Zoological Journal of the Linnean Society, 2007, **150**, 755–813. With 43 figures

A phylogenetic study of the neotropical catfish family Cetopsidae (Osteichthyes, Ostariophysi, Siluriformes), with a new classification

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Received December 2005; accepted for publication December 2006

A hypothesis on the phylogenetic relationships of the neotropical catfish family Cetopsidae is proposed on the basis of the parsimony analysis of 127 morphological characters and most of the species currently recognized. The family and its two recognized subfamilies, the Cetopsinae and Helogeninae, are corroborated as monophyletic, in agreement with recent studies. Previously proposed classifications of the Cetopsinae, however, were found to be poorly representative of the phylogenetic relationships within the subfamily. Major generic rearrangements are implemented in order that the classification of the Cetopsinae reflects the phylogenetic hypothesis. *Pseudocetopsis* Bleeker (1862) was found to be polyphyletic and to include several disjunct lineages. One of these lineages, recently named as the genus *Cetopsidium* Vari, Ferraris, and de Pinna (2005), is the sister group to the rest of the Cetopsinae. *Denticetopsis* Ferraris (1996) is the next sister group to the remainder of the Cetopsinae. The remaining species of the Cetopsinae belong to one of two sister genera, *Paracetopsis* Bleeker (1862) and *Cetopsis* Spix and Agassiz (1829). The latter genus includes species formerly assigned to *Hemicetopsis* Bleeker (1862), *Bathycetopsis* Lundberg and Rapp Py-Daniel (1994) and *Pseudocetopsis* Bleeker (1862). Continued recognition of *Hemicetopsis* and *Bathycetopsis* would have required the creation of several additional new genera for various species previously in *Pseudocetopsis* that form a series of sister groups to a clade composed of *Cetopsis oliveirai* (Lundberg and Rapp Py-Daniel, 1994), *C. coecutiens* (Lichtenstein, 1819) and *C. candiru* (Spix and Agassiz, 1829). *Cetopsis oliveirai* is a highly paedomorphic species that displays surprising similarities with conditions in juvenile specimens of *C. coecutiens*, a species that attains a large body size. Such similarities are not evident in adult specimens of the latter species. A new classification is proposed, within which the subfamily Cetopsinae consists of three tribes, the Cetopsidiini, the Cetopsini and the Denticetopsini. The results of the study form the basis for a discussion of the phylogenetic position of the family within the Siluriformes, the phylogenetic biogeography of the Cetopsidae, paedomorphosis and gigantism in the family, and the effect of different semaphoronts on the intrafamilial phylogeny.

ADDITIONAL KEYWORDS: evolution – gigantism – miniaturization – systematics – taxonomy – whale catfishes.

INTRODUCTION

The South American catfish family Cetopsidae (*sensu* de Pinna & Vari, 1995; Vari & Ferraris, 2003) consists of two externally distinctive clades. The first of these, the subfamily Cetopsinae, includes 37 recognized species (Vari, Ferraris & de Pinna, 2005) occurring over a large portion of northern and central South America, to both sides of the Andean cordilleras. In various portions of their range, the species of the Cetopsinae are called ‘bagre ciego’ (blind catfish) or ‘ciego’ (blind); names reflecting the reduced or absent eyes which characterize members of the subfamily. The common name of the subfamily in English, ‘whale catfishes’, is derived from the robust body and smoothly curved

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head and body profiles of the first described members of this group, features superficially reminiscent of those in some cetaceans. Species traditionally assigned to the genera *Cetopsis* Spix and Agassiz and *Hemicetopsis* Bleeker achieve among the largest body sizes in the family and are notorious for their voracious feeding habits, attacking not only carrion and dying animals but also on occasion healthy fishes (Goulding, 1980: 193; 1989: 184) and even humans (Goulding, 1989: 185). Most species in the Cetopsinae, however, are limited to smaller maximum body lengths and feed on allochthonous insects (Baskin, Zaret & Mago-Leccia, 1980: 184; Saul, 1975: 117; Lundberg & Rapp Py-Daniel, 1994: 387).

The second subfamily in the Cetopsidae, the Helogeninae, consists of four species in a single genus, *Helogenes* Günther (Vari & Ortega, 1986) and has a much more restricted distribution across the Amazon and Orinoco River drainage basins and the rivers of the Guianas. Species of the Helogeninae inhabit small rain forest streams where they feed primarily on allochthonous terrestrial insects (Vari & Ortega, 1986: 15).

The autapomorphic modifications of each of what are herein considered to be the subfamilies Cetopsinae and Helogeninae, together with the lack of detailed anatomical studies of these groups, long made them 'puzzles in catfish systematics', as noted by de Pinna & Vari (1995: 2). Some previous researchers associated species now assigned to the Cetopsinae with taxa that are now placed in the Trichomycteridae, an alignment that was shown to be erroneous by Peyer (1922) and subsequent studies (see de Pinna, 1998: fig. 1). The species of *Helogenes*, in turn, have been associated with various groups in the Siluriformes. Although authors beginning with Regan (1911) and Eigenmann (1912) recognized a separate Helogenidae (the Helogeninae of this study), there were no definitive statements about the relationships of that family to other catfish taxa. In their analysis, de Pinna & Vari (1995) proposed a series of synapomorphies that indicated that the Helogeninae and Cetopsinae were sister taxa and that each subfamily was monophyletic. Subsequently, de Pinna (1998: 292) noted that the Cetopsidae lacked some synapomorphies of all other families in the order Siluriformes except for the Diplomystidae, and in some instances also the fossil family †Hypsidoridae, and consequently placed the Cetopsidae near the base of the cladogram for that order (de Pinna, 1998: fig. 1). Such a hypothesis was in partial agreement with that of Mo (1991) and was later further corroborated by Diogo, Chardon & Vanderwalle (2005) and, with some modifications, Diogo (2005).

Interrelationships within the Helogeninae have not been examined in detail, and studies of the interrelationships within the Cetopsinae have been limited to two unpublished theses (Oliveira, 1988; Milani de Arnal, 1991). These studies provided some information on the internal anatomy of a few members of the Cetopsinae, but did not propose formal hypotheses of intrafamilial phylogenetic relationships. Although some subsequent authors (e.g. Ferraris & Brown, 1991; Lundberg & Rapp Py-Daniel, 1994; Ferraris, 1996) discussed specific phylogenetic questions within the context of their descriptions of new species and genera of the Cetopsinae, there is to date no detailed study of the phylogenetic interrelationships within that subfamily.

In this paper we address the question of the phylogenetic relationships within the Cetopsidae and bring the classification of the family into line with its hypothesized evolutionary history. These results also serve as the basis for an analysis of the biogeographical history of the Cetopsinae and of the phylogenetic position of the Cetopsidae within the Siluriformes.

METHODS

PHYLOGENETIC METHODOLOGY

The systematic methodology employed for proposing hypotheses of relationships was cladistic, or phylogenetic, as first proposed by Hennig (1950, 1966, 1968) and later elaborated upon by many other authors (e.g. Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981; Schoch, 1986; Rieppel, 1988; Swofford & Olsen, 1990; Wiley *et al*., 1991; Forey *et al*., 1996).

The method utilized to search for the hypothesis best supported by the data was strict (or Wagner) parsimony, where character reversals and convergences are allowed and quantified equally (Farris, 1983; Swofford & Maddison, 1987). Parsimony analyses were performed primarily with the computer program NONA, version 2.0 (Goloboff, 1999), in association with its shell WinClada, version 1.00.08 (Nixon, 2002), which was also used for tree manipulations and diagnostics. Data were also analysed with the program Hennig86, version 1.5 (by J. S. Farris; for information on the capabilities and options of that program, see Fitzhugh, 1989; Platnick, 1989; Lipscomb, 1994), implemented with the help of the shell, TreeGardener, version 2.2 (by T. Ramos). Characters with ambiguous state distributions were optimized according to Farris' optimization (Farris, 1970; also known as ACCTRAN, Swofford & Maddison, 1987), which maximizes reversals relative to convergences. That option is considered to be more efficient at preserving hypotheses of primary homology of apomorphic conditions (de Pinna, 1991). Whenever possible, multistate characters were ordered according to the similarity among character states (morphoclines). States in the outgroups or in the most distant outgroup (see below) provided the plesiomorphic end of the series which was coded ‘0’, while other states were ordered sequentially according to their divergence from that condition. Multistate characters for which no single obvious sequence of similarity could be determined were left unordered (i.e. non-additive).

The search for characters to be used as primary data for hypotheses of relationships followed a comparative-anatomical strategy, conducted on one body system at a time. Characters were chosen and coded with a directed effort to avoid preconceived ideas on relationships that would interfere with the process. Accordingly, similarities were chosen as characters no matter how implausible their derivative relationships might appear at first sight. This was done for two reasons. First, it makes the process of a character search and coding less biased. Second, many components of hypothesized relationships are supported mostly, or totally, by homoplastic characters which, if excluded, would result in decreased cladistic resolution. Autapomorphic character states were actively searched for and included in the data matrix. It is expected that at least some of these characters will be informative about relationships once the species of the Cetopsidae that could not be examined anatomically in this analysis become available for phylogenetic study.

Character coding was performed without a priori assumptions about polarity. All polarity inferences were derived a posteriori from the rooting of the tree at Diplomystidae (see below). The discussion and polarity inferences for each character provide a wider comparative framework for the variation described. Character states seen in the Diplomystidae were usually coded as ‘0’, because this would most often reflect a putatively plesiomorphic condition in a wide comparative framework and, thus, follow widespread coding practice. Autapomorphies in the Diplomystidae that were a priori obvious from wider comparisons and/or previously published information were coded as ‘1’, in order to maintain coding consistent with general polarity assumptions.

FRAMEWORK FOR OUTGROUP COMPARISONS, INGROUP AND TERMINAL DELIMITATION

Relationships for ingroup and outgroup taxa were resolved simultaneously, including all relevant terminals in a single analysis of global parsimony, as explained in Nixon & Carpenter (1993). Contrary to the suggestion of those authors, however, the root was not placed in the internode between ingroup and outgroup, which would result in both being monophyletic. Instead, the root was placed at the branch of the most basal clade in the data set according to current knowledge of siluriform relationships. In this case, the root was placed in the Diplomystidae, widely hypothesized to be the sister group to all other members of the Siluriformes, both Recent and fossil (Lundberg & Baskin, 1969; Arratia, 1987; Grande, 1987; Mo 1991; de Pinna, 1993). This hypothesis is generally accepted and provides a solid basis for the rooting decision implemented here (but see ‘Note added in proof’ at end of article). Characters relevant for the resolution of the outgroup portion of the tree were included in the data matrix, and were mainly taken from previous studies dealing with higher-level siluriform relationships (Mo, 1991; de Pinna, 1993).

The ingroup taxa were represented by species recognized in a recent revisionary study (Vari *et al*., 2005). Some of the species recognized in that study are known only from unique or a limited number of specimens, and could not be included in this analysis because relevant data from internal anatomy were unavailable. In all such cases, however, there is apparently a close relative based on external similarity that was represented by more abundant material that yielded specimens appropriate for anatomical study. The position of the more abundantly represented species in the phylogenetic hypothesis served as a guide to the putative phylogenetic position of those taxa not included in the matrix. At a minimum this permitted the correct generic allocation of their less well-known relatives. Data from radiographs permitted examination of some key phylogenetic characters and partial confirmation of the tentative placement of species that could not be examined in detail anatomically via cleared and stained specimens.

ANATOMICAL AND DESCRIPTIVE TERMINOLOGY

Nomenclature for bones and subdivisions of the braincase follows Patterson (1975); lower jaw terminology follows Nelson (1973); caudal skeleton morphology follows Lundberg & Baskin (1969) and Schultze & Arratia (1989); nomenclature of components of the hyoid bar follows Arratia & Schultze (1990) except that the parurohyal of those authors is called the urohyal; terminology for the suspensorium follows Arratia (1990) and Arratia & Schultze (1991); and pelvic-skeleton nomenclature follows Shelden (1937). Nomenclature for other osteological structures follows Weitzman (1962) and for muscles and associated tendons follows Winterbottom (1974). Exceptions to terminological suggestions of any of the above authors are noted and explained in the appropriate section.

PREPARATION OF MATERIAL AND MATERIAL EXAMINED

Specimens were cleared and counterstained for bone and cartilage according to a modified version of the procedure described by Taylor & Van Dyke (1985). Major cranial nerves in the Cetopsidae are usually visible in cleared and stained material even in the absence of special nerve stains. These nerves are somewhat darker than the surrounding macerated soft tissues and can be easily traced in most specimens. Illustrations were prepared either directly through a camera lucida attached to a stereomicroscope or on the basis of a colour printout from a video camera on the same stereomicroscope. Polarized transmitted light was used to examine tendons and ligaments in cleared and stained material, and also for examining fin-rays in very small specimens. Alcohol-preserved specimens were dissected for examination of myology and other features of the soft anatomy.

Species in this paper are those diagnosed for the Helogeninae by Vari & Ortega (1986) and the Cetopsinae by Vari *et al*. (2005). Appendix 1 includes only the cleared and stained specimens examined during this study, arranged by family and subfamily. Additional specimens examined only for external morphological characters (e.g. chromatophore form, extent of poring of the lateral line system on the body, and sexually dimorphic modifications of the dorsal, pectoral and anal fins) are listed in Vari & Ortega (1986) and Vari *et al*. (2005) and these extensive series are not repeated herein. One of the terminals of *Cetopsidium* included in this analysis (*Cetopsidium* sp.) is of uncertain taxonomic status. The sample came from Chimanta Tepui in Venezuela and the specimens in that lot are too poorly preserved to allow a conclusive comparison of their external anatomy with that of other species in the genus. A cleared and stained preparation, however, allows the examination of all characters utilized in the data matrix. The taxon is included in this analysis in order to provide elements for future studies which may investigate its taxonomic status more throughly.

Authorship and dates of publication of cetopsid taxon names follow Vari & Ferraris (2003) and Vari *et al*. (2005). Literature citations for taxon names can be found in those publications and are not included here.

INSTITUTIONAL ABBREVIATIONS

The following abbreviations for institutions and collections are used: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; INHS, Illinois Natural History Survey, Champaign; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; LACM, Los Angeles County Museum of Natural History, Los Angeles; MCNG, Museo de Ciencias Naturales, Guanare; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MEPN, Museo de La Escuela Politecnica Nacional, Quito; MRAC, Royal African Museum, Tervuren; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NMNH, National Museum of Natural History, Smithsonian Institution, Washington; NRM, Swedish Museum of Natural History, Stockholm; UF, University of Florida, Florida State Museum, Gainesville; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor; and USNM, National Museum of Natural History, Smithsonian Institution, Washington.

ANATOMICAL ABBREVIATIONS

AC, anterior ceratohyal; APC, anterior palatine cartilage; AVP, anterior ventral transverse process of a complex centrum; BB_n, basibranchial n; BBC, basal bifurcation of basipterygial cartilage; BC, barbel core; BO, basioccipital; BOL, branchiopercular ligament; BP, basipterygium; BPC, basal portion of basipterygial cartilage; CB_n, ceratobranchial n; CC, complex centrum; DFS_n, dorsal-fin spine n; DH, dorsal hypohyal; DPC, distal portion of basipterygial cartilage; DRA, distal radial of anal fin; DRP, distal radial of pectoral fin; EB_n, epibranchial n; ENT, entopterygoid; EP, epioccipital; ESC, extrascapular; ETC, ethmoid cartilage; EX, exoccipital; F, frontal; FR, fin ray; FA, anterior fontanel; FP, posterior fontanel; HB_n, hypobranchial n; HY, hyomandibula; HYB, hyoid branch of hyoideomandibular nerve; HYM, hyoideomandibular (facial) nerve; INH, interhyal; INT, interopercle; LBC, lateral branch of basipterygial cartilage; LE, lateral ethmoid; MAX, maxilla; MB, maxillary barbel; MBH, mandibular branch of hyoideomandibular nerve; ME, mesethmoid; MEC, mesethmoid cartilage; MET, metapterygoid; MNP, middle nuchal plate; MPC, median palatine cartilage; NS5, fifth neural spine; ON, superficial ophthalmic nerve; OP, opercle; ORB, orbitosphenoid; OS, os suspensorium; PAL, palatine; PAP_n, parapophysis of vertebra n; PAR, parasphenoid; PBC, parietal branch of laterosensory canal; PC, posterior ceratohyal; PHB_n, pharyngobranchial n; PMX, premaxilla; PNP, posterior nuchal plate; POP, preopercle; PPC, posterior palatine cartilage; PRA, proximal radial of anal fin; PRD1, first proximal radial of dorsal fin; PRP, proximal radial of pectoral fin; PSH, pterosphenoid; PT, pterotic; PVP, posterior ventral transverse process of complex centrum; QUA, quadrate; SB, swimbladder; SN, supraneural; SO, supraoccipital; SPH, sphenotic; T, teeth; TPT, transformator process of tripus; TRI, trigeminal nerve; TRR, transverse radial; UTP, upper pharyngeal toothplate; V, vomer; VC_n, vertebral centrum n; VH, ventral hypohyal; VT, ventral trabecula; WL, Weberian lamina.

CHARACTER DESCRIPTION AND ANALYSIS

This section is a comparative anatomical survey of the taxa treated in this study. It is arranged by morphological complex, ordered to the degree possible in a sequence corresponding approximately to that found in the body of a fish, from anterior to posterior. The information is organized so as to maximize the efficiency of description of phylogenetically relevant variation, which is presented as a sequence of numbered characters. Each character begins with a brief descriptive title, followed by its consistency and retention indices (CI and RI) in the two most parsimonious phylogenetic hypotheses. Characters which differ in fit among the most parsimonious trees are given minimum and maximum values for each index with these values separated by a slash. The retention index for characters that have one state in a single terminal and another state in all other terminals are mathematically indeterminate, and thus are indicated as 'AUT'. Most such cases are autapomorphies for individual terminals, but due to rooting assumptions, some are synapomorphies for all terminals except the Diplomystidae. The states recognized in each character are listed next, with a brief characterization for each of them. Additional considerations relevant for the understanding of our interpretation of the character and/or to provide information on previous concepts concerning the character states and their polarities are discussed in a separate paragraph.

The names for species of the Cetopsinae herein follow the new generic-level classification proposed in Vari *et al*. (2005) (see Appendix 1 and New classificatory scheme, below). Several changes from the generic classifications utilized prior to that in Vari *et al*. (2005) are of particular note: *Pseudocetopsis*, *Bathycetopsis* and *Hemicetopsis* are junior synonyms of *Cetopsis* which furthermore includes a number of recently described species (Vari *et al*., 2005); *Denticetopsis* is expanded beyond the species originally assigned to it (*D. sauli* and *D. royeroi*), to include *D. epa*, *D. iwokrama*, *D. macilenta*, *D. praecox* and *D. seducta*, some of which we described recently (Vari *et al*., 2005). *Cetopsidium* was erected by Vari *et al*. (2005) to accommodate *C. minutum*, *C. orientale* and *C. morenoi*, all previously included in *Pseudocetopsis*, and *C. ferreirai*, *C. pemon* and *C. roae*, all of which were described in that publication.

