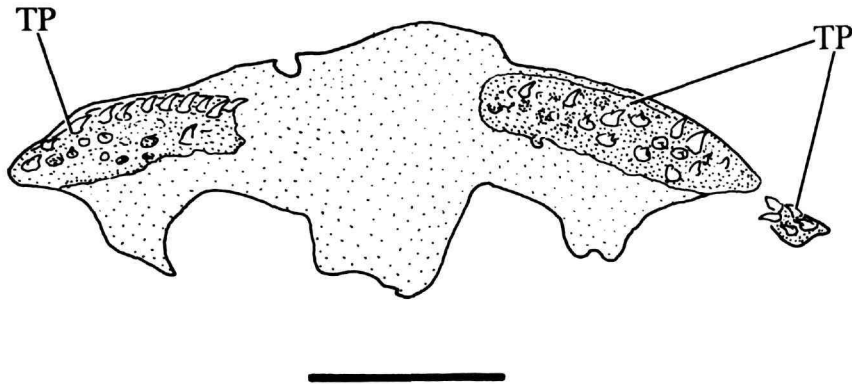
FIGURE 17.—*Helogenes marmoratus*, AMNH 91372, ventral view of vomer, anterior at top. (Scale bar = 1 mm.)
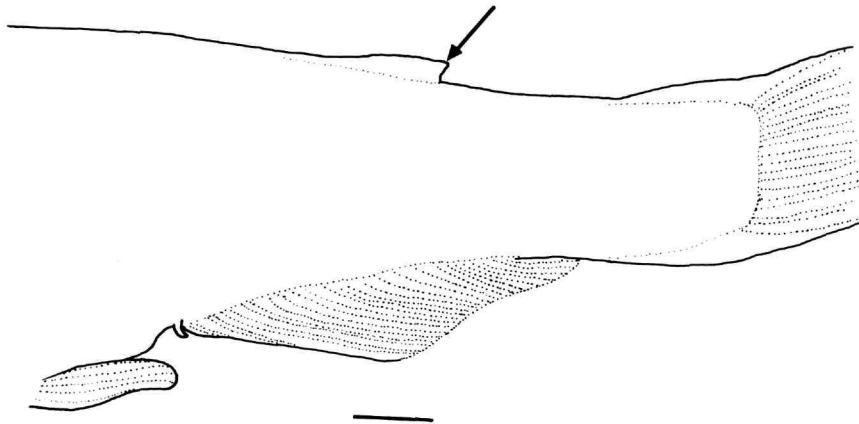
FIGURE 18.—*Cetopsis coecutiens*, juvenile, USNM 265707, 18.9 mm SL; posterior part of body, lateral view of left side. Arrow indicates adipose fin. (Scale bar = 1 mm.)

derived traits that are absent in a few representatives of the clades above. The nonuniversal distribution of these characters makes their phylogenetic implications uncertain at present. Some of the characters of interest present in the expanded Cetopsidae are shared with a few other catfish groups and eventually may prove useful in elucidating the position of the family within Siluriformes. Although a detailed discussion of that issue is not the objective of this paper, it is appropriate to call attention to these potentially informative features.

An adipose dorsal fin is absent in the adult stage of all members of the Cetopsinae; however, a well-developed adipose fin is present in the smallest juvenile examined of the subfamily (Figure 18, *Cetopsis coecutiens*, 18.9 mm SL, USNM 265707). This juvenile trait is clearly a differentiated adipose fin, and not simply a larval fin-fold, because the fold is otherwise almost absent in the specimen, and the putative fin clearly has a posterior free flap typical of well-formed adipose fins. In the Helogeninae, an adipose fin usually is present, but

it is always extremely reduced in size, and proportionally among the smallest of all siluriforms. As shown by Vari and Ortega (1986:4–5), the development of the adipose fin is variable within some populations of *Helogenes marmoratus*, with total absence one extreme. It also seems to be completely absent in some of the other populations of the species (Vari and Ortega, 1986). The tendency towards reduction and loss of the adipose fin in helogenines and the total absence of the fin in adult cetopsines may be considered further support for a hypothesis of cetopsid monophyly. Under this interpretation, the variable presence/reduction/absence of the adipose fin is a synapomorphy for helogenines plus cetopsines, whereas the more extreme state (complete absence) in adult cetopsines is, in turn, apomorphic for a less-inclusive clade. This evidence obviously relies on accepting the homology between variable presence of the adipose fin in helogenines and its invariant absence in adult cetopsines. Because acceptance of this premise may not be trivial theoretically, and also because the adipose

fin apparently has been lost independently in several catfish lineages (e.g., most trichomycterids, aspredinids, and some loricariids in South America, and clariids, chacids, and plotosids in the Old World), we do not consider the reduction and/or absence of the adipose fin to be as conclusive as the characters discussed above.