JAWS AND RELATED STRUCTURES

1. Thickness of dentary proximate to symphysis (multistate ordered) (CI = 50, RI = 50).
State 0: As thick as remainder of bone.
State 1: Slightly thicker than remainder of bone.
State 2: Approximately twice as thick as remainder of bone

In the diagnosis of the genus *Denticetopsis*, Ferraris (1996) reported on a remarkable lower jaw specialization in the two species that were then included in the genus, *D. royeroi* and *D. sauli*. In both species, the region of the dentary proximate to the symphysis is markedly thickened into a mass of bone projecting dorsally beyond the dorsal profile of the rest of the dentary (e.g. Ferraris, 1996: figs 8, 9). The teeth on that thickened region are also larger than are the remaining teeth on the dentary. The thickening of that portion of the jaw in conjunction with the enlargement of the teeth in that region results in an extensively modified anterior portion of the lower jaw relative to that of other species of the Cetopsidae. Although the degree of modification of the dentary and medial dentary teeth in those two species is unparalleled in all other members of the Cetopsinae, similar, albeit much less pronounced, modifications of the dentary also occur in all other species included herein in *Denticetopsis*, with the exception of *D. macilenta*. The thickening of the portion of the dentary proximate to the symphysis is considered to be derived given that in all relevant siluriform outgroups the dentary is either uniformly thick along its length, or the thickness decreases toward the symphysis. In this analysis, the pronounced thickening of the medial region of the dentary in *D. sauli* is coded as State 2, while the less extensive thickening of that portion of the bone in the species of *Denticetopsis* other than *D. macilenta* are coded as State 1.

2. Number of heads of articular end of maxilla (CI = 100, RI = AUT).
State 0: Two.
State 1: One.

Plesiomorphically in the Siluriformes the maxilla has two proximal heads that form a bifurcated condyle that articulates with, and partially surrounds, the cartilage at the anterior portion of the palatine (e.g. Mo, 1991: fig. 12C, D). Species of the Cetopsidae instead have a maxilla that is undivided proximally and articulates with the palatine via a single condyle. This modification was first proposed as a synapomorphy for the members of the family by de Pinna & Vari (1995: 4). The single articular head in the Cetopsidae is apparently homologous to the ventral articular head of the maxilla in the primitive catfish condition and contacts the ventral surface of the palatine cartilage. Although this less complex form of the maxilla is similar to that present in outgroups to the Siluriformes within the Ostariophysi, it is considered apomorphic within the context of the monophyly of that of the Siluriformes and the present hypothesis of relationships within that order (de Pinna, 1998). A proximally undivided maxilla is also present within the Neotropical catfish family Astroblepidae, but the presence of that feature in that family and the Cetopsidae is considered convergent given the well-corroborated phylogenetic hypothesis uniting the Astroblepidae to the Loricarioidea to the exclusion of the Cetopsidae (Howes, 1983; Schaefer, 1987).

Although the number of articular heads is in itself informative about relationships, there are a number of associated modifications in the maxilla of the Cetopsidae that deserve further discussion. In nearly all species in the Cetopsidae the maxilla is strongly twisted and angled, with its main axis forming a C-shaped structure that wraps around the anterolateral corner of the anterior palatine cartilage (Fig. 1; see also comments below concerning the condition in *Cetopsis oliveirai*). The distal end of the maxilla is flattened and supports the base of the maxillary barbel. Contrary to the typical catfish condition, the axis of the distal portion of the maxilla is not aligned with the axis of the associated barbel but is instead aligned approximately perpendicular to the axis of the barbel and fails to enter its base. It is possible that the modifications of the maxilla in the Cetopsidae comprise several independent pieces of evidence for the monophyly of the family; however, we herein conservatively interpret them as a single complex character.

There are several interesting modifications of the pattern described above that are probably informative about relationships at other levels of the phylogeny within the Cetopsinae. Preservation of the maxilla in some of the material examined in this study is often incomplete, with the bone lost on one or both sides of several specimens. Therefore, coding such variation as separate characters is at the present time unwarranted. We, however, note a few such variants as a potential source of information for future phylogenetic studies. The maxilla in *Paracetopsis bleekeri* is extremely small, being reduced to a tiny irregular bone, a condition that is certainly distinct from the morphology found in all other examined species of the Cetopsinae. The shaft of the maxilla is distinctly thickened in *Cetopsis coecutiens*, *C. candiru*, *C. fimbriata* and *C. motatanensis.* This may be additional evidence for the hypothesis that the species with that expansion form a monophyletic group.

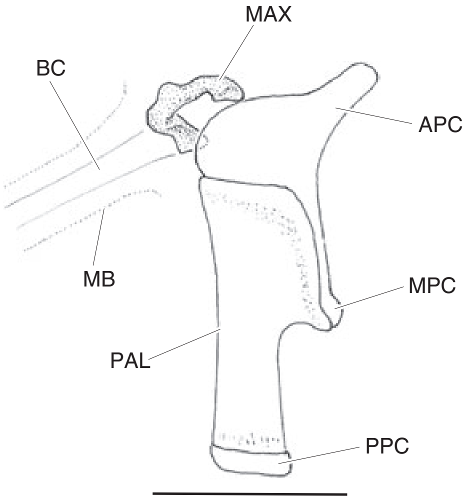

Figure 1. Palatine and maxilla of *Cetopsidium morenoi* (INHS 69416). Ventral view of right side, anterior facing top. Scale bar = 1 mm.

Cetopsis oliveirai is remarkable within the Cetopsinae because its maxilla, although one-headed as is the case in all other members of the family, is, however, straight and therefore resembles the overall shape hypothesized to be primitive for other groups in the Siluriformes. The maxilla of *C. oliveirai* also enters slightly into the base of the maxillary barbel, thereby differing markedly from the situation present in all other examined species in the Cetopsidae. A juvenile specimen of *C. coecutiens* of a size comparable with adults of the paedomorphic species, *C. oliveirai*, also has a mostly straight maxilla. The juvenile of *C. coecutiens*, however, exhibits a limited degree of dorsal bending of the maxilla which foreshadows the shape characteristic of adults of species of the Cetopsinae with the exception of *C. oliveirai*.

These observations lead to two important conclusions. First, the unusual morphology of the maxilla in the Cetopsidae seems to be a consequence of a dorsal 180° curvature of its primitively straight shaft, which results in a C-shaped bone. Associated with this curvature is the loss of the dorsal articular head. Second, the remarkably primitive-looking maxilla of *C. oliveirai* is probably a result of paedomorphosis, given the small body size of adults of that species and the phylogenetic evidence presented herein that indicates that the species is deeply nested within the Cetopsinae, rather than being a basal lineage.

The maxilla has been lost in available cleared and stained specimens of *Cetopsidium ferreirai*, *Denticetopsis praecox*, *Cetopsis othonops*, *C. pearsoni* and *Paracetopsis esmeraldas*, and those taxa are therefore assigned missing entries in the matrix.

3. Maxillary teeth (CI = 100, RI = 100)
State 0: Present.
State 1: Absent.

Maxillary teeth are absent in all families of the Siluriformes except the Diplomystidae and the †Hypsidoridae (e.g. Grande, 1987: fig. 7). Although this character has long been considered strong evidence for the basal position of the Diplomystidae (and more recently the †Hypsidoridae) within the Siluriformes, its polarity is somewhat ambiguous within the context of the currently accepted hypothesis of phylogenetic relationships within the Ostariophysi (Fink & Fink, 1981). Within that superorder, maxillary teeth are absent in all members of the Gonorynchiformes, Cypriniformes and Gymnotiformes, but are present in most groups in the Characiformes. This distribution across the Ostariophysi renders the state of maxillary dentition at the outgroup node for the Siluriformes ambiguous. Although we follow the traditional interpretation that assumes that the maxillary teeth are primitively present in the Siluriformes, the phylogenetic implications of the presence or absence of maxillary teeth within the Siluriformes are decidedly less clear than is usually considered to be the case. This character is included to help resolve the position of Cetopsidae relative to outgroups within the Siluriformes, but is irrelevant for the resolution of phylogenetic relationships within the family.

4. Number of dentary tooth rows in adult specimens (multistate ordered) (CI = 75, RI = 92).
State 0: More than one row of teeth extending along entire tooth-bearing surface of dentary.
State 1: More than one row of teeth present along the anterior half of length of tooth-bearing surface, plus some additional teeth located near symphysis.
State 2: Two rows of teeth located near symphysis (second row extending for approximately 4–5 teeth), with remainder of tooth-bearing surface of dentary with one row of teeth.
State 3: Only one row of teeth present along entire tooth-bearing surface of dentary.

The number of dentary tooth rows is a character that apparently involves phylogenetically informative variation, but it is a feature that must be used with caution because it is subject to a considerable degree of intraspecific and ontogenetic variation. On the basis of the material examined in this study, four conditions can be recognized that apparently represent discrete states in adult and half-grown specimens. State 0, in which there are two or more rows of teeth along most of the tooth-bearing surface of the dentary, is the presumed plesiomorphic condition in the Siluriformes. In addition to outgroups in the Siluriformes, State 0 is present within the Cetopsidae in the Helogeninae and, within the Cetopsinae, only in *Cetopsis arcana*. In that species, the primitive condition is seen only in the largest specimen examined (MZUSP 55965), which is taken to represent the adult condition. The examined juvenile specimen of *C. arcana* (MZUSP 41492) has, however, only a single row of teeth along most of the dentary. State 1, which was observed in most species of the Cetopsinae (Appendix 2), is defined as the presence of at least a second row of teeth along the anterior half of the tooth-bearing surface of the dentary. Often there are additional teeth located close to the symphysis, with those teeth either being irregularly distributed or arranged in a short third row. State 2, in turn, is characterized by the presence of a single primary row of teeth along the length of the tooth-bearing surface of the dentary, with a few, irregularly placed teeth situated close to the dentary symphysis. This is the condition found in *C. baudoensis*, *C. fimbriata* and *C. oliveirai*. Finally, a single row of teeth extending along the entire tooth-bearing portion of the dentary constitutes State 3, which was found only in *C. candiru* and *C. coecutiens*. The states are ordered as a progression toward the reduction in the number of tooth rows, with the plesiomorphic condition as the initial state of the transition series.

Lundberg & Rapp Py-Daniel (1994: 385) reported the presence of a single row of teeth on the dentary of *Cetopsis oliveirai*. However, both specimens of that species examined during this study have a second short series of teeth located external to the main tooth row in the region of the symphysis of the dentary. This condition was also found in juveniles of *C. coecutiens*. The fact that *C. coecutiens* loses the second row of dentary teeth as growth progresses provides ontogenetic support for the ordering and polarity hypothesized herein for this character.

Adult specimens of *C. coecutiens* have an inner series of teeth which may be mistaken for a second dentary tooth row. However, these are clearly replacement, rather than functional, teeth as indicated by the fact that they are unattached to the underlying dentary and are calcified only along their distal portions.

5. Shape of dentary teeth (multistate ordered) (CI = 100, RI = 100).
State 0: Conical with narrow base and single pointed tip.
State 1: Anterior teeth caniniform, but most teeth broad and tricuspidate with three, short, pointed cusps.
State 2: All teeth broad and tricuspidate, with middle cusp being blade-like, with expanded straight edge.

The dentary teeth in the Siluriformes are primitively conical, rounded in cross-section, and pointed distally (e.g. Ferraris, 1996: fig. 9). In the taxa exhibiting States 1 and 2, most, or all, of the dentary teeth are broad and flattened along their entire length. In *Cetopsis coecutiens* the anterior dentary teeth may be caniniform, and the remaining teeth are semi-incisiform, with a broad base and three short tooth cusps distally (State 1; Fig. 2A). These modifications of the teeth become more evident as one moves posteriorly along the dentary tooth series. In *C. candiru* the dentary teeth are strongly incisiform and situated very close to each other such that the distal portions of these teeth are nearly in contact. This combination results in the teeth forming a continuous cutting edge along the toothed portion of the dentary (State 2; Fig. 2B). The tricuspidate

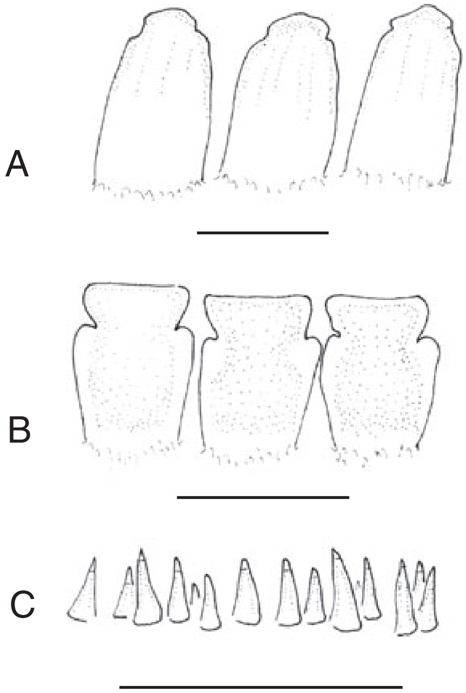

Figure 2. Dentary teeth in some species of *Cetopsis*. Mesial view of left side. A, *C. coecutiens* (MZUSP 23354); B, *C. candiru* (MZUSP 24688); C, *C. coecutiens*, juvenile specimen (LACM 43102-3). Scale bars = 1 mm.

structure of the teeth in *C. candiru* is evident, albeit with the distal margin of the middle cusp straight and expanded along the long axis of the tooth into a cutting blade. *Cetopsis candiru* has comparable modifications in the opposing teeth of the premaxilla and the vomer, which jointly form a highly efficient cutting apparatus.

Juveniles of *C. coecutiens* bear only conical teeth on the dentary (Fig. 2C). Thus, the ontogenetic sequence from conical to broad tricuspidate teeth in this species corroborates the polarity and ordering proposed herein for this character.

6. Spacing and form of teeth in outer dentary tooth row (CI = 100, RI = 100).
State 0: When more than one row of teeth present on dentary, teeth of outer row only slightly larger than other teeth and spacing between teeth in all rows relatively uniform.
State 1: Teeth in anterior portion outer row of dentary much larger and more widely spaced apart than other teeth on jaw.

Most species of the Cetopsinae having more than one row of teeth on the dentary and outgroups in the Siluriformes in general have the teeth of the external dentary tooth row separated by spaces approximately uniform among the different tooth rows. Furthermore, these groups have the teeth of all series of a nearly uniform size with the individual teeth gradually slightly increasing in size towards the outer margin of the bone. In the Helogeninae, in contrast, the teeth on the external row of the dentary are proportionally larger and more widely separated than is the case in the remaining dentition on that bone. State 1 of this character was proposed by de Pinna & Vari (1995: 13) as a synapomorphy for the Helogeninae.

7. Degree of development of the adductor mandibulae muscle (CI = 50, RI = 87).
State 0: Muscle not expanded, but restricted to lateral portions of head, and not significantly covering roof of skull.
State 1: Muscle hypertrophied and extending dorsally to midline of neurocranium.

The adductor mandibulae muscle in the Siluriformes is often massively developed when compared with the form of the muscle that is present in other orders in the Ostariophysi. As a consequence of that pronounced enlargement, the muscle often extends onto at least a portion of the skull roof, a situation that is present even in the Diplomystidae. The development of the adductor mandibulae across the Cetopsinae, with the exception of *Cetopsis oliveirai*, is, however, carried to an extreme degree, resulting in that muscle enveloping practically all of the dorsal surface of the braincase. This morphology is clearly a derived condition (de Pinna & Vari, 1995: 10, fig. 13). Despite the extension of the muscle over the skull roof in nearly all members of the Cetopsinae, most of the roof of the neurocranium does not actually serve as an area for direct muscle attachment. The attachment of the adductor mandibulae is instead restricted to the region of the neurocranium proximate to the dorsal midline.

The only species of the Cetopsinae that lacks a hypertrophied adductor mandibulae in adults is *Cetopsis oliveirai* (Lundberg & Rapp Py-Daniel, 1994: 382), a species of small body size (to 36 mm SL). The presence of the plesiomorphic condition of that muscle in *C. oliveirai* is a reversal within the context of the final phylogeny and may be a result of paedomorphosis. Two juvenile specimens examined of *Cetopsis montana* (LACM 41735-1, 13.0 mm SL, and LACM 41736-1, 14.1 mm SL) lack an extension of muscle on the roof of the neurocranium. Nonetheless, a limited invasion of the adductor mandibulae onto that region is evident in the posterior part of the neurocranium in a slightly larger 18.7-mm SL specimen in LACM 41735-1. Further corroboration for the interpretation of paedomorphosis comes from the lack of invasion of the skull roof by the adductor mandibulae in juvenile specimens of *C. coecutiens* (MZUSP 83336) at a size (21.9–24.6 mm SL) comparable with that of adult *C. oliveirai*. Interestingly, not all diminutive species in the Cetopsinae demonstrate the less extensive development of the adductor mandibulae found in *C. oliveirai*. For example, two small species of the Cetopsinae, *Denticetopsis sauli* and *D. royeroi*, nonetheless retain the derived, extensive development of the adductor mandibulae that is characteristic of nearly all species in the Cetopsinae (Ferraris, 1996).

8. Position of coronoid bone (CI = 100, RI = 100).
State 0: Coronoid bone located dorsomedially on Meckel's cartilage, not visible from lateral view of lower jaw.
State 1: Coronoid bone located laterally, visible in lateral view of lower jaw.

In nearly all members of the Siluriformes the coronoid bone is a small ossification located on the dorsomedial surface of Meckel's cartilage near the base of the coronoid process. The coronoid bone in the condition general for the Siluriformes is visible only from a medial view of the lower jaw. In contrast, the coronoid bone is located more laterally from the hypothesized plesiomorphic position in the Helogeninae (State 1) and, as a consequence, a part of that ossification is visible from a lateral view of the lower jaw.

9. Degree of ossification of coronoid process of lower jaw (CI = 100, RI = 100).
State 0: Fully ossified.
State 1: Composed mostly of unossified ascending process of Meckel's cartilage.

In the Cetopsinae and examined outgroups in the Siluriformes, the coronoid process is formed by ossifications of the dentary and anguloarticular. The ascending process of Meckel's cartilage in this condition contributes only the cartilaginous lining of the medial surface of this complex process. The coronoid process in the Helogeninae, in contrast, is composed almost entirely of the unossified ascending process of Meckel's cartilage (State 1).

10. Relative size and orientation of lateral-most premaxillary teeth (CI = 100, RI = 100).
State 0: Lateral-most premaxillary tooth same size as remaining premaxillary teeth and orientated approximately perpendicular to ventral surface of premaxilla.
State 1: Lateral-most one or two premaxillary teeth larger than remaining premaxillary teeth, with their longitudinal axis parallel, or nearly parallel, to ventral surface of premaxilla.

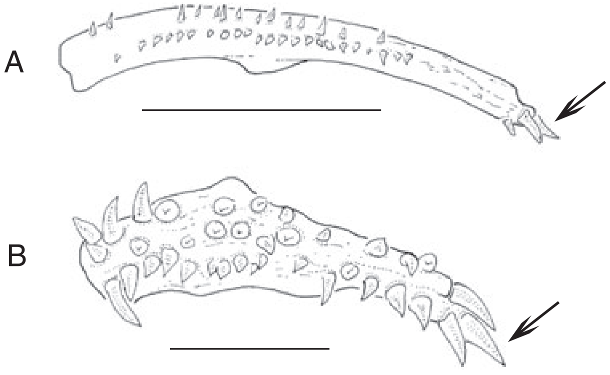

Figure 3. Premaxillae in various species of *Denticetopsis*. Ventral view of left side, anterior facing top. A, *D. sauli* (ANSP 161432, paratype); B, *D. epa* (MZUSP 83228). Arrows indicate hypertrophied and horizontally orientated distal teeth. Scale bars = 1 mm.

The upper jaw dentition in most members of the Cetopsidae and other families in the Siluriformes typically consists of a relatively uniform band of similarly sized teeth positioned on the ventral surface of the premaxilla, with the individual teeth orientated approximately perpendicular to the ventral surface of the premaxilla, albeit with a slight posteroventral inclination. All species of *Denticetopsis* have the lateral-most one or two teeth of the premaxilla directed laterally and, as such, have their longitudinal axis parallel, or nearly parallel, to the ventral surface of premaxilla (State 1, Fig. 3). The lateral-most one or two teeth in all species of *Denticetopsis* also differ from the usual condition of the dentition across the Siluriformes in being larger than the other premaxillary teeth, a condition that is most highly developed in *D. sauli* (Fig. 3A). In that species, the lateral teeth are, furthermore, separated from the rest of the premaxillary dentition by an edentulous region.