Most catfishes have strong spine-like structures anteriorly on their dorsal and pectoral fins. The particular morphogenesis of these "spines" is unique to siluriforms (Reed, 1924) and constitutes a synapomorphy for the order. In view of the presence of these spines in diplomystids, hypsidorids, and most other catfishes, it is probable that their presence is primitive for siluriforms. The spines are weakly developed or totally absent, presumably as a result of reduction, in a number of catfishes, including the Cetopsidae, Trichomycteridae (exclusive of *Nematogenys*), some members of the Ictaluridae, Amphiliidae, Sisoridae, and the subfamily Rhamdiinae in the Pimelodidae. It is clear that all these "reductions" are not a single character state, because the degree of reduction and details of anatomy indicate that the morphological basis for the absence of a spine-like structure varies fundamentally among these groups.

The most extreme cases are those in which the first ray is structurally indistinguishable from the remaining rays of the fin, being composed of unmodified and unfused rectangular lepidotrichial segments (e.g., most trichomycterids). The identity of the element as a modified spine is indicated by its being unbranched, undivided, and having a slightly thicker base. The degree of pectoral-spine reduction varies to a degree in cetopsids, but no member of the family has either a plesiomorphic pectoral- or dorsal-fin spine or a completely soft first ray. In all cases, the proximal third of the first ray is rigid near the base, where it retains the primitive spine-like morphology with near complete fusion between fin-ray segments. The distal portion, however, remains highly flexible with unfused ray segments. All other catfish clades with similar reductions (see listing above) seem to be more closely related to forms with fully formed pectoral- and dorsal-fin spines than they are to cetopsids (de Pinna, 1993), indicating that fin-spine reductions arose independently a number of times within siluriforms. If this hypothesis is correct, the fin-spine reduction in cetopsids constitutes an additional synapomorphy for the group.

Arratia (1987) observed that the Diplomystidae is characterized by a lap joint between the hyomandibula and metapterygoid. The character was offered as a synapomorphy for the family and is actually absent in practically all other siluriforms. It is not, however, unique to diplomystids. As noted above, the Cetopsidae has a very similar configuration of the articulation between the hyomandibula and the metapterygoid, and it is apparently the only taxon other than for diplomystids with this condition (Figures 6, 7). The lap joint can be considered derived within siluriforms in view of the absence of the trait in related ostariophysan outgroups. Nonetheless, the phylogenetic implications of the lap joint are ambiguous in the context of our present knowledge about catfish interrelationships. The hypothesis of relationships derived solely from the lap joint is that diplomystids and cetopsids form a clade excluding other siluriforms. This hypothesis, however, is untenable in view of the overwhelming evidence (see Chardon, 1968; Fink and Fink, 1981; Grande, 1987; Arratia, 1987; de Pinna, 1993) supporting the Diplomystidae as the sister group of all other catfishes, living and fossil. The latter hypothesis of relationships can be considered sufficiently well corroborated to serve as a topological constraint in this discussion. Given that constraint, there are only two phylogenetic interpretations for the presence of a lap joint exclusively in diplomystids and cetopsids. The first one is that the character originated independently in the two taxa and thus constitutes a synapomorphy supporting the monophyly of cetopsids and diplomystids separately. The second interpretation is that the lap joint is a synapomorphy for siluriforms, which secondarily reversed to the primitive condition in all members of the order except diplomystids and cetopsids. This view implies that cetopsids and diplomystids are adjacent in catfish phylogeny. The most interesting corollary of this interpretation is that it indicates that the Cetopsidae may be the sister group to all other living nondiplomystid catfishes. This possibility agrees with previous observations about various conspicuously primitive characteristics in some members of the Cetopsidae. These include the presence of six separate hypurals in the caudal skeleton of Cetopsinae (Lundberg and Baskin, 1969), and the clear separation of the fourth and fifth vertebrae and the independence of their neural arches from one another in helogenines (Chardon, 1968:155). Interestingly, Mo (1991) proposed the Helogeninae (his Helogenidae) as the sister-group of all nondiplomystid catfishes, and the Cetopsinae (his Cetopsidae, depicted as a paraphyletic group) as the next sister group to remaining siluriforms. More in accordance with the findings of the present paper, de Pinna (1993) proposed the Cetopsinae and Helogeninae (therein recognized as families) as forming a clade, itself the sister group of all other nondiplomystid, nonhypsidorid siluriforms.

A critical evaluation of the putatively primitive characters mentioned above lies outside the scope of this study, but we believe, however, that the admittedly limited evidence available thus far indicates that the rather poorly known Cetopsidae may occupy an important phylogenetic position within Siluriformes, and it is certainly deserving of further study within such a broader context.

New Classificatory Scheme

The following classification expands the current Cetopsidae to incorporate the Helogenidae. The composition of the subfamilies Cetopsinae and Helogeninae is identical to that of current Cetopsidae and Helogenidae (Regan, 1911; Greenwood et al., 1966; Chardon, 1968; Nelson, 1984; Burgess, 1989). The phylogenetic hypothesis is consistent either with the retention

of cetopsids and helogenids as separate families, the present situation, or their recognition as a single family. We prefer to unite them into an expanded Cetopsidae given that the recognition of two families in a relatively nonspeciose lineage (a combined total of approximately 20 species) serves little purpose.

The family name Cetopsidae is attributable to Bleeker (1858), who erected his Cetopsini as group "A" of his subfamily Silurichthyoidei. Cuvier and Valenciennes (1840) previously had referred to *Cetopsis* in the French vernacular as "Des Cétopsis." There is no clear indication that Cuvier and Valenciennes' "Des Cétopsis" was intended as a suprageneric name (it included only the genus *Cetopsis*), as required by the International Code of Zoological Nomenclature for the availability of family-group names. Therefore, the family Cetopsidae is considered Bleeker's and not Cuvier and Valenciennes'. A family-group name based on *Cetopsis* has priority over that based on *Helogenes* (Regan's Helogenidae dates from 1911), hence the family formed by former cetopsids and helogenids is referred to as Cetopsidae.

Helogenes was first assigned a family-group taxon by Regan (1911:573), who ranked it as family Helogenidae. Eigenmann (1912:207) published Helogeneidae [sic] as a new family, presumably unaware of Regan's nearly simultaneous publication. However, Regan has priority and is the author of family-group names based on *Helogenes*.

The name Cetopsidae has not been used previously with the composition proposed here (i.e., former Cetopsidae plus former Helogenidae). Consequently, our use of the name constitutes a new usage. A subfamily-level name based on *Helogenes* has not been employed previously, therefore use of Helogeninae constitutes a new rank. Use of Cetopsinae is not a new rank because Eigenmann and Eigenmann (1890), Regan (1911), and Miranda Ribeiro (1912), among others, used it with identical composition and rank, although as a subfamily of the Trichomycteridae.

As mentioned by Vari and Ortega (1986:4), several authors adopt the erroneous form "Helogeneidae," most likely following Eigenmann's (1912) spelling. That derivation of the family name is wrong, as pointed out by Steyskal (1980:174), because a family based on *Helogenes* should be Helogenidae, as correctly done by Regan (1911).

Family CETOPSIDAE Bleeker, 1858, new usage

CETOPSINI Bleeker, 1858 [Siluroidei, Silurichthyoidei, in part].
CETOPSINAE Gill, 1872 [Siluridae, in part].—Eigenmann and Eigenmann, 1890 [Pygidiidae, in part].—Regan, 1911 [Trichomycteridae, in part].
HELOGENIDAE Regan, 1911.—Burgess, 1989.
CETOPSIDAE Miranda Ribeiro, 1912.—Berg, 1940.—Schultz, 1944.—Greenwood et al., 1966.—Chardon, 1968.—Nelson, 1984.—Burgess, 1989.
HELOGENEIDAE Eigenmann, 1912.—Berg, 1940.—Greenwood et al., 1966.—Chardon, 1968.—Nelson, 1984.
HELOGENIIDAE Robins et al., 1991.