11. Shape of posterior portion of palatine (CI = 100, RI = 100).
State 0: Dorsoventrally flattened and horizontally expanded.
State 1: Rod-shaped.

Most members of the Siluriformes have the posterior part of the palatine rod-shaped and approximately round in cross-section (State 1). In the Cetopsidae, the posterior portion of the palatine is dorsoventrally flattened and horizontally expanded (Fig. 4). The flattened portion of the bone extends to the centre of ossification in the Cetopsidae and the flattening is a consequence of a complete restructuring of that region of the ossification rather than simply a result of expansion of the superficial bone layers. Among outgroups examined, a dorsoventrally flattened posterior part of the palatine was observed in *Olivaichthys* and *Nematogenys*. In view of the relatively basal position of the Diplomystidae and the Cetopsidae within the Siluriformes (Mo, 1991; de Pinna, 1993, 1998; see also comments under Discussion below), it is most parsimonious to hypothesize that the morphology of the dorsoventrally flattened posterior part of the palatine in those families (and

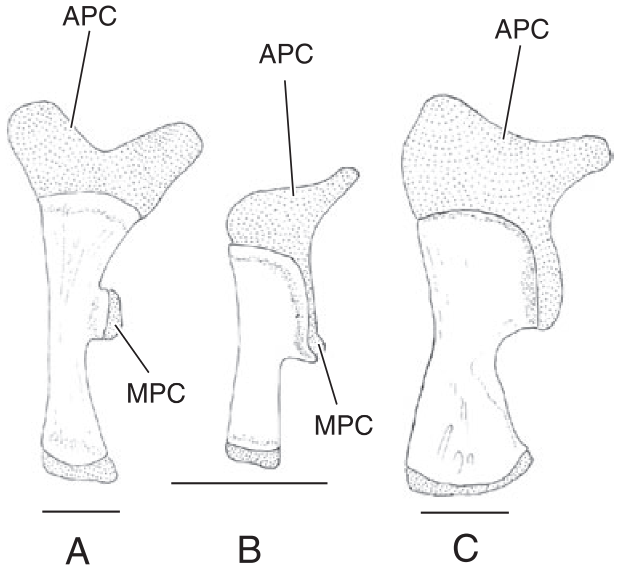

Figure 4. Palatine. Ventral view of right side. A, *Cetopsis coecutiens* (MZUSP 38765); B, *Cetopsidium morenoi* (INHS 69416); C, *Cetopsis gobioides* (MZUSP 38808). Scale bars = 1 mm.

possibly also in the Nematogenyidae and some other loricarioids) is plesiomorphic.

The posterior part of the palatine is also flattened in the superfamily Sisoroidea (de Pinna, 1996), but in that group the bone is laterally compressed rather than dorsoventrally depressed. In some members of the subtribe Glyptosternina of the family Sisoridae, the posterior part of the palatine appears to be depressed but is actually rotated relative to the anterior region of the bone such that its expanded surface lies in the horizontal plane, rather than exhibiting the vertical orientation of the flattened portion that is characteristic of the bone in other members of the Sisoroidea. The obvious torsion of the bone within the Glyptosternina, however, leaves little doubt that the conditions in that component of the Sisoroidea on the one hand, and the Cetopsidae, Nematogenyidae and Diplomystidae on the other, are non-homologous.

The marked dorsoventrally flattening and horizontal expansion of the posterior portion of the palatine was proposed as a synapomorphy for the Cetopsidae by de Pinna & Vari (1995: 4). Although our partition of the character states agrees with that observed in de Pinna & Vari (1995), the polarity interpretation herein is opposite to the one proposed in that publication.

12. Shape of anterior portion of palatine (CI = 100, RI = 100).
State 0: Dorsoventrally depressed and laterally expanded.
State 1: Rod-like.

In most members of the Siluriformes the anterior portion of the palatine is rod-like and circular in cross-section. The anterior part of the palatine in the Diplomystidae (Grande, 1987: fig. 8B), the Cetopsidae (Fig. 4), the †Hypsidoridae (Grande, 1987: fig. 4) and the Nematogenyidae is, however, dorsoventrally flattened and laterally expanded. This character and Character 11 are considered as separate herein because of the condition in the †Hypsidoridae, which has the combination of an expanded anterior portion of the palatine and a rod-like posterior portion of that bone (Grande, 1987). This mosaic combination of character distributions indicates that the shape of the anterior and posterior portions of the palatine change as independent units in the Siluriformes.

13. Degree of development of anterior cartilage of palatine (CI = 50, RI = 66).
State 0: Cartilage small, forming cap on anterior end of palatine.
State 1: Cartilage large, extending anteriorly for distance equivalent to one-third or more of length of bony portion of palatine.

In the plesiomorphic condition within the Siluriformes, the anterior palatine cartilage is small, forming a short cap on the anterior end of the bone. In all members of the Cetopsidae the anterior cartilage of the palatine is prolonged anteriorly for a distance equivalent to at least one-third of the length of the bony portion of the palatine (State 1, Fig. 4A–C). Additionally, the cartilage is also expanded laterally, thereby matching the width of the broad anterior end of the palatine. The markedly expanded anterior cartilage of the palatine characteristic of the Cetopsidae was initially proposed as a synapomorphy for the family by de Pinna & Vari (1995: 5). Among outgroups, a similarly elongated palatine cartilage is seen in *Austroglanis* and *Nematogenys*. In *Austroglanis* (Skelton, 1981: fig. 11), however, the shape of the cartilage, and that of the palatine itself, is cylindrical and thus markedly distinct from that present in the Cetopsidae.

14. Position on palatine of articular facet with lateral ethmoid (CI = 100, RI = 100).
State 0: On dorsal surface of palatine.
State 1: On lateral surface of palatine.

In the Diplomystidae the facet on the palatine that articulates with the lateral ethmoid is located on the dorsal surface of the palatine (Fink & Fink, 1981: fig. 11). This condition is unusual in the Siluriformes, and occurs elsewhere only in the Loricarioidea (represented by *Nematogenys* in the present analysis) and the Cetopsidae. In all other examined members of the Siluriformes the facet is located on the lateral surface of the palatine, even in those species in which the facet is overlain by the lateral wings of the lateral ethmoid. In the Cetopsidae the lateral ethmoid articulates only with the anterior cartilage of the palatine (see Character 15), but retains the primitive position of articulation, being located on the dorsal surface of that bone.

15. Condition of anterior and medial cartilages of palatine and their role in articulation of palatine with cranium (multistate ordered) (CI = 50, RI = 89).
State 0: Anterior and medial cartilages of palatine completely separated, with articulation of palatine with lateral ethmoid entirely by way of medial cartilage.
State 1: Anterior and medial cartilages of palatine continuous with each other, but with medial cartilage still partly differentiated; articulation of palatine with lateral ethmoid located midway between anterior and medial portions of palatine cartilage.
State 2: Anterior and medial cartilages entirely united, without any differentiation between those components; articulation of palatine with lateral ethmoid entirely through anterior portion of cartilage.

The plesiomorphic and widespread condition of the articulation between the palatine and lateral ethmoid in the Siluriformes is one in which there occurs a separate cartilage and facet medially midway along the length of the palatine with these structures serving as the articular surface of that bone with the lateral ethmoid (State 0). One of the synapomorphies for the Cetopsidae proposed by de Pinna & Vari (1995: 5) was the articulation of the palatine with the lateral ethmoid by way of the anteriorly expanded cartilage of the palatine. This character, as defined in that paper, is herein confirmed as synapomorphic at the level proposed de Pinna & Vari (1995). Examination of additional taxa, however, revealed intrafamilial variation that permits a more refined coding and description of this feature than that advanced by de Pinna & Vari (1995). An articulation between the palatine and the lateral ethmoid limited exclusively to the anterior cartilage of the palatine is partly the result of the fusion of the anterior and medial palatine cartilages, with subsequent anterior displacement of the latter. The condition of the palatine cartilage in the species of *Cetopsidium* demonstrates the sequence of modifications that apparently took place phylogenetically. In species of that genus there occurs a single long cartilage covering the anterior and part of the mesial margins of the palatine. The small region of the palatine serving for the articulation with the lateral ethmoid is still slightly differentiated from the remainder of the palatine as reflected in both the indentation of the bony part of the palatine and in the angled cartilage overlying that region (Fig. 4B). The articular surface of the palatine with the lateral ethmoid in *Cetopsidium* is also positionally close to the primitive state, i.e. approximately at the middle of the length of the mesial margin of the palatine. This condition is coded as State 1, and is also present in the Helogeninae. More pronounced modifications of this system were found in nearly all other components of the Cetopsidae other than the Helogeninae and *Cetopsidium*. All genera of the Cetopsinae other than *Cetopsidium* have the medial cartilage apparently displaced anteriorly and entirely fused with the anterior cartilage that now serves as the point of articulation of the palatine with the lateral ethmoid (State 2; Fig. 4C). The medial and anterior cartilages are uniquely independent in *Cetopsis coecutiens* within the Cetopsidae (Fig. 4A), a morphology comparable with that of the primitive condition of these cartilages in the Siluriformes and which presumably reflects a reversal from the derived condition that is present in all other members of the Cetopsidae according to the phylogenetic hypothesis arrived at in this study.

16. Degree of development of levator arcus palatini muscle (CI = 50, RI = 87).
State 0: Levator arcus palatini muscle with little or no dorsal component, and not evident in dorsal view.
State 1: Levator arcus palatini muscle very developed and clearly visible in dorsal view.

Plesiomorphically in the Siluriformes, the levator arcus palatini is mostly, or entirely, a vertically orientated muscle attached to the ventrolateral surface of the skull in the region posterior to the orbit. Although the muscle is clearly visible in lateral view, it has little or no extension onto the dorsal surface of the neurocranium. In nearly all members of the Cetopsinae (see below), the levator arcus palatini is more massively developed and expanded onto the dorsal surface of the anterior part of the roof of the neurocranium. As a result of this expansion the levator arcus palatini is broadly visible from a dorsal view in members of the subfamily (de Pinna & Vari, 1995: 10, fig. 13). Within the Cetopsinae, the only instance of the presence of a plesiomorphic, less-developed, condition of the levator arcus palatini, with little or no extension of the muscle onto the dorsal surface of the roof of the neurocranium, was observed in *Cetopsis oliveirai*. This is a case of reversal according to the phylogenetic hypothesis herein proposed and is perhaps associated with the paedomorphosis of that species.

SUSPENSORIUM AND OPERCULAR COMPLEX

17. Form of articulation between hyomandibula and neurocranium (CI = 100, RI = 100).
State 0: Dorsal portion of hyomandibula without any anterior process articulating with ventrolateral margin of neurocranium, or with only slightly developed process.
State 1: Dorsal portion of hyomandibula with distinct anterior process forming long, direct articulation with ventrolateral margin of neurocranium.

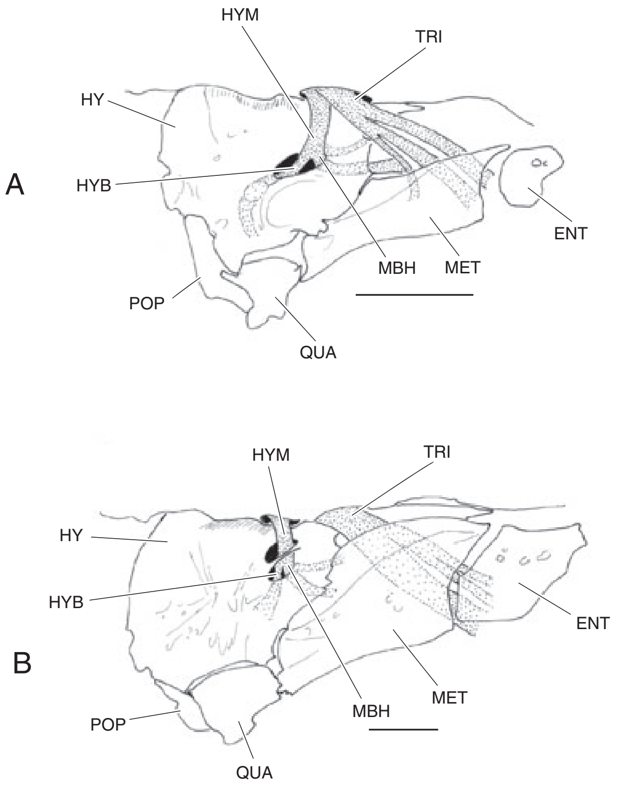

Figure 5. Suspensorium and associated major nerve trunks. Left side, medial view, anterior to right. A, *Cetopsidium pemon* (UF 26156); B, *Denticetopsis epa* (MZUSP 83228). Scale bars = 1 mm.

The species of the Helogeninae and most other members of the Siluriformes lack any notable anterior process of the dorsal portion of the hyomandibula articulating with the ventrolateral margin of the neurocranium, or at most have a slightly developed process (de Pinna & Vari, 1995: fig. 7). In all species of the Cetopsinae, however, the dorsal portion of the hyomandibula is prolonged anteriorly as a large process extending along the floor of the skull (Fig. 5; de Pinna & Vari, 1995: fig. 6). State 1 of this character was proposed by de Pinna & Vari (1995: 12) as a synapomorphy for the Cetopsinae, a hypothesis that is supported by the results of this study. The anterior extension of the hyomandibula present in the Diplomystidae (Fink & Fink, 1981: fig. 11) is far less developed than the extension of the bone present in the Cetopsinae and, thus, coded as state 0 for this character.

18. Path of hyoid branch of hyoideomandibular nerve on hyomandibula (CI = 50, RI = 83).
State 0: Nerve running through tunnel in hyomandibula.
State 1: Nerve crossing hyomandibula and running exposed on lateral surface of that bone.

The hyoideomandibular nerve (also called the facial nerve) in the Siluriformes exits the skull through a foramen near, or confluent with, the opening for the trigeminal nerve (Fig. 5). The paths of these two nerves diverge immediately after exiting the skull, with the hyoideomandibular nerve extending ventrolaterally and the trigeminal nerve extending anterolaterally. The hyoideomandibular nerve then divides into two branches, an anterior mandibular branch and a posterior hyoid branch. The two branches diverge approximately as they enter the hyomandibula, with the bifurcation sometimes occurring amidst the bony trabeculae of the hyomandibular foramen. The hyoid branch can either run through a short tunnel inside the bone before exiting on the lateral surface of the hyomandibula (State 0, Fig. 5A) or cross the surface of the hyomandibula in a path approximately transverse to the surface of the bone (State 1, Fig. 5B). The passage of the hyoid branch directly through the hyomandibula (Fig. 5B), a condition that occurs only in *Helogenes* and *Denticetopsis* among examined members of the Siluriformes, is considered derived in view of the lack of such a passage in examined siluriform outgroups.

19. Passage of trigeminal nerve through suspensorium (CI = 100, RI = 100).
State 0: Wide and situated within distinct gap between metapterygoid and skull.
State 1: Narrow and constricted by dorsal lamina of metapterygoid.

The trigeminal nerve exits the neurocranium through a ventrally, or ventrolaterally, positioned foramen and then continues anteriorly along the margin of the suspensorium, normally through a space between the dorsal margin of the metapterygoid and the ventral surface of the neurocranium. In the Cetopsinae the hyomandibula has an anterior extension running along the ventrolateral margin of the neurocranium (see Character 17) and the trigeminal nerve passes between the metapterygoid and the anterior portion of the hyomandibula. Notwithstanding, the presence of this anterior process of the hyomandibula, nearly all species in the Cetopsinae retain a wide space for the passage of the nerve in that region (Fig. 5A). In the derived condition that occurs only in the species of *Denticetopsis*, the metapterygoid is expanded dorsally as a lamina that closely approaches the anterior margin of the hyomandibula. As a consequence of this expansion, there remains a narrow slit between the metapterygoid and the hyomandibula for the passage of the trigeminal nerve (State 1, Fig. 5B).

20. Position of medial opening for hyoideomandibular nerve on hyomandibula (CI = 100, RI = AUT).
State 0: On dorsal margin of hyomandibula and close to area of exit of hyoideomandibular nerve from neurocranium.

State 1: Approximately at centre of hyomandibula and distant from area of exit of hyoideomandibular nerve from neurocranium.

The hyoideomandibular nerve passes through the hyomandibula as it continues anteriorly from the neurocranium to the more anterior portion of the head. The corresponding foramen in the hyomandibula for the hyoideomandibular nerve is normally located among members of the Siluriformes on the dorsal part of the bone proximate to the exit of the hyoideomandibular nerve from the neurocranium (Fig. 5A–B). Uniquely in *Cetopsis othonops* among the species examined, the foramen is located on the central or ventral part of the hyomandibula, and the facial nerve consequently travels for a considerable distance along the medial surface of the hyomandibula between its exit from the neurocranium and its entrance into the hyomandibula (State 1).

21. Form of articulation between metapterygoid and entopterygoid (CI = 50, RI = 87).
State 0: Metapterygoid not extending posteromedial of entopterygoid.
State 1: Metapterygoid extending posteromedial of entopterygoid.

The bone in the pterygoid series anterior to the metapterygoid in the Cetopsidae is apparently homologous to element identified as the entopterygoid in *Channalabes apus* (Clariidae), as illustrated by Howes & Teugels (1989: 453, fig. 7c), the mesopterygoid of Oliveira (1988) and Milani de Arnal (1991), and the ectopterygoid of de Pinna & Vari (1995). Despite the resulting terminological confusion, there is little question that the bone is homologous across the species of the Cetopsidae and probably of most, if not all, other groups in the Siluriformes. All species of the Cetopsinae with the exception of *Cetopsis oliveirai* have a metapterygoid that has a large anteromedial expansion which extends along the posteromedial margin of the entopterygoid (Fig. 5; see also de Pinna & Vari, 1995: fig. 6). Despite much variation in the shape of the metapterygoid of outgroups in the Siluriformes, none of these outgroups exhibits an expansion of the metapterygoid comparable with that present in most species of the Cetopsinae.

22. Form of articulation between opercle and interopercle (CI = 100, RI = 100).
State 0: Articular surfaces not overlapping.
State 1: Articular surfaces overlapping and forming a lap suture.

In most outgroups in the Siluriformes, the opercle and interopercle meet each other along the same plane without overlap at their borders and are united by a sheet of connective tissue. As first observed by de Pinna & Vari (1995: 6, fig. 4), the partly overlapping articulation between the opercle and interopercle is a synapomorphy for the Cetopsidae. The overlapping surfaces each exhibit some modification in the bone structure, with the lateral surface of the opercle having a slight recess along the plane of contact into which the posterior edge of the interopercle fits, thereby forming the lap suture of State 1. The details of the joints differ slightly between the Cetopsinae and Helogeninae. The plane of contact of the bones in the Helogeninae is at a 90° angle relative to the plane of the opercle and interopercle, while in the Cetopsinae the plane of contact is parallel to the surfaces of the bones. The only other known occurrence of such a lap joint between the opercle and preopercle within the Siluriformes outside of the Cetopsidae is the previously unreported occurrence of this modification in the electric catfish family Malapteruridae (*Malapterurus* sp.; MZUSP 62600). The presence of an interopercle/opercle lap suture in the Malapteruridae and the Cetopsidae must be considered homoplastic under current concepts of phylogenetic relationships within Siluriformes (cf. de Pinna, 1998; Diogo, 2005).

23. Point of attachment of interoperculo-mandibular ligament on interopercle (CI = 100, RI = 100).
State 0: Attachment located on anterior tip of interopercle.
State 1: Attachment located on dorsal margin of interopercle.