DIAGNOSIS.—Diagnosed as a monophyletic group on the basis of the following synapomorphies:

1. Maxilla with a single proximal head.
2. Posterior portion of palatine depressed, expanded lateromesially.
3. Anterior distal cartilage of palatine extending onto mesial surface of the bone.
4. Anterior cartilage of palatine expanded anteriorly.
5. Lap joint present between opercle and interopercle.
6. Attachment of interoperculo-mandibular ligament located on dorsal portion of interopercle.
7. Interopercle expanded along dorsoventral axis, deeper than long.
8. Shaft of second basibranchial expanded laterally, with convex lateral margins (reversed to primitive condition in some small paedomorphic cetopsines).
9. Metapterygoid elongate, roughly rectangular in shape.

External characters not unique to the Cetopsidae but which are useful, in combination, to identify the family include: orbital margin not free; dorsal and pectoral fins without pungent spines; anal-fin base long (23 to 34 rays); all barbels thread-like along their entire lengths, thickening very little from tip to base; and nasal barbels absent.

Subfamily CETOPSINAE Bleeker, 1858

CETOPSINI Bleeker, 1858 [Siluroidei, Silurichthyoidei, in part].
CETOPSINAE Gill, 1872 [Siluridae, in part].—Eigenmann and Eigenmann, 1890 [Pygidiidae, in part].—Regan, 1911 [Trichomycteridae, in part].
CETOPSIDAE Miranda Ribeiro, 1912.—Berg, 1940.—Schultz, 1944.—Greenwood et al., 1966.—Chardon, 1968.—Nelson, 1984.—Burgess, 1989.

DIAGNOSIS.—Diagnosed as a monophyletic group on the basis of the following synapomorphies:

1. Posterior cartilaginous process of basipterygium elongate, dorsoventrally flattened, and ramified distally (ramifications lacking in the extremely paedomorphic *Bathycetopsis*).
2. Anterior tip of third epibranchial curved anteriorly to articulate directly with third pharyngobranchial.
3. Palatine articulating with lateral ethmoid only through its anterior cartilage.
4. Adductor mandibulae muscle hypertrophied, extending dorsally to the midline of neurocranium. (See also "Note Added in Proof" following the previous discussion of this character.)
5. Levator arcus palatini muscle enlarged and prominent in dorsal view.
6. Dorsal portion of hyomandibula extended anteriorly along ventrolateral margin of neurocranium.
7. Olfactory capsule partly protected by wall of trans-

parent cartilage-like tissue originating on mesethmoid.

External characters not unique to the Cetopsinae but which are useful, in combination, to identify the subfamily include: anterior nostrils located on upper lip, directed anteriorly on the anteriormost point of head; upper and lower lobes of caudal fin of similar size; origin of dorsal fin located on anterior half of SL; branchiostegal membranes united to isthmus to some degree; barbels shorter than head length; all barbels fitting into a well-defined groove on skin for most or all of their lengths; adipose fin absent in adults; and snout protruded anteriorly well beyond mouth.

Subfamily HELOGENINAE Regan, 1911, new rank

HELOGENIDAE Regan, 1911.—Burgess, 1989.
HELOGENEIDAE Eigenmann, 1912.—Berg, 1940.—Greenwood et al., 1966.—Chardon, 1968.—Nelson, 1984.
HELOGENIIDAE Robins et al., 1991.

DIAGNOSIS.—Diagnosed as a monophyletic group on the basis of the following synapomorphies:

1. Third basibranchial and associated cartilage greatly expanded posteriorly.
2. Second cartilaginous hypobranchial with anterior concavity.
3. Distal cartilage of fifth ceratobranchial with independent ossification at posterior tip.
4. Outer row of teeth on dentary enlarged and widely spaced.
5. Mesethmoid unossified medially in adults.
6. Sphenotic not contacting supraoccipital.
7. Large paired fontanel in frontal.
8. Posterior process of vomer reduced or absent.

External characters not unique to the Helogeninae but which are useful, in combination, to identify the subfamily include: anal-fin base very long, with 32 to 49 rays; ventral lobe of caudal fin longer and wider than dorsal lobe in adults (the inverse situation occurs in very young juveniles, see below); adipose fin minute or absent, when present its length distinctly greater than width of base; and dorsal fin short, with five rays, its origin located on posterior half of SL.

Comparisons with Previous Hypotheses and Classifications

The first time *Helogenes* was assigned to a higher-level group more restrictive than catfishes was by Günther (1864:66), who placed it together with the Neotropical *Hypophthalmus* in his group Hypophthalmina, erected on the basis of the common possession of an anal fin with an elongate base. A family Hypophthalmidae including both *Hypophthal-*

mus and *Helogenes* was adopted by Eigenmann and Eigenmann (1888:120; 1890:312; 1891:35) and Eigenmann (1910:398).

Regan (1911:573) placed *Helogenes* in its own family and stated that "the relationships of this genus [*Helogenes*] appear to be about equally close with the Pimelodidae and with *Cetopsis*." Regan, however, did not have access to skeletal material of helogenids and was therefore unable to formulate any precise ideas on the phylogenetic affinities of the genus.

Eigenmann (1912) also adopted a separate Helogenidae (his Helogeneidae) and pointed out various significant differences between *Helogenes* and *Hypophthalmus*. In Eigenmann's view, the differences far outweighed the similarities between those two taxa and, thus, justified familial distinctiveness. The possible relationships of the two families to other catfishes were not, however, discussed. A separate Helogenidae was adopted by most authors subsequent to Regan (1911) and Eigenmann (1912), including Jordan (1923), Berg (1940), Gosline (1945), Greenwood et al. (1966), Chardon (1968), Lundberg and Baskin (1969), Nelson (1984), Burgess (1989), and Ferraris (1991).

Bertin and Arambourg (1958) included *Helogenes* in their family Schilbidae, which included not only today's schilbids, but also pangasiids and hypophthalmids. The union of this heterogenous assemblage was based mainly on the common possession of an elongate anal fin; however, that feature is present in several other catfish groups. Although Bertin and Arambourg (1958:2303) mention *Cetopsis* in passing in their general overview of catfishes, they do not refer to cetopsids in their taxonomic account. Their opinion about the systematic position of the family is therefore unclear.

Dahl (1960) was the only previous author to suggest that the Cetopsidae and Helogenidae (in the sense of the period) might be closely related. In referring to *Leyvaichthys castaneus* Dahl (= *Helogenes castaneus*), he stated that "...the total lack of an adipose fin also reminds of the Cetopsidae, to which the Helogenidae may be phylogenetically allied" (Dahl, 1960:304). Dahl failed to identify characters other than for the absence of adipose fin in support of his hypothesis, nor did he address the problem that the adipose fin is variably present in *Helogenes*. His opinion probably was based on some undefined sense of overall similarity between the two families.

The internal anatomy of *Helogenes* was first reported on in some detail by Chardon (1968:152–155). He described the absence of contact between the sphenotic and supraoccipital (synapomorphic for the genus and subfamily, see above). Chardon also stated that the shape of the frontal-supraoccipital suture was peculiar to *Helogenes*, an observation we could not corroborate. He also pointed out similarities in overall body shape between *Helogenes* and the Siluridae and Schilbidae, in particular the presence of an elongate and ventrally curved caudal peduncle. More importantly, Chardon (1968:155) observed that *Helogenes* has some primitive conditions that

occur elsewhere among catfishes only in diplomystids. These were the distinct separation between the fourth and fifth vertebrae and the independence of their neural arches. Concerning the Cetopsinae (his Cetopsidae), Chardon (1968) remarked that the group is more primitive than the Pimelodidae and Bagridae because of the very flexible attachment of its posttemporal bone. That author also observed a number of similarities between the Cetopsinae and Siluridae, but Chardon correctly pointed out that these traits were present in other primitive siluriforms (i.e., symplesiomorphies) and therefore not appropriate evidence to unit members of Cetopsinae with another family. As part of his argument, Chardon also reviewed and dismissed characters previously used to align cetopsines and trichomycterids in the same taxon (a common view at one time, see Eigenmann and Eigenmann, 1890; Regan, 1911; Berg, 1940). The alignment of cetopsines and trichomycterids was first shown to be erroneous in an insightful, but frequently overlooked, paper by Peyer (1922). Peyer unambiguously demonstrated that cetopsines are not closely related to trichomycterids because they lacked all the traits that characterize the larger group of loricarioids, which includes trichomycterids.