Most taxa in the Siluriformes and most other teleosts have the interoperculo-mandibular ligament attached to the anterior tip of the interopercle. In the Cetopsidae, instead, the posterior attachment of the interoperculo-mandibular ligament is more dorsally positioned to a location at or near the dorsal portion of the interopercle (de Pinna & Vari, 1995: fig. 4).

24. Form of interopercle (multistate ordered) (CI = 100, RI = 100).
State 0: Interopercle approximately triangular, being either equally as long as, or longer than, deep.
State 1: Interopercle with reduction of its anteroposterior axis, so that it is as deep as, or slightly deeper than, long.
State 2: Interopercle extremely reduced anteroposteriorly, restructured into vertically elongated bone.

The interopercle in most families in the Siluriformes is longer than deep, with the result that its longest axis is approximately horizontal (e.g. Fink & Fink, 1981: fig. 11; Skelton, 1981: fig. 10). As reported by de Pinna & Vari (1995: 7), the interopercle in the Cetopsidae is apparently unique within the Siluriformes in being either as deep as long, or deeper than long and thereby forming a vertically elongate ossification (de Pinna & Vari, 1995: fig. 4B). As coded in this study, this character includes two states. The condition in the Helogeninae has a more pronounced degree of anteroposterior compression of the interopercle than occurs in the Cetopsinae (de Pinna & Vari, 1995: fig. 4A) and this vertically elongate form of the bone is therefore coded as State 2.

25. Shape of metapterygoid (CI = 100, RI = 100).
State 0: Irregular, quadrangular or approximately round.
State 1: Rectangular.

In the Siluriformes, the metapterygoid is highly variable in shape but in most members of the order that bone is as long as deep (e.g. Fink & Fink, 1981: fig. 11, *Diplomystes*; Mo, 1991: fig. 14, *Bagrus*) and it is not rectangular overall. As noted by de Pinna & Vari (1995: 7), the metapterygoid in the Cetopsidae is anterodorsally elongated into an irregular, roughly rectangular, ossification that is longer than deep (State 1, Fig. 5A, B). These modifications were not encountered elsewhere in the Siluriformes and as in de Pinna & Vari (1995) are hypothesized as apomorphic for the members of the Cetopsidae.

26. Number of suprapreopercles (CI = 100, RI = AUT).
State 0: One or two.
State 1: Four or five.

The suprapreopercles are dermal ossifications that develop around the dorsal portion of the preopercular branch of the laterosensory canal dorsal to the body of the preopercle. These bones are typically simple tubules of bone lining the canal, often exhibiting a feeble, irregular ossification pattern. Most members of the Siluriformes have one or two suprapreopercles, whereas several taxa in the order lack those ossifications. *Denticetopsis epa* differs markedly from the typical siluriform pattern in alternatively having four or five suprapreopercles. The number of suprapreopercles could not be clearly determined in the specimen available of *D. sauli*, because of its small size, and poor ossification of the relevant region of the body.

NEUROCRANIUM

27. Fenestra between lateral ethmoid and orbitosphenoid (CI = 100, RI = 100).
State 0: Large.
State 1: Small or absent.

Most otophysans have the lateral ethmoid and orbitosphenoid primitively separated by a large fenestra. A large fenestra between the lateral ethmoid and orbitosphenoid is found within the Siluriformes only in the Diplomystidae, Cetopsidae and Pangasiidae (de Pinna, 1993: 167). In all other groups in the Siluriformes, the fenestra is either absent or very small. Although Mo (1991) indicated the presence of the primitive condition of a large fenestra in several catfish families in addition to the Diplomystidae, Cetopsidae and Pangasiidae, we found State 0 to be present only in those three families. In all other families of the Siluriformes, the fenestra is clearly reduced in size relative to the larger aperture present in other groups within the Otophysi.

28. Anterior cranial fontanel in adults (CI = 50, RI = 93)
State 0: Anterior cranial fontanel present throughout ontogeny.
State 1: Anterior cranial fontanel reduced or absent in adults.

Members of the Siluriformes usually have two median fontanels on the skull roof, an anterior opening bordered anteriorly by the mesethmoid and laterally and posteriorly by the frontals, and a posterior aperture bordered anteriorly by the frontals and posteriorly by the supraoccipital. Usually, the anterior fontanel is wider and shorter than the posterior fontanel (e.g. Skelton, 1981: fig. 8, *Austroglanis*; Mo, 1991: fig. 6, *Bagrus*). Within the Cetopsidae, that presumed plesiomorphic configuration of the two medial cranial fontanels occurs only in the Helogeninae (de Pinna & Vari, 1995: fig. 16), *Cetopsidium*, *Denticetopsis sauli* and *Paracetopsis* (Fig. 6). All other genera of the family have some degree of fontanel closure, with the anterior fontanel completely absent in some of these taxa (e.g. *Cetopsis coecutiens*, *C. fimbriata*; Fig. 7).

The degree of fontanel reduction seems to vary markedly ontogenetically, with small and juvenile specimens of a species usually having proportionally larger apertures. The ontogenetic closure of the fontanel is evident in different-sized specimens of *Denticetopsis macilenta* (AMNH 55332) and *D. epa* (MZUSP 83228), in which small specimens have distinctly open fontanels whereas large ones lack the openings. Similarly, a small juvenile specimen of *Cetopsis coecutiens* (LACM 43102-3) has fontanels of a degree of proportional development comparable with the openings present in the plesiomorphic condition, a situation that contrasts markedly with the absence of fontanels in large adults of this species. In view of that, it seems that the homoplastic presence of a large anterior fontanel in *Denticetopsis sauli* is probably a result of the paedomorphic condition of that species.

29. Shape of posterior margin of posterior fontanel (CI = 20, RI = 33).
State 0: Broad and rounded.
State 1: Narrow and pointed.

The posterior region of the posterior fontanel exhibits either of two distinct morphologies among the examined ingroup and outgroup taxa. In the first of these (State 0), the fontanel is broad, usually with a rounded or somewhat truncated posterior margin (e.g. Fig. 6; Grande & Lundberg, 1988: fig. 5). In the alternative condition (State 1), the nearly straight sides of the posterior fontanel converge posteriorly to a fine point. The examined specimens of *Helogenes*, *Cetopsidium* and *Denticetopsis* exhibit State 0, all species of *Paracetopsis* exhibit State 1, and the species of *Cetopsis* exhibit either of these two states (Appendix 2). Missing entries are assigned to *Cetopsis montana*, because the small examined specimens of that species show an intermediate condition between the two recognized states, and to the outgroup species *Pimelodus ornatus*, because the anterior margin of the posterior fontanel in that species is modified beyond meaningful comparison.

30. Extent of posterior fontanel (CI = 33, RI = 50).
State 0: Long and extending anteriorly to frontal.
State 1: Short and not bordered anteriorly by frontal.

The posterior fontanel in the Siluriformes primitively extends anteriorly into the frontal region of the skull, thereby separating the posterior regions of the frontals at the midline (Fig. 6). In some species of *Cetopsis* (*C. baudoensis*, *C. candiru*, *C. coecutiens* and *C. fimbriata*), the posterior fontanel falls short anteriorly of the posterior margin of the frontals (State 1; Fig. 7). The condition of this character in large specimens of *C. candiru* and *C. coecutiens* can be obscured because of the partial (*C. candiru*) or complete (*C. coecutiens*) closure of the fontanel. Half-grown specimens of both of these species have the posterior fontanel clearly identifiable in the posterior part of the supraoccipital as a medial slit that does not extend anteriorly to the margin of the frontals. Thus, these species are coded as having State 1. The primitive condition seen in *C. oliveirai*, which is judged homoplastic to the condition in many species in the Cetopsidae and many outgroups, is hypothesized to be a reversal that is probably the result of paedomorphosis.

31. Paired fontanels in frontals (CI = 100, RI = 100).
State 0: Frontal without fontanel.
State 1: Frontal with large fontanel.

Most members of the Siluriformes lack large openings on the dorsal surface of the neurocranium, except for the medial cranial fontanels. One character that serves to diagnose the Helogeninae (State 1) is the presence of an opening entirely within the frontal, with the aperture situated close to the articulation of the frontal with the sphenotic (de Pinna & Vari, 1995: 15, fig. 16). The opening is apparently a structural fontanel, insofar as it opens to the interior of the braincase but does not appear to serve for the passage of nerves or blood vessels either in cleared and stained material or in dissected alcohol-preserved specimens. The fontanel enclosed within the frontal is unique to the Helogeninae within the Siluriformes.

32. Form of dorsal surface of cranium (CI = 20, RI = 42).

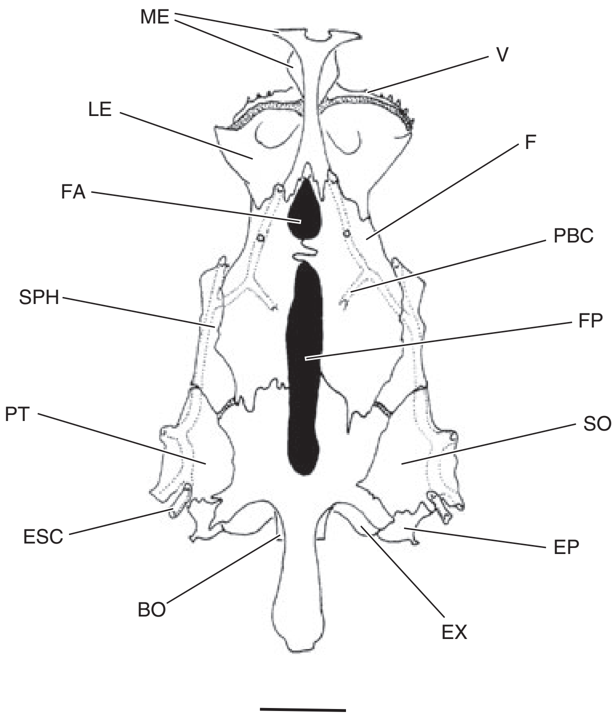

Figure 6. Neurocranium of *Cetopsidium ferreirai* (INPA 6501). Dorsal view. Anterior to top. Scale bar = 1 mm.

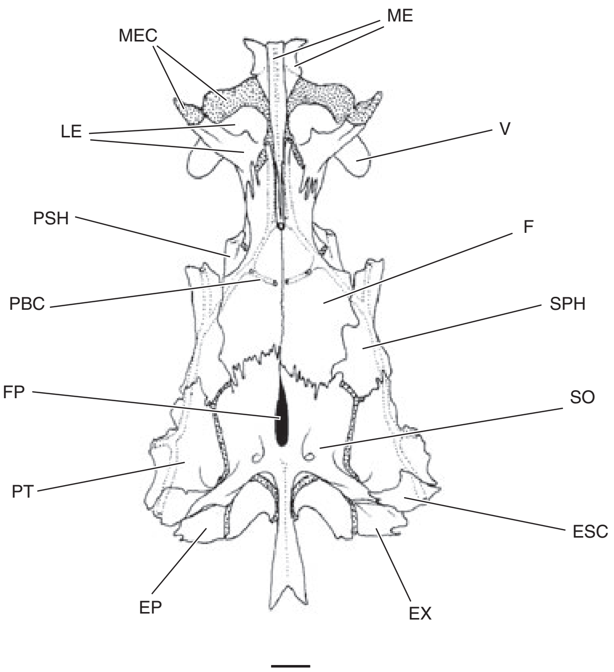

Figure 7. Neurocranium of *Cetopsis fimbriata* (USNM 257763). Dorsal view. Anterior to top. Part of sphenotic of left side damaged, but drawn to match its counterpart. Scale bar = 1 mm.

State 0: Dorsal surface of cranium relatively smooth and without pronounced median ridge.
State 1: Dorsal surface of cranium with pronounced median ridge formed by frontals and supraoccipital.

The dorsal surface of the neurocranium in members of the Siluriformes and most other groups in the Otophysi has a relatively smooth surface without a pronounced median ridge. In some species of *Denticetopsis* and *Cetopsis* (Appendix 2), there is a pronounced vertical ridge formed by vertical expansions or curvatures of the supraoccipital and frontals that extends along the dorsal midline of the skull (State 1). The ridge serves as the median area of attachment for the hypertrophied adductor mandibulae muscle that covers most of the dorsal surface of the skull in those taxa (see character 7, above).

33. Position of canal-bearing portion of sphenotic (CI = 50, RI = 90).
State 0: Extending parallel to lateral margin of skull.
State 1: Diverging laterally from lateral margin of skull.

The anterior portion of the sphenotic in members of the Siluriformes usually consists primarily of a process supporting the branch of the laterosensory canal system that extends somewhat anterolaterally through that bone, regardless of the shape of the sphenotic. This portion of the sphenotic is normally either continuous with the rest of the lateral profile of the neurocranium or runs parallel to the lateral margin of the other bones in that region. The main axis of the anterior portion of the sphenotic, thus, typically has either an anterior or an anteromedial alignment (Fig. 6). Within the Cetopsidae, this presumed plesiomorphic condition of the canal-bearing portion of the sphenotic is limited to *Helogenes* (de Pinna & Vari, 1995: fig. 16) and *Cetopsidium*. All other genera in the Cetopsidae have the anterior portion of the canal-bearing portion of the sphenotic diverging anterolaterally from the rest of the lateral margin of the skull (Fig. 7).

34. Contact between the sphenotic and supraoccipital (CI = 100, RI = 100).
State 0: Present.
State 1: Absent.

Members of the Siluriformes plesiomorphically have the supraoccipital as the main bone of the posterodorsal part of the cranium with that bone having a broad contact along its anterolateral margin with the sphenotic. As noted by de Pinna & Vari (1995: 14) the rearrangement of the neurocranial bones in the Helogeninae is among the most dramatic across the Siluriformes. One of the more striking results of these alterations is the lack of contact between the sphenotic and supraoccipital in the members of that subfamily (Chardon, 1968: 153; Lundberg, 1975: 70; de Pinna & Vari, 1995). The loss of such contact between these bones is largely the result of a reduction in proportional size of the supraoccipital which in the Helogeninae is a relatively narrow bone.

35. Structure of supraoccipital spine (CI = 50, RI = 50).
State 0: With both vertical and horizontal components.
State 1: With only vertical blade and lacking horizontal component.

The supraoccipital spine in the Siluriformes is normally a large structure composed of both a vertical lamina and a dorsally positioned horizontal roof that is aligned transverse to the vertical lamina and continuous with the more anterior components of the skull roof (e.g. Ferraris, 1996: fig. 7). A derived condition present in the species of *Paracetopsis* is the absence of the roof of the supraoccipital spine, such that the spine is composed only of the vertical lamina. Missing entries were assigned to *Nematogenys* (Arratia & Chang, 1975: fig. 1) and *Noturus*, which have the supraoccipital spine either absent or too reduced for the meaningful recognition of character states.

36. Shape of tip of supraoccipital spine (CI = 50, RI = 92).
State 0: Undivided and either pointed or truncated.
State 1: Bifurcated.

The supraoccipital spine among the examined taxa has either an undivided or a bifurcated tip (compare Figs 6, 7). The bifurcated tip is hypothesized to be synapomorphic for the species of *Cetopsis* within the Cetopsidae, a condition that is homoplastic, however, with various outgroup taxa (e.g. *Pelteobagrus*, *Mystus*, *Bagrus* and *Pimelodus*; see Mo, 1991: figs 26, 27). In the species of *Cetopsis*, however, the bifurcated spine does not extend posteriorly to the anterior nuchal plate, in contrast to the condition seen in most other catfishes with bifurcated supraoccipital spines, including the cited genera, in which the spine contacts that plate. Missing entries were assigned to *Nematogenys* (Arratia & Chang 1975: fig. 1) and *Noturus*, where the supraoccipital spine is greatly reduced or absent.

37. Vomerine dentition (CI = 33, RI = 50).
State 0: Present.
State 1: Absent.

The vomer in ostariophysans is primitively edentulous, a condition present in the Cypriniformes, Gymnotiformes and most members of the Characiformes. Many taxa in the Siluriformes, including the relatively basal lineages Diplomystidae and †Hypsidoridae (Grande, 1987: figs 5, 6), have vomerine teeth. The distribution of this feature suggests that the vomer is primitively toothed in catfishes, and that the absence of dentition on that bone is a secondary loss

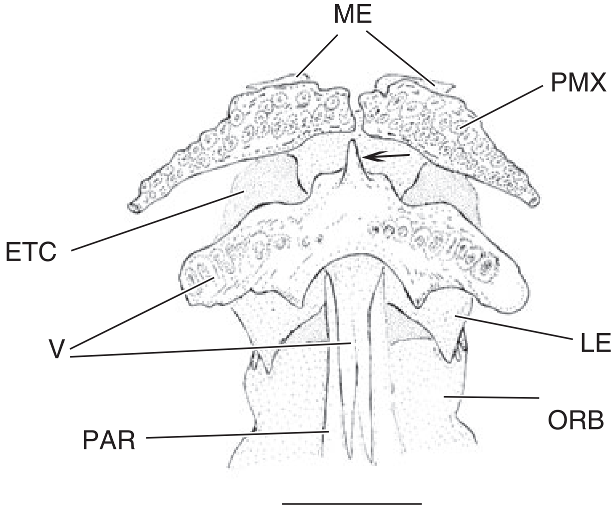

Figure 8. Ethmoid region of skull and associated structures of *Denticetopsis macilenta* (AMNH 55332). Ventral view. Arrow indicates ventromedial protuberance of vomer. Premaxillary and vomerine teeth have fallen off in this specimen. Irregularities on surfaces of vomer and premaxilla are sites of original tooth insertions. Scale bar = 1 mm.

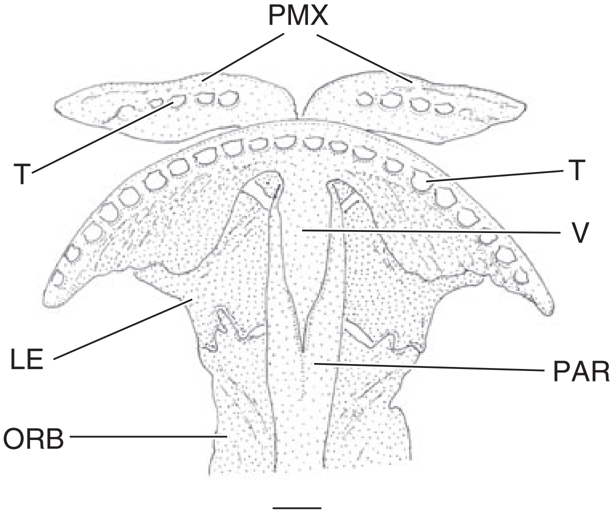

Figure 9. Ethmoid region of skull and associated structures of *Cetopsis candiru* (MZUSP 24688). Ventral view. Scale bar = 1 mm.

that, in the Cetopsidae, is found only in *Denticetopsis sauli*.

38. Form of vomerine teeth (CI = 100, RI = 100).
State 0: Conical.
State 1: Incisiform.

Vomerine teeth in the Siluriformes are primitively conical in shape, a condition seen in the Diplomystidae (Arratia, 1987), †Hypsidoridae (Grande, 1987; Grande & de Pinna, 1998) and the majority of other catfish taxa in which such teeth are present. In *Cetopsis coecutiens* and *C. candiru*, vomerine teeth are incisiform, with a sharp, flattened edge. These teeth are aligned to form a long and nearly continuous cutting surface extending across the roof of the mouth. The polarity of this character is further corroborated ontogenetically, in that examined juvenile specimens of *C. coecutiens* have conical vomerine teeth comparable with those in the hypothesized plesiomorphic condition. *Denticetopsis sauli* is coded as inapplicable for this character because it lacks vomerine teeth (Ferraris, 1996: 165).