Mo (1991:194) tentatively proposed that the Cetopsinae (his Cetopsidae) was a nonmonophyletic group, with *Hemicetopsis* and the remaining cetopsines as successive branches close to the base of the siluriform cladogram. As previously noted (de Pinna and Ferraris, 1992), his conclusion about cetopsine nonmonophyly relies mostly on the fact that none of the unique characteristics of the group was included in the analysis. The additional data supplied in the present work includes numerous synapomorphies for the Cetopsinae, further countering the hypothesis of the group's paraphyly. Mo (1991) also proposed some uniquely derived features for the Helogeninae (his Helogenidae) and proposed the group as the sister group to all nondiplomystid catfishes. Although that author did not recognize a sister-group relationship between his cetopsids and helogenids, interestingly his cladograms (Mo, 1991:203, 206) place the two taxa in adjacent positions (i.e., as successive branches).

Description of the Juvenile of *Helogenes*

Juveniles of the Helogeninae have not been reported to date, and apparently they are extremely rare in collections. During this study we located a few small juveniles of *Helogenes* that we describe below, with particular emphasis on a number of unusual features not previously reported in catfishes.

The smallest known specimen of Helogeninae is a 10.4 mm SL individual (ZSM 28285) collected by E.J. Fittkau, 8 June 1962, at riffles in Igarapé Aracu, located 15 km from Manaus, on a road to Rio Branco, State of Amazonas, Brazil. This specimen of *Helogenes* is tentatively identified as *Helogenes*

marmoratus. Although diagnostic characters for the species cannot be unambiguously observed in this juvenile, the collection locality is within a region (vicinity of Manaus, Brazil) where only *H. marmoratus* is known to occur (Vari and Ortega, 1986, fig. 9).

The gap between the ZSM specimen and adults is filled by three somewhat larger specimens of *H. marmoratus*, 13.9, 14.8, and 20.3 mm SL. The first (USNM 269975) was collected by R.P. Vari et al., 2 Dec 1984, in a small stream close to Puerto Ayacucho, Departamento Ature, Estado Amazonas, Venezuela. The other two (MUSM 2717) were collected by H. Ortega and F. Chang, 26 Jan 1990, in a stream at km 3.7 of a road to Cocococha, Río Tambopata drainage, Zona Reservada Tambopata-Candamo, Departmento Madre de Dios, Peru.

It is interesting to note that the two smallest juveniles (ZSM 28285 and USNM 269975) were collected in June and December, respectively. The small size difference between these specimens is perhaps an indication that *Helogenes marmoratus* does not have a rigid yearly seasonality in its reproductive cycle across its range.

We base our description on the ZSM specimen and compare it with adult individuals of *H. marmoratus*, with reference to the intermediate-size USNM and MUSM specimens whenever pertinent. We also provide a section on the integument pigmentation of the USNM specimen, whose skin pigmentation is particularly well preserved.

The ZSM specimen, in reasonable condition, was apparently fixed originally in alcohol, and it has very little integument pigmentation (possibly a result of long preservation). The fins are reasonably intact, and it is still possible to make out their general shape and determine fin-ray counts (Figure 19). The musculature of the caudal peduncle is strongly constricted, seemingly as a consequence of previous damage.

The juvenile of *Helogenes marmoratus* is laterally compressed, albeit less so than adults, and moderately deep. The large head has a subterminal mouth and from a dorsal view an almost semicircular anterior profile. The branchiostegal membranes are free from each other and the isthmus. The tubular anterolaterally directed anterior nostril is located on the anterolateral surface of the upper lip. The tubular posterior nostril is shorter than the anterior nostril and located close to the anterior margin of eye. The barbels have a location similar to those of adults, but they are proportionally shorter and thicker, with blunt tips, a distinct contrast with the very fine tips of adults.

Remnants of a dorsal fin-fold occur anterior and posterior to the dorsal fin. The posterior fold is posteriorly confluent with the dorsal lobe of the dorsal fin and extends along the entire dorsal margin of the caudal peduncle. A notch on the anterior half of this fold constitutes the primordium of the adipose fin. The adipose fin primordium in the juvenile is located immediately posterior to the posterior tip of the dorsal fin in contrast to the adult condition in which the dorsal and adipose
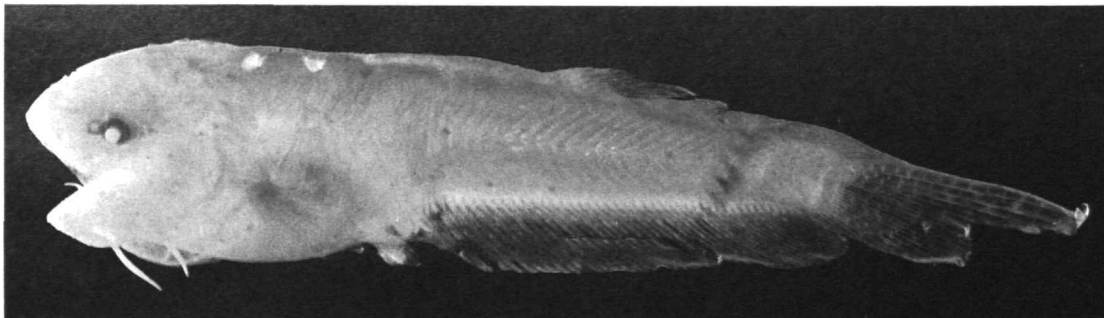
FIGURE 19.—*Helogenes marmoratus*, juvenile, ZSM 28285, Brazil, Amazonas, vicinity of Manaus.
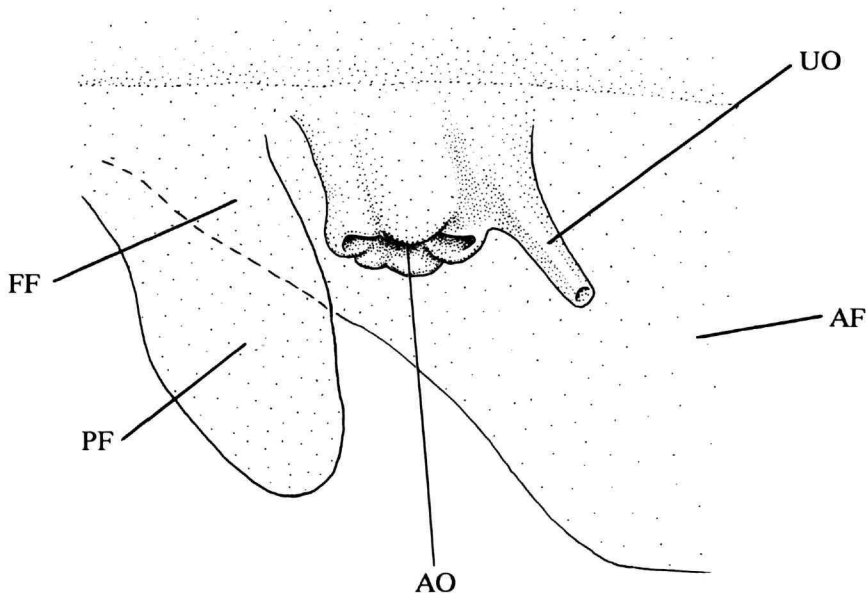

FIGURE 20.—*Helogenes marmoratus*, ZSM 28285, anal and urogenital openings and surrounding structures, lateral view of left side, anterior to left. Pelvic- and anal-fin rays not represented.

fins are distinctly separated. The apparent ontogenetic divergence in the position of the two fins is confirmed by the intermediate position of the adipose fin in the smaller specimen in MUSM 2717.

The small pectoral fin is considerably shorter than HL (in adults it is approximately as long as HL). The pelvic fins are small, but fully independent from the skin covering the remainder of the body. The forked caudal fin has the dorsal lobe longer than the ventral, a condition the inverse of that in adults in which the ventral lobe is always the longer. The transition between the two conditions cannot be observed in intermediate-sized juveniles, all of which have the caudal fin badly damaged. The origin of the dorsal fin is located on the posterior half of the

SL, similar to the condition in adults and unlike the situation in most other siluriforms.