39. Distribution of vomerine teeth (multistate ordered) (CI = 60, RI = 87).
State 0: More than one irregular row of teeth arranged in contralateral patches.
State 1: One row of teeth arranged in contralateral components separated at midline.
State 2: One continuous row of teeth arranged in separate arches on each side of midline.
State 3: One row of teeth in single, continuous, semicircular arc across midline.

The vomerine dentition in the Cetopsinae shows pronounced variation that has been previously utilized to underpin the taxonomy of the group. While there is certainly taxonomically relevant variation in that character complex, previous interpretations were flawed by their use of stages of ontogenetic variation as characters, a problematic practice inasmuch as vomerine dentition patterns change dramatically during ontogeny in the Cetopsinae. We coded the observed variation in four different states which reflect objective qualitative gaps in the range of observed configurations. These states apply only to adult stages of the examined species.

State 0 was observed in the Diplomystidae, in which the vomerine teeth are arranged in two separate patches, a condition that is hypothesized to be plesiomorphic given its occurrence in this basal siluriform family and numerous other families. In State 1 there is a single row of teeth on each side of the vomer, with the contralateral tooth rows not meeting at the midline (Fig. 8). In State 2 the teeth are arranged in a single tooth row without a gap at the midline, but with the teeth forming two separate arches, one on each side of the vomer. In State 3 the teeth are arranged in a single row in forming a continuous semicircular arch across the midline of the vomer (Fig. 9). Species of *Cetopsidium*, *Denticetopsis* and *Paracetopsis* exhibit State 1. Species of *Cetopsis* have either State 1, 2 or 3. State 1 is present in *C. montana*, *C. orinoco*, *C. othonops*, *C. pearsoni* and *C. sandrae*; State 2 in *C. amphiloxa*, *C. arcana*, *C. gobioides* and *C. plumbea*; and State 3 in *C. baudoensis*, *C. candiru*, *C. coecutiens*, *C. fimbriata*, *C. motatanensis* and *C. oliveirai*.

This character was ordered according to similarity among its states. Taxa assigned missing entries are those lacking vomerine teeth. The outgroup taxon *Bagrus bayad* has vomerine teeth that are irregularly disposed in a band continuous across the midline. This condition does not fit any of the recognized states within the Cetopsidae and is therefore not relevant for the resolution of the cladogram of the family and is therefore coded as a missing entry.

Lundberg & Rapp Py-Daniel (1994: 385) reported that the vomerine tooth row is interrupted across the midline in *Cetopsis oliveirai*. One of two cleared and stained specimens of this species examined in this study has a continuous vomerine tooth row and the other has the row interrupted in the middle, but with the gap in the series obviously a consequence of the loss of a tooth at that position. Therefore, we code the vomerine tooth rows in *C. oliveirai* as continuous.

40. Position of tooth-bearing part of vomer relative to ventral portion of neurocranium (CI = 100, RI = 100).
State 0: Lateral arms approximately parallel to surface of other bones of ventral portion of neurocranium.
State 1: Lateral arms arched ventrally relative to surface of other bones of ventral surface of neurocranium.

Siluriformes plesiomorphically have the plane of the head of the vomer parallel to that of the adjoining bones of the ventral portion of neurocranium, both in those species with tooth-bearing and in those species with edentulous vomers. In all species of *Denticetopsis*, except *D. macilenta* and *D. sauli*, the lateral arm of the head of the vomer is curved ventrally, such that the lateral end of that bone is markedly divergent ventrally from the rest of the floor of the cranium. The vomerine teeth in the species of *Denticetopsis* with the derived condition also increase in size laterally. The combined effect of these two modifications results in the tips of the teeth on the vomer delimiting a markedly ventrally concave plane. The ventral curvature of the lateral arm of the vomer found in most species of *Denticetopsis* is absent in *D. macilenta*, and in *D. sauli* the arm is reduced in size (Ferraris, 1996: fig. 1), a condition that does not allow a determination of character states.

41. Ventral surface of vomer (CI = 50, RI = 83).
State 0: Vomer without median protruberance anteriorly on ventral surface.
State 1: Vomer with median protuberance anteriorly on ventral surface.

The vomer in most members of the Cetopsidae and other groups in the Siluriformes has a relatively flat ventral surface without well-defined protuberances or processes (Fink & Fink, 1981: fig. 2D, *Diplomystes*; Mo, 1991: figs 7, 8, *Bagrus*). The species of *Denticetopsis* have, instead, a conspicuous ventromedial protuberance on the vomer arising slightly posterior to the posterior limit of the premaxillary symphysis (Fig. 8, arrow). A median ligamentous sheet extends anteriorly from the protuberance of the vomer to the premaxillary symphysis. The protuberance varies slightly in shape and orientation among the species of *Denticetopsis*. In *D. sauli* the protuberance extends directly ventrally, whereas in *D. macilenta* it is directed anteriorly, and *D. praecox* has an intermediate alignment of the process. Uniquely within the species of *Cetopsis*, *C. montana* has a slight thickening of the vomer in the position where the ventral vomerine protuberances occurs in the species of *Denticetopsis.* However, the thickening in *C. montana* is distinctly less developed than are the protuberances found in the species of *Denticetopsis* and therefore *C. montana* is considered to have State 0 for this character. Elsewhere in the Cetopsidae, two species of *Cetopsidium*, *C. pemon* and *Cetopsidium* sp., also have a protuberance similar to that in *Denticetopsis*, although proportionally smaller in size than is the process in that genus. Because of the similarity in form, this process is coded as State 1 in these two taxa.

42. Relative position of teeth on vomer and premaxilla (CI = 100, RI = 100).
State 0: Tooth-bearing surface of vomer distinctly separated from posterior dentition of premaxilla, with anterior process of vomer falling short of premaxilla.
State 1: Tooth-bearing surface of vomer located very close to dentition of premaxilla, with anterior process reaching and extending dorsal to premaxilla.

In the Siluriformes, the lateral arm of the anterior head of the vomer, whether tooth-bearing or edentulous, is primitively separated from the posterior margin of the premaxilla by a broad space (e.g. Grande, 1987: fig. 6; Mo, 1991: fig. 31). The tooth-bearing surface of the vomer thus forms a biting surface clearly separate from that of the premaxilla. In *Cetopsis coecutiens* and *C. candiru*, the tooth-bearing portion of the vomer is markedly displaced anteriorly, with the result that the vomerine dentition lies proximate to the premaxillary dentition (Fig. 9). Consequently the vomer and premaxillae jointly form a single biomechanically functional biting surface. Indeed, the presence of teeth on the vomer that are both longer and stouter than the dentition present on the premaxilla suggests that the vomerine dentition is the primary functional component of the dorsal portion of the biting complex in those two species of *Cetopsis*. The anterior displacement of the vomer furthermore results in the dorsal overlap by the anterior process of the vomer of part of the premaxilla. This arrangement contrasts with the primitive condition of the vomer in the Siluriformes in which the anterior process of the vomer falls short of the posterior margin of the premaxilla. The positional modification of the vomer is clearly associated with the feeding habits of *Cetopsis coecutiens* and *C. candiru*, both of which bite off large chunks of flesh from living prey and carrion.

43. Dorsal surface of shaft of mesethmoid (CI = 50, RI = 80).
State 0: Flat or convex.
State 1: Strongly concave.

The dorsal surface of the anterior portion of the mesethmoid in the Siluriformes is primitively transversely convex or flat. In *Cetopsis amphiloxa* and the species of *Denticetopsis* that region of the mesethmoid is strongly concave, such that the lateral edges of the mesethmoid shaft form elevated rims laterally bordering the deeper central groove on the shaft. The mesethmoid shaft in the species of *Denticetopsis* is also much wider than in other species of the Cetopsidae (Ferraris, 1996: fig. 7), a condition apparently correlated with the dorsally concave shape of the bone and which is therefore not coded herein as a separate character. The transverse concavity of the mesethmoid in the species of *Denticetopsis* is considered to be homoplastic to the presence of that feature in *Cetopsis amphiloxa* under the final most parsimonious hypophysis of relationships.

44. Shape of anterior process of vomer (CI = 20, RI = 42)
State 0: Either uniformly wide with truncate distal margin, or narrowing anteriorly to rounded tip.
State 1: Expanding anteriorly and terminating in broad truncate margin.

The anterior process of the vomer in most members of the Cetopsidae and indeed the Siluriformes either has a relatively uniform width along its length and a truncate distal margin or it narrows anteriorly and terminates in a rounded tip. In the species of *Paracetopsis* and some species of *Cetopsis* (*C. amphiloxa*, *C. othonops*, *C. pearsoni*, *C. plumbea* and *C. sandrae*), the anterior process expands anteriorly and terminates in a broad, truncate, anterior margin, with the overall form of the process somewhat fan-shaped.

45. Relative length of anterior process of vomer (CI = 100, RI = AUT).
State 0: Slightly broader than long, or as long as broad.
State 1: Longer than broad.

The anterior process of the vomer is the portion of the bone that extends anteriorly along the ventral surface of the anterior part of the mesethmoid and which extends anterior to the lateral arms of the vomer. In most species of the Cetopsidae and other families of the Siluriformes, this process has an overall irregular or somewhat square shape. In *Cetopsis montana*, this process is uniquely markedly elongated, having an overall slender rectangular shape.

46. Width of lateral wing of vomer (CI = 100, RI = 100).
State 0: Wide, approximately as wide as, or wider than, premaxilla.
State 1: Narrow, less than one-half width of premaxilla.

The lateral wing of the vomer provides support for the vomerine tooth plate in those members of the Siluriformes with such dentition. Even taxa lacking vomerine teeth usually have a vomer with lateral wings present on the ventral surface of the skull. In the plesiomorphic condition in the Siluriformes the vomerine wing is a broad structure, approximately as wide as, or wider than, the premaxilla (Fig. 8). Uniquely in the species of *Paracetopsis*, the arm of the vomer is narrower, with its maximum dimension along the anteroposterior axis not exceeding half the width of the premaxilla. The broad lozenge-shaped vomer in the Diplomystidae lacks well-defined lateral wings, which makes an identification of relevant homologous points impossible. That taxon is therefore coded a missing entry for this character.

47. Posterior process of vomer (CI = 100, RI = 100).
State 0: Present.
State 1: Reduced or absent.

The vomer in species of the Siluriformes plesiomorphically has an anterior laterally expanded portion that sometimes bears tooth plates, and a long, median, posterior process that is typically ankylosed to the ventral surface of the anterior portion of the parasphenoid (Figs 8, 9). As reported previously by de Pinna & Vari (1995: 15, fig. 17), this posterior median process of the vomer is either absent or greatly reduced in the species of the Helogeninae with the overall form of the reduced vomer markedly variable intraspecifically. Such reduction was proposed as a synapomorphy for the species of the Helogeninae by de Pinna & Vari (1995), a conclusion congruent with the results of this study.

48. Posterior extension of lateral portion of ethmoid cartilage (CI = 100, RI = AUT).
State 0: Present.
State 1: Absent.

Otophysans primitively have a narrow process of the ethmoid cartilage extending posteriorly, ventral of the orbitosphenoid. This extension is absent in all families in the Siluriformes except for the Diplomystidae (de Pinna, 1993). The primitive state is very evident in that family, in which the posterior extension of the ethmoid cartilage stretches along the limit between the orbitosphenoid dorsally and the vomer and parasphenoid ventrally (Fink & Fink, 1981: fig. 2D). The cartilaginous process extends posteriorly to the middle of the length of the orbitosphenoid in adults, and almost to the pterosphenoid in younger individuals. This character is included in this analysis to help resolve the position of the Cetopsidae relative to siluriform outgroups, albeit being irrelevant for the resolution of relationships within the family.

49. Degree of ossification of medial portion of mesethmoid (CI = 100, RI = 100).
State 0: Ossified.
State 1: Unossified.

The mesethmoid in the Siluriformes is primitively ossified as a single element that is composed of anterolaterally diverging arms (mesethmoid cornua) and a medial shaft forming the roof of the anterior-most portion of the skull (Fink & Fink, 1981: fig. 7). In the Helogeninae, the medial portion of the mesethmoid fails to ossify even in adults (de Pinna & Vari, 1995: 13–14, fig. 16). The cartilaginous condition of the central region of the mesethmoid leaves the ossified mesethmoid cornua unattached directly to bone, or attached by narrow, ossified, dorsolateral bridges on each side of the neurocranium. This limited degree of ossification of the mesethmoid has not been encountered in other examined taxa in the Siluriformes and is consequently considered a derived condition within that order.

50. Degree of development of ossified portion of mesethmoid cornua (CI = 100, RI = 100).
State 0: Well developed, forming conspicuous diverging arms on anterior part of mesethmoid.
State 1: Poorly developed or absent.

Mesethmoid cornua are primitively present in most groups in the Siluriformes and other orders in the Ostariophysi, forming an important component of the suspension of the upper jaw. In adults of *Cetopsis candiru* and *C. coecutiens*, in contrast, the mesethmoid cornua are entirely absent in adults. The cornua in these species are replaced by a structure that is similar in shape to the cornua, but which is composed of rigid, soft tissue, probably fibrous cartilage (see Character 52, below). Juveniles of *C. coecutiens*, contrastingly, have the bony cornua present and well developed (Fig. 43). Apparently, the bony portion of the cornua of this species progressively decreases in size ontogenetically and is replaced by fibrous cartilage. This modification may be related to the shift in biting force from the premaxillae to the vomer in these two species of *Cetopsis* (see Character 42, above).

51. Vertical lamina of mesethmoid (CI = 25, RI = 0).
State 0: Not pierced by well-defined fenestra.
State 1: Pierced by well-defined, round fenestra.

The vertical lamina of the mesethmoid in most species in the Cetopsidae and other families in the Siluriformes is a continuous sheet of bone that fills the space between the vomer ventrally and the shaft of the mesethmoid dorsally. The lamina sometimes bears small depressions and superficial concavities that occasionally completely pierce the bony surface, but the plesiomorphic condition of the lamina in the Siluriformes lacks any large, well-defined opening. *Cetopsis amphiloxa*, *C. candiru*, *C. orinoco* and *C. plumbea* have a conspicuous and well-defined fenestra located in the middle of the mesethmoid lamina (Fig. 11, arrow). Some variation in the size of the fenestra occurs among the species with this opening, and it reaches its maximum development in *C. amphiloxa*, in which it is enlarged into a large, posteriorly open hiatus leaving the bony portion of the lamina restricted to dorsal and ventral horizontal struts. No blood vessels or nerve branches appear to pass through the opening, which implies that it is not technically a foramen. In *Helogenes*, the central part of the mesethmoid is entirely cartilaginous and the condition of this character is thus coded as a missing entry for that genus.

52. Rigid layer of fibrous cartilage associated with anterolateral margins of mesethmoid, forming protective wall surrounding anteromedial portions of olfactory capsule (CI = 100, RI = 100).
State 0: Absent.
State 1: Present.

As noted in de Pinna & Vari (1995: 12), the prominent snout in all members of the Cetopsinae accommodates a pair of significantly enlarged olfactory organs and associated nasal cavities. A number of modifications contribute to this modified snout in the species of the Cetopsinae, with one of the more striking being a peculiar, transparent, laminar shelf formed of soft tissue that extends from the dorsolateral rim of the snout. This shelf is mechanically resistant and extends anteriorly into the posterodorsal margin of the mesethmoid cornua. The shelves form a conspicuous anteromedial shield for each of the nasal capsules and are apparently unique to members of the Cetopsinae within the Siluriformes (de Pinna & Vari, 1995: 12).

Although a histological examination of these shelves lay beyond the scope of this study, the appearance, diffraction and consistency of the shelves are very similar to those characteristics for cartilage as apparent from a gross morphological examination of cleared and stained specimens. Consequently, it seems likely that the shelves of the mesethmoid are formed by fibrous cartilage. The shelves failed to stain with alcian blue, but such staining is also absent in other structures, such as intervertebral discs, that are composed of fibrous cartilage.

53. Morphology of anterior part of mesethmoid cornua (CI = 100, RI = 100).
State 0: Round or with horizontal laminar edge.
State 1: With vertical ventral lamina.

The mesethmoid cornua are either round in cross-section or extended as a posteroventral lamina of bone in most groups in the Siluriformes, in general, and in species of the Cetopsidae (e.g. Ferraris, 1996: fig. 1) other than for *Paracetopsis*, in particular. Species of *Paracetopsis* have a peculiar morphology of the mesethmoid cornua, in which the anterior margin of the cornua is extended ventrally as a vertical lamina. The premaxilla articulates with the posterior part of this lamina.

54. Shape of anterior margin of anterior process of vomer (CI = 100, RI = 100).
State 0: Straight or convex, with smooth anterior margin.
State 1: With jagged anterior margin.

The anterior margin of the anterior process of the vomer in outgroups in the Siluriformes and most species of the Cetopsidae is primitively truncate with a straight or anteriorly convex edge (Fig. 8). In *Paracetopsis* the anterior margin of the vomer is, in contrast, distinctly jagged.

55. Medial attachment of transcapular process (CI = 50, RI = 66).
State 0: Directly onto facet on basioccipital.
State 1: Onto lateral process of basioccipital.

The transcapular process in the Siluriformes is an ossification of Baudelot's ligament that connects a portion of the pectoral girdle with the posterior portion of the neurocranium. When the ossification of the ligament is complete, there is bony contact between the transcapular process and the basioccipital. In the plesiomorphic condition, as observed in the Diplomystidae, †Hypsidoridae (Grande & de Pinna, 1998: fig. 7) and most other outgroups in the Siluriformes included in this study (e.g. Grande & Lundberg, 1988: fig. 6), the proximal portion of the process articulates directly with a facet on the basioccipital. In the derived state, present in *Cetopsis coecutiens*, *C. candiru* and *C. oliveirai*, the basioccipital has a lateral process on each side of the bone that acts as a counterpart of, and contacts, the transcapular process. As a result, the medial portion of the transcapular bar of these three species is formed by a process of the basioccipital.

56. Shape of dorsal limb of supracleithrum (CI = 100, RI = AUT).
State 0: Straight.
State 1: Curved posteriorly.

The dorsal limb of the supracleithrum corresponds to the region of that bone which articulates with the posterior region of the neurocranium. Normally, members of the Siluriformes have the dorsal limb of the supracleithrum poorly differentiated from the rest of the bone and the limb is either straight or has a slight curve. In *Cetopsis gobioides* the dorsal part of the supracleithrum is curved posteriorly (Fig. 10). Some variation was observed in the form of the dorsal limb of the supracleithrum among examined specimens. One cleared and stained specimen of *C. arcana* (MZUSP 55965) has a curvature of the dorsal portion of the supracleithrum whereas a second specimen of the species (MZUSP 41492) shows the hypothesized plesiomorphic straight condition of this character. *Cetopsis arcana* is consequently coded as a missing entry for this character. *Cetopsis orinoco* has a slight curvature of the supracleithrum, a condition that is intermediate between States 0 and 1. In light of that indefinite condition, this species is also coded as a missing entry for this character. In *C. gobioides*, the curvature seems to be more pronounced in large specimens and very slight in small ones and it is possible that the variation observed in other species is also a function of growth.

57. Posterior process on ventral limb of supracleithrum (CI = 100, RI = 100).
State 0: Absent or poorly defined.
State 1: Well defined.

The ventral limb of the supracleithrum in the Siluriformes primitively lacks any well-defined processes along its posterior margin. In all species of *Cetopsis* the ventral part of the ventral limb of the supracleithrum that lies adjacent to the body wall bears a short, finger-like, posteriorly directed process (Fig. 10).