The anal and urogenital openings are not median, but instead they are strongly displaced laterally to the left side of the ventral fin-fold (Figure 20). In the slightly larger USNM specimen, the anal opening already is situated along the ventral midline, but the urogenital opening is still markedly shifted laterally, this time to the right side of the fin-fold. In both specimens the urogenital opening is at the tip of a long, slender, distally narrowing tube. Neither the lateral displacement nor the tubular urogenital opening occur in larger juveniles and adults. The highly unusual asymmetry of the anal and urogenital openings is unknown in other catfish juveniles for

which data are available (Ihering and Azevedo, 1936; Mooker-
jee and Mazumdar, 1950; Karamchandani and Motwani, 1955,
1956; David, 1961; Saigal and Motwani, 1962; Devaraj et al.,
1972; López Rojas and Machado Allison, 1975; Machado
Allison and López Rojas, 1975; Godinho et al., 1978; Fuiman,
1984; Mago-Leccia et al., 1986; Gopinantha Menon et al.,
1989; Xie, 1989; Kossowski and Madrid, 1991). Outgroup
comparisons with other ostariophysans (cf., Fuiman, 1984)
indicate that such displacements are likely derived and possibly
autapomorphic for helogenines. However, the smallest cetop-
sine examined is far larger than the *Helogenes* specimens
showing the asymmetry, with this size difference perhaps
accounting for the apparent absence of the character in
cetopsines. Although the data presently available are too
incomplete to permit a precise assessment of the generality of
the lateral location of the anal and urogenital openings in
juveniles of *Helogenes*, such modifications are certainly an
unusual characteristic of the subfamily that deserves further
research.

PIGMENTATION.—The whole body of the USNM specimen
is covered with a uniform scattering of very small dark
chromatophores, denser dorsally, laterally, and on the dorsal
surface of the head. Overlying that background pigmentation is
a series of five large dark spots widely disposed along the
lateral line. A second series of six spots is located along the
middorsal line, and a few other large spots are irregularly
distributed over the ventral half of caudal region. Smaller, very
dark spots are evenly distributed over the abdomen. A
well-defined, narrow, dark stripe that narrows posteriorly,
extends along the body dorsal to the entire base of the anal fin.

Large, poorly defined spots are irregularly distributed over
the anal, dorsal, and pectoral fins, being most numerous on the
anal. The pelvic fins have a concentration of dark chromato-
phores near their base, with the remainder of the fin hyaline.
The caudal-fin pigmentation is unknown because the fin is
almost completely severed in this specimen.

The pigmentation of the nares is notably dark, more so on the
posterior pair. The barbels have faint concentrations of dark
pigment only near their bases.

The smaller MUSM specimen shows a pigmentation pattern
transitional between that of juveniles and adults. The large dark
spots alongside the lateral line are present but proportionally
smaller and not as dark as in smaller juveniles.

The conspicuous narrow white stripe seen along the lateral
line in adults is absent in all juveniles, except the largest
MUSM specimen (which is nearly an adult), where the stripe is
beginning to develop.

RESUMO

Os bagres neotropicais atualmente considerados como famílias Cetopsidae e Helogenidae são propostos como grupos-irmãos. Os dois taxa compartilham numerosas sinapomorfias, incluindo uma articulação sobreposta entre o opérculo e o interopérculo, um deslocamento dorsal da inserção do ligamento interoperculo-mandibular no interopérculo, e um palatino fortemente deprimido. Alguns destes caracteres derivados são únicos em Siluriformes. Com base na nova hipótese de parentesco, os atuais Cetopsidae e Helogenidae são unidos em um Cetopsidae expandido, por sua vez subdividido nas subfamílias monofiléticas Cetopsinae e Helogeninae. Os Cetopsinae são diagnosticáveis por, entre outros caracteres, um processo posterior do basipterígio expandido e ramificado, uma curvatura anterior do terceiro epibranquial, e uma articulação do palatino com o neurocrânio exclusivamente através da cartilagem anterior do primeiro. Sinapomorfias corroborando monofiletismo de Helogeninae incluem uma redução da ossificação entre os cornua do mesetmoide e o restante do neurocrânio, uma grande fontanela par no frontal, o terceiro basibranquial expandido posteriormente, e a ausência de contato entre o esfenótico e o supraoccipital. Diagnoses filogenéticas são oferecidas para Cetopsidae revisado, Cetopsinae e Helogeninae. A morfologia do estado juvenil de *Helogenes*, que inclui algumas características incomuns talvez únicas ao gênero, é descrita pela primeira vez.

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