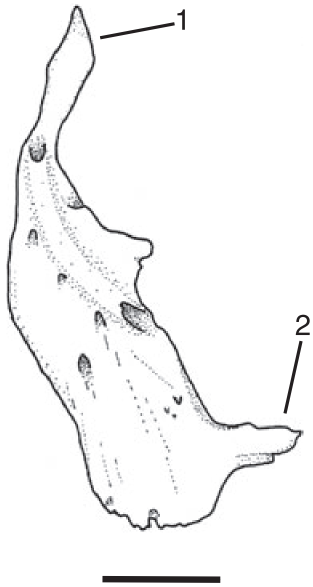

Figure 10. Supracleithrum of *Cetopsis gobioides* (MZUSP 38808). Lateral view. Left side. Anterior to left. Arrow 1 indicates dorsal limb, arrow 2 indicates posterior process of ventral limb. Scale bar = 1 mm.

58. Distance between laterosensory canals along anterior halves of frontals (multistate ordered) (CI = 50, RI = 86).
State 0: Widely separated, with gap at least six times width of canal.
State 1: Moderately separated, with gap approximately four or five times width of canal.
State 2: Closely set, with gap no more than two times width of canal.

The sensory canals along the anterior halves of the frontals are primitively well separated from one another in the Siluriformes. For consistency in comparisons in light of the anterior convergence of the canals in some species, we measure the distance between the canals immediately anterior to the epiphyseal bar. The typical maximum separation between the canals in catfishes is approximately 6–8 times the width of one canal from dorsal view (e.g. de Pinna & Vari, 1995: fig. 16). The only taxa within the Cetopsidae in which the sensory canals retain the plesiomorphic condition are the species of *Helogenes* and *Cetopsidium* (Fig. 6). Among other species of the Cetopsidae the canals are more closely positioned, to varying degrees (States 1 and 2; Ferraris, 1996: fig. 6). At the extreme of their proximity, the canals are nearly adpressed to each other along the dorsal midline, as found in *Cetopsis coecutiens*, *C. fimbriata* (Fig. 7), *C. oliveirai* (Lundberg & Rapp Py-Daniel, 1994: fig. 1) and *C. orinoco* (State 2).

59. Separation of the contralateral parietal branches of laterosensory canal system (CI = 50, RI = 92).
State 0: Canals widely separated.
State 1: Canals converging posteromedially to midline and then running dorsally in soft tissue and adpressed to each other.

The parietal branch of the laterosensory canal system in the Siluriformes is a short canal that extends posteriorly from the sensory canal system on the frontal toward the supraoccipital. The parietal canal is plesiomorphically directed posteriorly and the contralateral canals open onto the dorsal surface of the head as two small pores that are positioned distant from one another. In the derived condition, which is present in all species of *Cetopsis* except *C. oliveirai*, the parietal canals converge posteriorly toward the midline, and then exit the skull and continue as proximate soft-tissue canals to the surface of the skin. This revamping of the parietal branch is clearly associated with the extensive invasion of the skull roof by the adductor mandibulae muscle, which restricts the area of potential passage of the canals to the median muscle septum. The greater separation of the pores in *Cetopsis oliveirai* probably reflects the paedomorphic less-developed adductor mandibulae muscle that uniquely characterizes that species in the Cetopsidae (see Character 7).

In groups within the Siluriformes with a less pronounced envelopment of the skull roof by muscle, such as the *Noturus* in the Ictaluridae, the parietal canals converge until the dorsal limit of muscle, which in this genus is still distant from the midline. The relevant soft-tissue parts are damaged in the single available specimen of *Denticetopsis sauli*, and the taxon is assigned a missing entry for this character.

60. Size and orientation of exit for ophthalmic nerve from neurocranium (multistate ordered) (CI = 66, RI = 0).
State 0: Small, not evident in dorsal view.
State 1: Large, partially visible in dorsal view.
State 2: Very large, located on roof of skull and completely visible in dorsal view.

In most members of the Cetopsidae and outgroup taxa, the ophthalmic nerve exits the neurocranium through a narrow, vertical foramen that is not visible from a dorsal view. This nerve branch innervates the snout region. The form of the exit for the ophthalmic nerve in *Cetopsis oliveirai* is apparently unique within the Siluriformes and possibly across the Ostariophysi in having a hypertrophied superficially situated ophthalmic nerve that exits the skull through a large, dorsally positioned foramen that is bordered by the frontal, sphenotic and orbitosphenoid bones (Fig. 12; see also Lundberg & Rapp Py-Daniel, 1994: fig. 1). The hypertrophied ophthalmic nerve in *C. oliveirai* is associated with the extremely large olfactory organ and related cranial restructurings characteristic of that species (Lundberg & Py-Daniel, 1994: 382) which are unique to that species among examined taxa in the Siluriformes. *Cetopsis coecutiens* has, however, homologous modifications of the ophthalmic nerve and neurocranium, albeit somewhat less developed. The exit for the ophthalmic nerve in *C. coecutiens* is also more dorsally positioned than found in most cetopsids, but the nerve branch in that species is proportionally much smaller than in *C. oliveirai* and is therefore coded as State 1, an intermediate condition.

61. Condition of frontals at midline (CI = 100, RI = AUT).
State 0: Unfused.
State 1: Fused.

Cetopsis oliveirai has the frontal bones fused to each other, with the result that the frontals jointly form a single gently convex bony plate on the skull roof (Fig. 12), without any indication of the primitive joint between the contralateral frontals. Such fusion represents a nearly unique condition within the Siluriformes (the genus *Platyallabes* in the Clariidae also has such fusion; Poll, 1977; Devaere *et al*., 2005) and the Ostariophysi. Lundberg & Rapp Py-Daniel (1994:

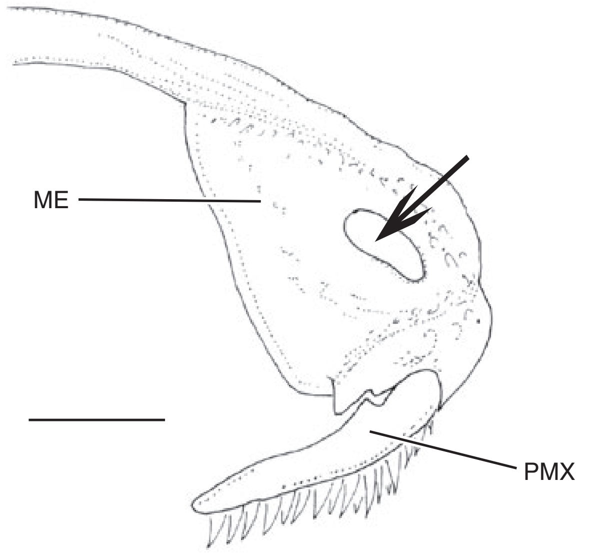

Figure 11. Mesethmoid and premaxilla of *Cetopsis orinoco* (MCNG 5375). Lateral view, anterior to right. Arrow indicates fenestra in mesethmoid lamina. Scale bar = 1 mm.

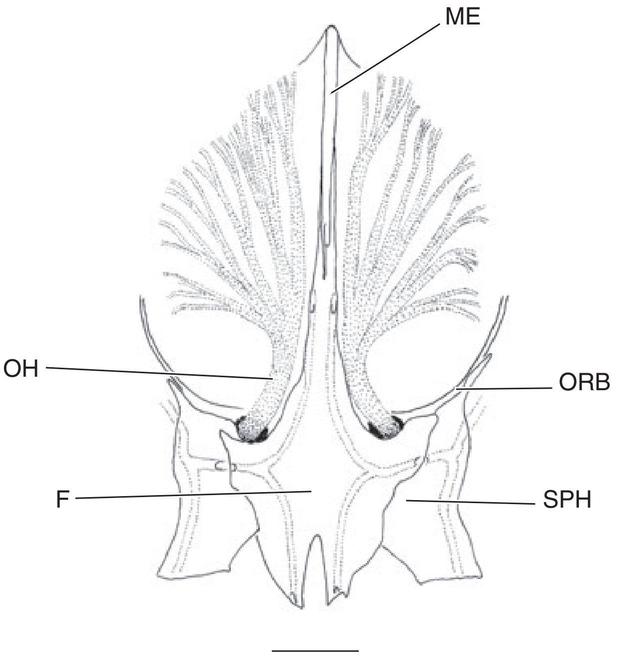

Figure 12. Anterior portion of skull and associated portion of ophthalmic nerves of *Cetopsis oliveirai* (MZUSP 79338). Dorsal view. Scale bar = 1 mm.

fig. 1) show a line of separation between the frontals in *C. oliveirai*, but such a division was not apparent in either of the specimens examined for this study. A similar median fusion of the frontals may occur in *C. coecutiens*, but in that species the medial portions of the frontals are extended vertically as a median crest, with the fusion of these bones, if present, occurring along the middle of that crest. In cleared and stained preparations of adult and medium-sized specimens, the bones of the crest seem to form a continuous surface, but that cannot be confirmed without a histological examination of the bones in that region. For that reason, *C. coecutiens* is scored as a missing entry for this character. This character, if confirmed, provides evidence that *C. coecutiens* and *C. oliveirai* are sister groups, contrary to the most parsimonious hypothesis arrived at in this study, in which *C. coecutiens* and *C. candiru* are sister species (see Discussion).

BRANCHIAL ARCHES

62. Anterior bony end of second basibranchial (CI = 50, RI = 92).
State 0: Not developed anteriorly and falling short of transverse line through anterior bony margin of first hypobranchial.
State 1: Developed anteriorly and extending to transverse line through anterior bony margin of first hypobranchial.

The bony portion of the anterior end of the second basibranchial in the Siluriformes is normally truncate or convex, and does not extend significantly into the region between the first hypobranchials. In the derived condition, which occurs in *Paracetopsis* and most species of *Cetopsis*, the anterior margin of the bone is developed anteriorly, such that its anterior margin is aligned with the transverse line through the anteromedial corners of the first pair of hypobranchials.

63. Lateral margins of second basibranchial (CI = 25, RI = 78).
State 0: Approximately following profile of centre of ossification of bone.
State 1: Expanded laterally and forming convex lateral shelf.

In most members of the Siluriformes the second basibranchial (the anterior-most ossified element in the series, because both the basihyal and the first basibranchial are absent in the Siluriformes) is a simple cylinder of bone that is often slightly expanded along its anterior and posterior portions. The lateral margins of the main shaft of the bone are, in turn, either straight or slightly concave, with little or no ossification present beyond the ossification centre of the second basibranchial. In the hypothesized derived condition the lateral margins of the second basibranchial are expanded laterally by the development of horizontal shelves that result in convex lateral profiles to the bone from a dorsal view (de Pinna & Vari, 1995: 7, fig. 5). These expansions are sometimes asymmetrical with the expansions more pronounced on the anterior than the posterior half of the bone.

Some species of the Cetopsinae of small body sizes retained the plesiomorphic morphology of the second basibranchial and, on that basis, de Pinna & Vari (1995: 7) postulated that such cases represented reversals. The lack of detailed knowledge about the intrafamilial relationships for the Cetopsidae at the time of de Pinna and Vari's study, however, prevented a conclusive assessment of the evolution of the character. The second basibranchial shows the plesiomorphic state (State 0) in *Cetopsis oliveirai*, all species of *Denticetopsis*, and all species of *Cetopsidium* with the exception of *C. ferreirai* (the miniature cetopsins including *Pseudocetopsis macilenta* reported by de Pinna & Vari, 1995: 7). *Cetopsidium morenoi* has an intermediate condition that is difficult to assign unambiguously to either of the states, and the species is coded as a missing entry. All of these taxa are species that achieve among the smallest maximum body sizes within the Cetopsinae, with all species except *Cetopsis oliveirai*, however, belonging to relatively basal clades within the subfamily. It is possible that the presence of the plesiomorphic state of this character in at least some of these taxa, in particular *C. oliveirai*, may be a result of paedomorphosis.

64. Degree of development of posterior portion of third basibranchial (CI = 100, RI = 100).
State 0: Bone and associated cartilage not expanded posteriorly.
State 1: Bone and associated cartilage greatly expanded posteriorly.

The posterior region of the third basibranchial (the second ossified element in the basibranchial series) in the Siluriformes is plesiomorphically smaller than the anterior part of that bone. The third basibranchial ossification, and associated cartilage, is markedly expanded and flared posteriorly in adults of the Helogeninae, thereby making the posterior region of the third basibranchial is as large as, or larger than, the anterior portion of that bone (de Pinna & Vari, 1995: 13, fig. 5). A somewhat less pronounced expansion is found in smaller specimens of the Helogeninae. In light of the unique nature of this feature, it is hypothesized to be a synapomorphy of the subfamily.

65. Size of uncinate process of first hypobranchial (CI = 100, RI = 100).
State 0: Shorter than free anterior margin of bone.
State 1: Longer than free anterior margin of bone.

The presence of an anterior uncinate process on the first hypobranchial is a common trait in the Siluriformes. This anteromedially directed process is usually located at the anterior or anterolateral corner of the bone. The size of the uncinate process of the first hypobranchial varies widely, ranging from being a short knob of bone to having the form of a well-defined process (de Pinna & Vari, 1995: fig. 5). Within the taxa examined in this study, the uncinate process is markedly enlarged (State 1) in the species of *Cetopsidium*, in which the process extends anteromedially to the space between the dorsal and ventral hypohyals (Fig. 13). As a consequence of this expansion of the uncinate process, the anterior half of that structure is dorsally covered by the dorsal hypohyal. The degree of development of the uncinate process on the first hypobranchial of *C. orientale* is less pronounced than in its congeners, but the process is, nonetheless, larger than that present in the non-*Cetopsidium* species of the Cetopsidae examined in this study. This lesser degree of development of the first hypobranchial in *C. orientale* is probably a consequence of the relatively small size of the single cleared and stained specimen of that species examined, in which the skeleton had probably not yet fully ossified.

66. Form of first hypobranchial (CI = 100, RI = 100).
State 0: Straight or slightly arched, without posteromedial concavity.
State 1: Strongly arched, with posteromedial concavity.

In the Siluriformes, the posteromedial margin of the first hypobranchial is plesiomorphically either straight, convex or slightly curved posteriorly (de Pinna & Vari, 1995: fig. 5). In contrast, the species of *Denticetopsis* have a deep concavity along the posteromedial margin of the first hypobranchial (State 1: Fig. 14).

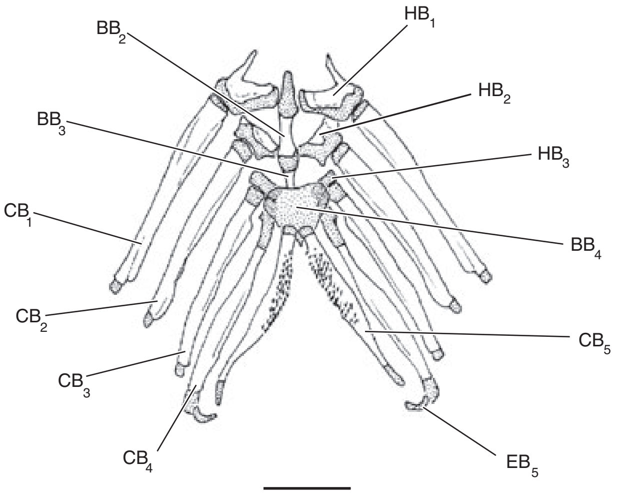

Figure 13. Lower branchial arches in *Cetopsidium morenoi* (UF 26156). Dorsal view. Anterior to top. Scale bar = 1 mm.

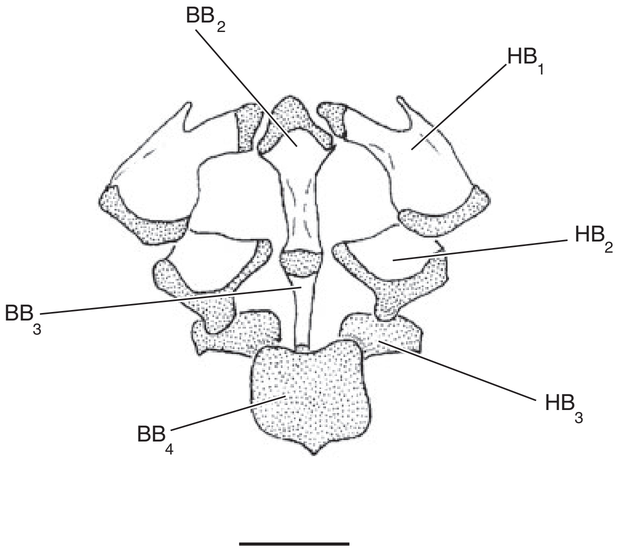

Figure 14. Anterior ventral branchial-arch elements in *Denticetopsis praecox* (AMNH 74449SW). Dorsal view. Anterior to top. Scale bar = 1 mm.

67. Ossification of second hypobranchial (CI = 33, RI = 33).
State 0: Present, cartilage restricted to posterior margin of bone.
State 1: Absent, hypobranchial entirely cartilaginous.

The second hypobranchial in the Siluriformes is usually ossified as a perichondral layer of bone that originates ontogenetically in the middle of the anterior margin of the bone and expands posteriorly until only a margin of cartilage remains along the posterior margin of the bone. Within the Cetopsidae, the second hypobranchial is unossified in all species of *Helogenes* (de Pinna & Vari, 1995: fig. 5) and in *Cetopsis sandrae* (State 1). The single examined cleared and stained specimen of the *C. sandrae* is apparently not completely grown. Nonetheless, the cartilaginous condition of its second hypobranchial in that specimen does not appear to be directly correlated to the apparently juvenile condition of the specimen, inasmuch as similar-sized specimens of other species of *Cetopsis* exhibit a pronounced ossification of the second hypobranchial element.

68. Anterior profile of second hypobranchial (CI = 100, RI = 100).
State 0: Convex or straight.
State 1: With well-defined concavity.

The anterior margin of the second hypobranchial in nearly all taxa in the Siluriformes is either convex or straight. However, in the Helogeninae, the second hypobranchial is entirely cartilaginous and has a well-defined concavity in its anteromedial corner when examined from a dorsal view (de Pinna & Vari, 1995: fig. 5). This modification was proposed as a synapomorphy for the Helogeninae by de Pinna & Vari (1995: 13), a conclusion congruent with the results of this study.

69. Orientation of third hypobranchial (CI = 33/50, RI = 50/75).
State 0: Long axis perpendicular to basibranchial series.
State 1: Long axis oblique relative to basibranchial series.

The third hypobranchial normally has the same orientation as the remaining elements in the hypobranchial series (i.e. approximately perpendicular to the longitudinal line formed by the basibranchials; see de Pinna & Vari, 1995: fig. 5). In *Denticetopsis sauli* and in the species of *Cetopsidium*, with the exception of *C. orientale*, the medial terminus of the third hypobranchial is posterior of lateral portion and, as a consequence, that ossification has an oblique alignment relative to the longitudinal axis (Fig. 13).

70. Shape of uncinate process on second epibranchial (CI = 100, RI = AUT).
State 0: Straight.
State 1: Angled distally.

When present, the uncinate process on the second epibranchial in the Siluriformes and other orders in the Otophysi is a slightly angled or curved either posteriorly or posteromedially directed process (Fink & Fink, 1981: fig. 13). *Cetopsis sandrae* is unique among the species examined in this study in having the uncinate process on the second epibranchial both markedly elongate and anteromedially angled, thereby forming an almost angled hook on the posterior portion of the bone.

71. Distal ends of uncinate processes on third and fourth epibranchials (CI = 100, RI = AUT).
State 0: With cartilaginous tips.
State 1: Without cartilaginous tips.

The uncinate processes of the epibranchials in the Gonorynchiformes, when present, usually have cartilaginous caps at the tips. In the Otophysi, the uncinate processes of the first and second epibranchials sometimes lack distal cartilages, whereas the uncinate process on the third and/or fourth epibranchials usually retain such cartilages (Fink & Fink, 1981: fig. 13). The Diplomystidae are the only group in the Siluriformes that retains the primitive condition for the Ostariophysi of distal cartilages on the uncinate processes on the third and fourth epibranchials (de Pinna, 1993). All other members of the Siluriformes lack cartilages associated with the uncinate processes of the epibranchials (de Pinna & Vari, 1995: figs 10, 11). Although this character is irrelevant for resolution of relationships within the Cetopsidae, it is included to facilitate the resolution of the position of the family relative to siluriform outgroups.

72. Form of anterior portion of third epibranchial and of articulation of third epibranchial with third and fourth pharyngobranchials (CI = 25, RI = 80).
State 0: Anterior portion of third epibranchial relatively straight and articulating equally with both third and fourth pharyngobranchials.
State 1: Anterior portion of third epibranchial anteriorly curved and associated more closely with third than with fourth pharyngobranchial.

The primitive condition of the anterior portion of the third epibranchial in the Siluriformes is a relatively straight ossification that articulates equally with the anterodorsal margin of the third and fourth pharyngobranchials (de Pinna & Vari, 1995: fig. 10). In most members of the Cetopsinae, the anterior portion of the third epibranchial is anteriorly curved and, as a consequence, its medial articulation is primarily with the posterior cartilage of the third pharyngobranchial, rather than equally with the cartilaginous interface of both the third and the fourth pharyngobranchials (Fig. 15; see also de Pinna & Vari, 1995: 10, fig. 11). On the basis of the species examined in that study, de Pinna & Vari (1995) proposed that an articulation of the anterior extremity of the third epibranchial primarily with the third pharyngobranchial was apomorphic for the Cetopsinae. The more encompassing taxonomic representation of the Cetopsidae included in this study showed, however, that the form of the articulation of the third epibranchial with the third and fourth pharyngobranchials varies across the Cetopsinae. The plesiomorphic condition for the Siluriformes (State 0) is present in species of the genus *Cetopsidium*, in which it is most parsimoniously hypothesized to represent the primitive condition. State 0 is also found in *Cetopsis othonops* and *C. sandrae*, an occurrence which we interpret as reversals within the context of the final phylogeny. Elsewhere within the Cetopsidae, the plesiomorphic condition of the third epibranchial is also present in *Denticetopsis sauli*, as previously noted by Ferraris (1996: 163). The occurrence of the condition in that species has an ambiguous optimization in this analysis.

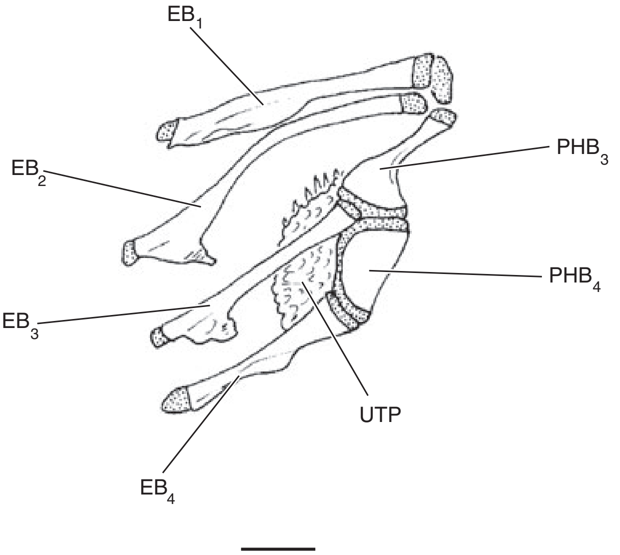

Figure 15. Upper branchial arches in *Cetopsis coecutiens* (MZUSP 38765). Left side, dorsal view. Anterior to top. Scale bar = 1 mm.

73. Anterior portion of third pharyngobranchial (CI = 100, RI = 100).
State 0: Poorly differentiated from remainder of bone, with overall bone gradually narrowing anteriorly.
State 1: Clearly differentiated from remainder of bone and abruptly narrowing from wide posterior portion of bone.

The third pharyngobranchial in most species of the Cetopsidae, and generally in the Siluriformes, is an approximately triangular bone with a narrow anterior portion and a wide posterior portion (e.g. Fink & Fink, 1981: fig. 13B; de Pinna and Vari, 1995: figs 10, 11). A relatively gradual transition in width occurs along the length of the third pharyngobranchial and, as a result, the anterior and posterior portions of the bone are not clearly differentiated. In *Cetopsis candiru* and larger specimens of *C. coecutiens*, the third pharyngobranchial narrows markedly and abruptly anteriorly, such that the anterior portion of the bone has the form of a slender, parallel-sided rod (Fig. 15). A young specimen of *C. coecutiens* has the plesiomorphic condition, and the apparent ontogenetic transition in the form of the third pharyngobranchial provides further corroboration for the hypothesis that State 1 is apomorphic.

74. Size of medial teeth of upper pharyngeal toothplate (CI = 50, RI = 0).
State 0: Approximately same size as other teeth on toothplate.
State 1: Markedly smaller than other teeth on toothplate.

The teeth on the upper pharyngeal toothplate in the Siluriformes are usually approximately equal in size across the tooth-bearing surface of the bone. Variation of tooth size is, at most, minor with any changes in tooth size across the toothplate being gradual. *Cetopsis coecutiens*, uniquely within the Cetopsidae, has the medial teeth on the plate markedly and abruptly smaller in size than the remaining teeth on that bone, thereby forming a narrow band of small, closely set teeth.

75. First pharyngobranchial (CI = 50, RI = 0).
State 0: Present.
State 1: Absent.

The first pharyngobranchial is primitively present in the Ostariophysi (Fink & Fink, 1981: fig. 13) and other lower teleosts. The bone is present in the Diplomystidae and *Bagrus* among examined outgroups, but is otherwise apomorphically absent in the majority of the Siluriformes (de Pinna, 1993). Although this character is irrelevant for resolution of relationships within the Cetopsidae, it is included in this analysis to help resolve the position of the family relative to siluriform outgroups.

76. Second pharyngobranchial (CI = 100, RI = AUT).
State 0: Present.
State 1: Absent.

The second pharyngobranchial, like the first pharyngobranchial, is primitively present in the Ostariophysi but it is nearly always absent in the Siluriformes. The only taxa in the Siluriformes that have second pharyngobranchials are the genus *Horabagrus* (a group of uncertain familial allocation), and members of the families Diplomystidae, Plotosidae and Pangasiidae (de Pinna, 1993). Although this character is irrelevant for resolution of relationships within the family Cetopsidae, it is included to provide a realistic framework for the outgroup portion of the tree and to corroborate our rooting on the Diplomystidae.

77. Number of gill raker rows on first ceratobranchial (CI = 100, RI = 100).
State 0: Two.
State 1: One.

The Otophysi primitively have two rows of gill rakers along their dorsal surface of the ceratobranchials. Within the Siluriformes, this primitive condition occurs only in the Diplomystidae, the Cetopsidae and some species of the Auchenipteridae and Aspredinidae (de Pinna, 1993). The overall relative size of gill rakers is reduced in the Helogeninae, but these vestigial ossifications still form two distinct rows, indicating that the subfamily retains the plesiomorphic otophysan condition for this character. In the derived condition, there is a single row of gill rakers along the first ceratobranchial, a reduction that often extends also to the second ceratobranchial. This character is included to help resolve the position of Cetopsidae relative to siluriform outgroups, albeit being irrelevant for the resolution of relationships within the family.

HYOID ARCH

78. Form of distal portion of posterior ceratohyal (CI = 33, RI = 81).
State 0: Narrow, with a narrow, blunt distal tip.
State 1: Broadened.

The posterior ceratohyal in the Siluriformes, as in other members of the Otophysi, usually narrows gradually posteriorly and terminates in a narrow blunt tip. In all species of the Cetopsinae, with the exception of *Denticetopsis sauli*, *Cetopsis coecutiens*, *C. candiru* and *C. oliveirai*, the posterior ceratohyal is broad posteriorly, and the distal tip is represented by a small posterodorsal knob (Figs 16A, 17).

79. Shape and size of interhyal (CI = 100, RI = 100).
State 0: Cylindrical bone approximately one-third to one-quarter length of posterior ceratohyal.
State 1: Small rounded knob, distinctly smaller than in State 0.

The plesiomorphic condition of the interhyal, present in outgroup taxa in the Siluriformes and most species of the Cetopsidae, is a well-formed, cylindrical bone with an evident conical ossification centre (Figs 16, 17). In *Cetopsis candiru*, *C. coecutiens* and *C. oliveirai*, the interhyal is reduced in size to a tiny nodule of bone, with a barely visible, or invisible, ossification centre in adults. *Cetopsidium ferreirai* is assigned a missing entry because the interhyal is not preserved in the only specimen of that species available for osteological examination.

80. Interhyal length (CI = 100, RI = 100).
State 0: Relatively short, with length approximately 3–4 times its width.
State 1: Distinctly elongate, with length approximately six or more times its width.

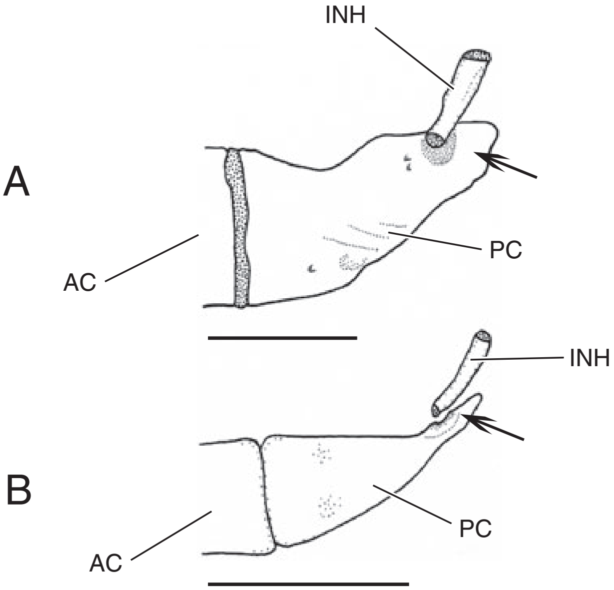

Figure 16. Posterior portion of hyoid bar and interopercle. Medial view of right side, anterior facing left. A, *Denticetopsis seducta* (MZUSP 37813); B, *D. sauli* (ANSP 161432, paratype). Arrow indicates posterior process of posterior ceratohyal. Scale bar = 1 mm.

The plesiomorphic condition of the interhyal in most species of the Cetopsidae and other groups of Siluriformes is a relatively short, cylindrically shaped bone, with the length of the bone approximately 3–4 times its width (Fig. 17). In the species of *Denticetopsis*, the interhyal is proportionally much longer than that observed in most groups in the Siluriformes, and it is approximately six or more times as long as wide (Fig. 16). *Cetopsidium ferreirai* is assigned a missing entry because the interhyal is not preserved in the only specimen of that species available for osteological examination.

81. Association of branchiostegal rays with opercle (CI = 33, RI = 33).
State 0: Without strong ligamentous connection.
State 1: With strong ligamentous connection.

In all members of the Cetopsidae, except for the Helogeninae and *Denticetopsis sauli*, the two posterior-most branchiostegal rays are connected to the ventral corner of the opercle by a strong and well-defined ligament (Fig. 17, BOL), the branchiopercular ligament (State 1). The ligament extends continuously along the medial margins of the distal portions of the two posterior-most branchiostegal rays, and inserts on the medial surface of the posteroventral corner of the opercle. This ligament forms a strong, yet elastic, mechanical link between the posterior branchiostegal rays and the poorly ossified, weak lower portion of the opercle in those fishes. In the Helogeninae and *Denticetopsis sauli*, the ligament is either absent or too fine to be detected by stereomicroscopical examination, and the branchiostegal rays and the opercle are connected only, or mostly, by integument. Missing entries in the matrix for *Cetopsidium ferreirai*, *Paracetopsis esmeraldas* and *Cetopsis othonops* represent species for which the relevant body parts are poorly preserved in the available cleared and stained material.

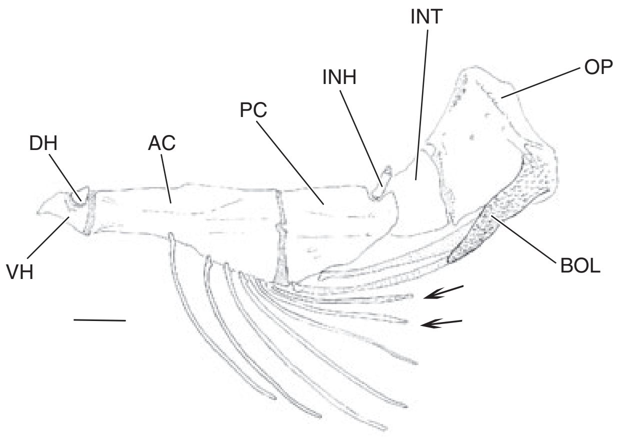

Figure 17. Hyoid bar, branchiostegal rays, and some opercular elements of *Cetopsis sandrae* (MZUSP 61051). Medial view of right side. Arrows indicate comparatively smaller third and fourth branchiostegal rays. Scale bar = 1 mm.

82. Relative length of branchiostegal rays (CI = 100, RI = 100).
State 0: Rays gradually increasing in length posteriorly.
State 1: Posterior third and fourth rays distinctly shorter than other rays.

Branchiostegal rays typically gradually increase in size posteriorly in members of the Siluriformes and, as a result, their posterior tips define a continuous semicircular or sinusoidal margin to that series. Species of the Cetopsinae are unique among examined taxa in the Siluriformes in having such typically smooth size gradient interrupted by the abruptly shorter posterior third and fourth branchiostegal rays (Fig. 17, arrows). These rays are markedly shorter than are the rays situated both anterior and posterior of them, and often also slightly thinner. This foreshortening of these branchiostegal rays is often visible externally in whole specimens as a concave recess positioned along the margin of the branchiostegal membrane.

Diogo *et al*. (2005) proposed 'large, stout medial branchiostegal rays' as synapomorphic for the Cetopsidae. We presume that their observations have some relation to the present character; however, we did not observe any particular increase in length or thickness of anterior branchiostegal rays relative to the condition in examined outgroups. Examination of the whole branchiostegal series in the Cetopsinae makes it clear that the relevant anatomical modification is a decrease in size of the third and fourth rays, as described above, rather than an increase in size of more anterior rays. We did not observe any equivalent modifications in Helogeninae. It seems that the apparent larger size of anterior rays is just a result of the smaller third and fourth rays, which make subsequent rays look larger by comparison.

83. Shape of interhyal along long axis (CI = 50, RI = 50).
State 0: Straight.
State 1: Slightly bent.

In the plesiomophic state of the interhyal that is present in outgroups in the Siluriformes and most species in the Cetopsidae, the interhyal is a straight bone (Fig. 16A). In *Denticetopsis epa*, *D. praecox* and *D. sauli*, the interhyal has a bend at the middle of its length. The illustrated specimen of *D. sauli* (ANSP 161432) in Figure 16B is a juvenile, in which the interhyal is only slightly angled. The flexure of the bone is more pronounced in the larger cleared and stained specimen of that same lot. A missing entry is assigned to *Cetopsidium ferreirai*, because the interhyal is not preserved in the available cleared and stained specimen of that species.

84. Shape of anterior ceratohyal (CI = 100, RI = 100).
State 0: Anteriorly narrow.
State 1: Roughly rectangular.

The anterior ceratohyal in most groups of the Siluriformes, including the majority of the species of the Cetopsidae, narrows anteriorly, so that its anterior half is distinctly shallower than its posterior half (Fig. 17). In *Cetopsis coecutiens* and *C. candiru*, the depth of the anterior ceratohyal is approximately constant along the length of the bone, with the overall shape of the bone being rectangular. An examined juvenile specimen of *C. coecutiens* has, in contrast, the plesiomorphic condition of the anterior ceratohyal, indicating that there is an ontogenetic shift in the form of the ossification in that species.

85. Posterior process of posterior ceratohyal (CI = 100, RI = 100).
State 0: Poorly defined or absent.
State 1: Long and well defined, extending posteriorly or posterodorsally along posterior margin of interhyal.

The posterodorsal tip of the posterior ceratohyal is short and poorly differentiated, without any distinct process, in outgroups in the Siluriformes and most species of the Cetopsidae (cf. Arratia, 1987: fig. 27A). The posterodorsal tip of the posterior ceratohyal in the species of *Denticetopsis* is either elongated into a spear-like posterior process (*D. sauli*, Fig. 16B, arrow) or is paddle-shaped (all other species of *Denticetopsis*, Fig. 16A, arrow), and clearly differentiated from the remainder of the bone.

WEBERIAN APPARATUS AND ANTERIOR VERTEBRAE

86. Relation between parapophysis of fifth vertebra and Weberian lamina (CI = 50, RI = 85).
State 0: Basal portion mostly free.
State 1: Basal portion broadly attached to posterior margin of Weberian lamina.

The transverse process of the fifth vertebrae in the Siluriformes is involved in the skeletal support for the dorsal surface of the swimbladder in a way comparable with that of the more anteriorly located Weberian lamina. The anterior margin of the transverse process and the posterior margin of the Weberian lamina are closely set or overlap only very close to their bases in the majority of taxa in the Siluriformes (Fig. 18). In this condition, most of the transverse process of the fifth vertebra is free from the posterior margin of the Weberian lamina. Within the Cetopsidae, this primitive condition of the transverse process of the fifth vertebra is found only in the species of *Helogenes* and *Cetopsidium*. In all other taxa of the family, the proximal one-half of the process is tightly attached or ankylosed anteriorly to the posterior margin of the Weberian lamina, such that the two structures form a conjoined or partially conjoined complex (Figs 19, 20).

87. Connection between fifth vertebral centrum and complex centrum (CI = 100, RI = 100).
State 0: Synchondral.
State 1: Sutural.

The fifth vertebral centrum in the Siluriformes is primitively articulated synchondrally to the fourth centrum, as is the case in other groups of the Otophysi (Fink & Fink, 1981: fig. 17; Grande, 1987). Such a synchondral articulation between those elements is, however, limited to the Diplomystidae and Cetopsidae among Recent families of the Siluriformes (Figs 18–20). In the derived state, the fifth centrum is sutured to the posterior part of the complex centrum and lacks

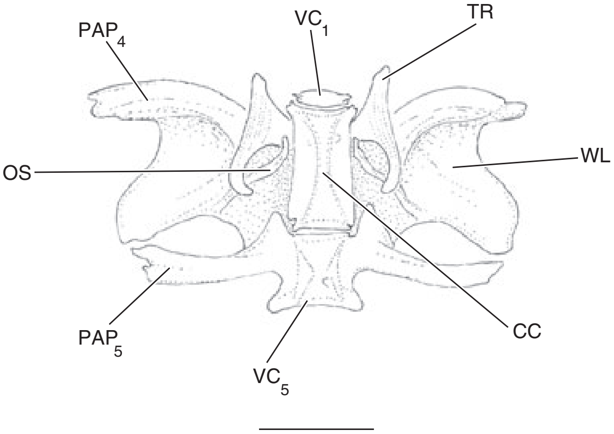

Figure 18. Weberian apparatus of *Cetopsidium ferreirai* (INPA 6501). Ventral view, anterior facing top. Scale bar = 1 mm.

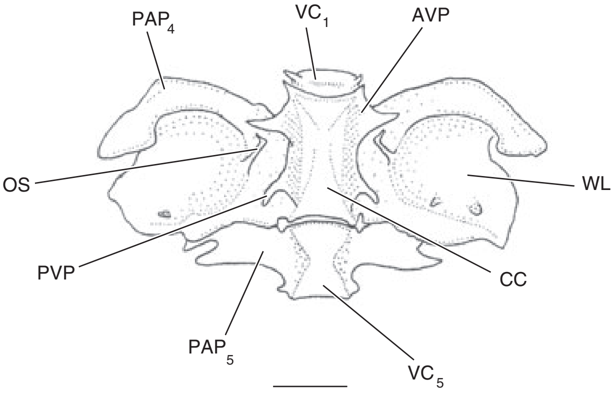

Figure 19. Weberian apparatus of *Cetopsis pearsoni* (MZUSP 27812, paratype). Tripus not shown. Ventral view. Scale bar = 1 mm.

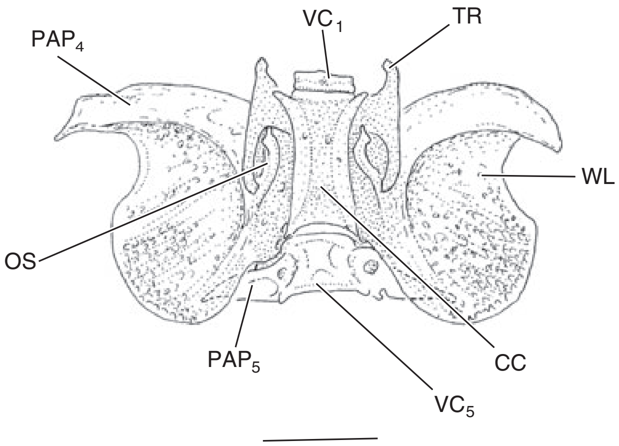

Figure 20. Weberian apparatus of *Denticetopsis macilenta* (AMNH 55332). Ventral view. Anterior to top. Scale bar = 1 mm.

an intervertebral cartilage disc. Although this character is irrelevant for resolution of relationships within the Cetopsidae, it is included to help resolve the position of the family relative to siluriform outgroups.

88. Posterior profile of the Weberian lamina (CI = 50, RI = 90)
State 0: With well-defined concave recess.
State 1: In single convex arc.

The Weberian lamina in members of the Siluriformes generally has a concave posterior margin, or at least a posterior recess or concavity that delimits an open space between the lamina and the transverse process of the fifth vertebra. This condition is hypothesized to be plesiomorphic for the Siluriformes in light of its similarity to the form of the lamina seen in outgroups of the Ostariophysi such as the Characiformes (Fink & Fink, 1981: figs 15, 16). Within the Cetopsidae, the primitive siluriform configuration of the Weberian lamina was found only in *Helogenes* (where the recess may be partly covered by the parapophysis of the fifth vertebra, but is still clearly present) and *Cetopsidium* (Fig. 18). In all other genera of Cetopsidae, the Weberian lamina is expanded posteriorly such that its posterior margin is convex and does not delineate a space between itself and the transverse process of the fifth vertebra (Figs 19, 20). The posterior expansion of the Weberian lamina is correlated with the degree of swimbladder encapsulation (Character 89).

89. Degree of encapsulation of swimbladder (multistate ordered) (CI = 50, RI = 85).
State 0: No encapsulation.
State 1: Partially encapsulated.
State 2: Completely encapsulated.

Bony encapsulation of the swimbladder occurs in various groups within the Siluriformes. Loricarioids are the largest subgroup within the Siluriformes with entirely encapsulated swimbladders. Other cases of swimbladder encapsulation within the Siluriformes are present, as more or less patchy occurrences, in the Clariidae, Auchenipteridae, Sisoridae, Amphiliidae and Cetopsidae. These different instances of encapsulation of the swimbladder often have, however, distinct anatomical bases. These differences, and the phylogenetic distance among the different families that exhibit encapsulation, indicate that swimbladder encapsulation arose multiple times across the Siluriformes (Chardon, 1968; Baskin, 1973). There occurs a gradation in the level of swimbladder encapsulation within the Cetopsidae that ranges from a totally free swimbladder to an entirely encapsulated one. Most of the species in the family fall between the two extremes, with partially encapsulated swimbladders.

An entirely free swimbladder, similar to that found in the Diplomystidae and other generalized groups in the Siluriformes, is found in the Cetopsidae only in the species of *Helogenes* and *Cetopsidium* (Fig. 18). In species of those two genera, the Weberian lamina is primarily a bony sheet, curving only slightly around the dorsal surface of the swimbladder. The Müllerian ramus (parapophysis of the fourth vertebra) curves around the anterodorsal surface of the swimbladder, but with only a limited extension ventrally. A partially encapsulated condition (State 1), which is found in *Denticetopsis*, *Paracetopsis* and all species of *Cetopsis*, except *C. candiru*, *C. coecutiens* and *C. oliveirai*, exhibits a Weberian lamina that is strongly concave ventrally and forms a well-defined bony dome that covers the dorsal surface of the swimbladder (Figs 19, 20). Additionally, the Müllerian ramus in the partially encapsulated swimbladder extends further ventrally than in the unencapsulated condition and covers a small part of the ventrolateral surface of the swimbladder (Fig. 21). Nevertheless, in the partly encapsulated condition, most of the ventral surface of the swimbladder lacks a bony covering. In the fully encapsulated condition (State 2), found in *Cetopsis candiru*, *C. coecutiens* and *C. oliveirai*, the swimbladder is nearly entirely encased in bone, such that only a small portion of its lateral surface and a few pores remain unshielded by bone. Most of the additional encapsulation results from a hypertrophy of the ventral part of the Müllerian ramus that extends posteroventrally all the way to the posterior part of the Weberian lamina with the ventral part of the ramus also widened such that it covers most of the ventral surface of the swimbladder. The bony covering of the swimbladder in adults of these three species is so heavily consolidated that the structural components of the swimbladder capsule are difficult to discern. An examined juvenile

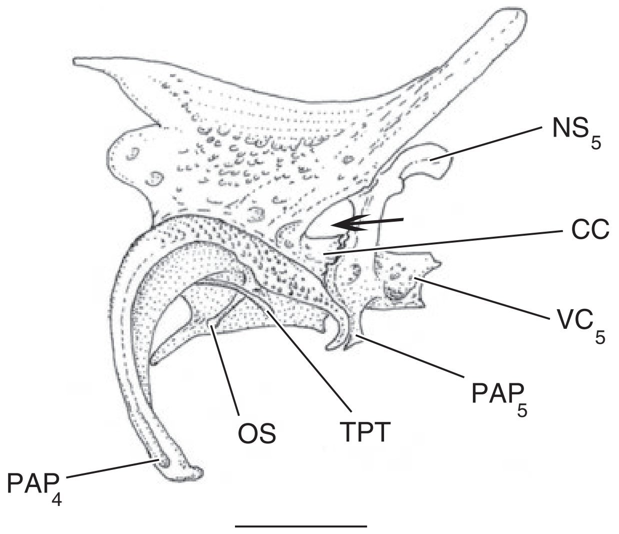

Figure 21. Weberian apparatus of *Cetopsis arcana* (MZUSP 41492). Lateral view. Anterior to left. Arrow indicates foramen between posterior margin of neural arch of complex centrum and anterior margin of neural arch of fifth centrum. Scale bar = 1 mm.

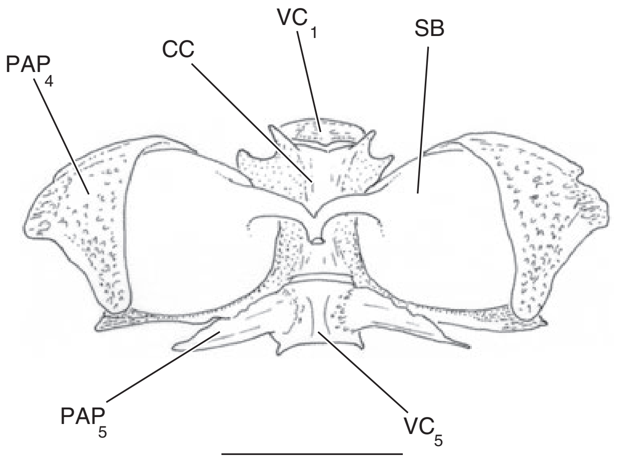

Figure 22. Weberian apparatus of juvenile specimen of *Cetopsis coecutiens* (LACM 43102-3). Ventral view. Scale bar = 1 mm.

specimen of *C. coecutiens* provides some insight into the early development of the Müllerian ramus, in that it clearly demonstrates the role of that process as the main component of the ventral wall of the swimbladder capsule (Fig. 22). In adults of *C. coecutiens* and *C. candiru*, the Müllerian ramus does not fuse with the ventral part of the complex centrum, with the result that a narrow space remains at the ventromedial surface of the swimbladder. Such fusion of the Müllerian ramus occurs in *C. oliveirai*, where the capsule is a continuous, vase-shaped structure.

90. Anterior ventral transverse process of complex centrum (multistate ordered) (CI = 60, RI = 90).
State 0: Absent.
State 1: Present and relatively short, not or only barely extending laterally past lateral limit of tripus.
State 2: Present and relatively long, extending laterally well past lateral limit of tripus.
State 3: Present and very long, extending laterally past the midwidth of the swimbladder.

The anterior margin of the ventral surface of the complex centrum in the Siluriformes primitively lacks any well-differentiated laterally directed bony extensions. In contrast, the ventral surface of the complex centrum in the species of *Cetopsis* bears a conspicuous laterally orientated process at its anterolateral corner. The length of this process varies markedly within the species of *Cetopsis* and three discrete states were identifiable in the examined species of the genus (Appendix 2). In State 1 the process is short, reaching at most to the horizontal through the lateral margin of the tripus (Fig. 19). In State 2 the tip of the process clearly extends lateral to the horizontal through the lateral margin of the tripus (Fig. 21). In the most extreme condition, State 3, the process extends to, or beyond, the midwidth of the swimbladder. The states were ordered according to similarity.

91. Length of transverse process of fifth vertebra (CI = 50, RI = 88).
State 0: Long, tip extending to lateral margin of Weberian lamina.
State 1: Short, tip falling short of lateral margin of Weberian lamina.

The transverse process of the fifth vertebrae, which in the Siluriformes is homologous to a vertebral parapophysis, usually extends laterally to approximately the same parasagittal plane as the lateral margin of the Weberian lamina. This plesiomorphic condition is limited to the species of *Cetopsidium* (Fig. 18) within the Cetopsinae. In all other members of that subfamily and in *Helogenes castaneus* of the Helogeninae, the transverse process of the fifth vertebrae is short, with its tip falling short of the lateral margin of the Weberian lamina (Figs 19, 20). In *Helogenes marmoratus*, there is considerable variation in the proportional length of the transverse process, making a definitive assessment of the state of that character impossible in that species.

92. Structure of neural arches of fifth to eighth vertebrae (CI = 100, RI = 100).
State 0: Without trabeculae.
State 1: With trabeculae.

The neural arches of the anterior free vertebrae in the Siluriformes are usually composed of a continuous bony sheet which sometimes bears superficial ridges and tiny foramina. Members of the Helogeninae are unique among examined taxa in the Siluriformes in having the arches strongly trabeculate, a modification that results in large irregular openings that extend into the inside of the neural canal.

93. Number of pleural ribs (CI = 50, RI = 50).
State 0: Six or more.
State 1: Four or five.

Members of the Siluriformes usually have six or more pleural ribs. This number of ribs is considered plesiomorphic because of its occurrence in the Diplomystidae, the †Hypsidoridae and most other groups in the Otophysi. Four or five ribs are variably present in both *Helogenes* and *Denticetopsis sauli*, reductions that are hypothesized to be a result of independent events under the final phylogenetic scheme presented here.

94. Position of insertion of os suspensorium (CI = 50, RI = 87).
State 0: Lateral to lateral margin of tripus.
State 1: Medial to lateral margin of tripus.

The os suspensorium is a bony process that extends ventrally from the roof of the Weberian lamina. The distal portion of the os suspensorium serves as the site for attachment of the ligamentous sheet that extends radially to the internal margin of the transformator process of the tripus. In the Siluriformes the plesiomorphic site of attachment of the os suspensorium on the Weberian lamina is situated markedly lateral to the lateral margin of the tripus, when examined from a ventral view. That plesiomorphic condition is limited, within the Cetopsidae, to the species of *Cetopsidium* (Fig. 18). In all other genera of the family, the insertion of the os suspensorium on the Weberian laminae is displaced medially toward the complex centrum and, as a consequence, the insertion lies medial to the lateral margin of the tripus from a ventral view (Fig. 20).

95. Shape of first centrum (CI = 50, RI = 0).
State 0: Rectangular in ventral view.
State 1: Lozenge-shaped in ventral view, with lateral margins compressed between basioccipital anteriorly and complex centrum posteriorly.

The first centrum in the Siluriformes, which is absent in some members of that order, is usually similar in form to the other free centra in the vertebral column, differing mostly in being considerably shortened along the anteroposterior axis (e.g. Fink & Fink, 1981: fig. 17) and, in ventral view, has the shape of a small, transversely elongate rectangle (Fig. 20). In *Cetopsis coecutiens* and *C. oliveirai*, the lateral margins of the first centrum in ventral view are constricted, so that the length along the middle of the centrum is much greater than that along the lateral margins of the ossification. The first centrum in these two species appears as a lozenge in ventral view, with fine lateral tips. An apparently similar configuration can be seen in some other species in the Cetopsinae, such as *C. pearsoni* (Fig. 19). The situation in these species is not homologous, however, with that present in *C. coecutiens* and *C. oliveirai* and derives only from the partial covering of the posterior margin of the centrum by superficial ossification of the complex vertebra. The body of the vertebra, nonetheless, retains its primitive rectangular shape rather than being laterally constricted as is the case in those two species.

96. Anterior ventral prezygapophysis of complex centrum (CI = 100, RI = 100).
State 0: Thin and with smooth distal margin.
State 1: Thickened and with jagged distal margin.

The anterior ventral prezygapophysis of the complex centrum in the Siluriformes is primitively a small, relatively thin flap of bone extending anteroventrally from the anteroventral surface of the complex centrum and has a smooth anterior edge (Figs 18–20). In the derived condition, found only in the species of *Paracetopsis*, the prezygapophysis of the complex centrum is thickened, with bony ridges on its ventral surface and an irregularly jagged anterior margin.

97. Shape of posterior margin of first centrum (CI = 20, RI = 50).
State 0: Straight or only slightly convex.
State 1: Strongly convex.

The posterior margin of the first centrum in the Siluriformes, when present, is usually straight from a ventral view (e.g. Fink & Fink, 1981: fig. 17). In the majority of the species of *Cetopsis* (Appendix 2), in contrast, the posterior margin of the exposed portion of the first centrum is strongly convex from a ventral view, assuming, in some species, a nearly semicircular shape.

98. Anterior ventral prezygapophysis of complex centrum (CI = 33, RI = 50).
State 0: Separate from, and ligamentously attached to, ventral surface of first centrum.
State 1: Adpressed against ventral surface of first centrum.

The anterior ventral prezygapophysis of the complex centrum in the Siluriformes, when present, is primitively orientated anteroventrally and lacks direct bony contact with the first centrum, to which it is connected only by a ligament (Figs 18–20). In the derived condition, the prezygapophysis is strongly deflected anteriorly, with the result that its dorsal surface is adpressed against the ventrolateral surface of the first centrum. Taxa assigned missing entries are those where the anterior ventral prezygapophysis of the complex centrum are not differentiated.

99. Well-defined fenestra between posterior margin of neural arch of complex centrum and anterior margin of neural arch of fifth centrum (CI = 33, RI = 71).
State 0: Absent.
State 1: Present.

The posterior margin of the neural arch of the complex centrum in the Siluriformes is primitively a continuous layer of bone that forms a shield connected to the anterior margin of the neural arch of the fifth centrum. The posterior part of the neural arch of the complex centrum may or may not overlap the anterior part of the fifth centrum but, regardless of the degree of development of the neural arch, there is no well-defined unossified space between the two neural arches. In the majority of species of *Cetopsis* (Appendix 2), the posterior margin of the neural arch of the complex centrum has a deep notch that forms a large triangular fenestra, with the posterior margin of that opening delimited by the straight anterior margin of the neural arch of the fifth centrum (Fig. 21, arrow). No evidence was found that this fenestra serves as a passage for either nerves or blood vessels.

Pectoral girdle

100. Number of ossified proximal pectoral-fin radials (CI = 50, RI = 90).
State 0: Two or more.
State 1: One.

Most members of the Siluriformes have two ossified proximal radials in the pectoral-fin skeleton. The compact cartilaginous (sometimes partly ossified) element anterior to those two radials is often referred to as the first proximal radial, but may be a compound element formed by the fusion of two or more distal radials (Mo, 1991). Most members of the Cetopsidae have a single ossified proximal pectoral-fin radial, in which a broad distal margin articulates with most, or all, of the pectoral-fin rays. This reduction in the number of radials is considered to be an apomorphic condition. The only genus of the Cetopsidae that retains the primitive condition is *Cetopsidium*(Fig. 23), which has two elongate ossified radials very similar to those present in outgroups in the Siluriformes. The one ossified radial (State 1) present in all genera of the Cetopsidae except *Cetopsidium* may represent either a fusion of the two primitively present elements or may be the result of the loss of one radial with the subsequent expansion of the remaining element to occupy the space originally filled by the two radials. The condition found in one asymmetrical specimen of *C. morenoi* (INHS 69416: Fig. 23B) suggests that the single radial present in most taxa in the Cetopsidae is a function of fusion, because the individual has two very closely positioned radials on one side, with a combined outline of the two elements that is very similar to that of the single enlarged radial present on the other side of that specimen as well as that in other species of the Cetopsidae with a single proximal radial (e.g. *Denticetopsis macilenta*; Fig. 24). Nonetheless, the examination of juvenile specimens of species of the Cetopsidae with a single proximal radial failed to reveal any hint of ontogenetic fusion, with the single radial apparently formed from a single cartilaginous precursor. The question of how the derived configuration of that element was reached, thus, remains unsettled.

101. Form of proximal pectoral-fin radial (CI = 25, RI = 40).
State 0: Narrow, leaving some open space between fin-ray bases and pectoral girdle.
State 1: Broad, encompassing nearly entire space between fin-ray bases and girdle.

The single proximal pectoral radial found in most species of the Cetopsidae other than *Cetopsidium* (see character 100), although broader than either of the primitive two radials in that area that are present in other examined members of the Siluriformes and *Cetopsidium*, nonetheless, fails to occupy the entire space that separates the bases of the pectoral-fin rays from the body of the pectoral girdle (Fig. 24) in some members of the subfamily. In the derived condition that is present in six species of *Cetopsis* (Appendix 2), the lateral margins of the proximal pectoral radial are markedly expanded and convex, filling almost all the space between the bases of the pectoral-fin rays and

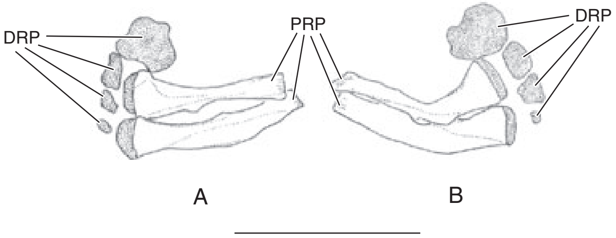

Figure 23. Pectoral-fin radials of *Cetopsidium morenoi* (INHS 69416). Ventral view. A, right side; B, left side. Scale bar = 1 mm.

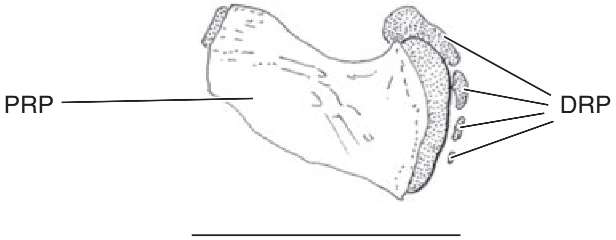

Figure 24. Pectoral-fin radials of *Denticetopsis macilenta* (AMNH 55332). Ventral view of left side. Scale bar = 1 mm.

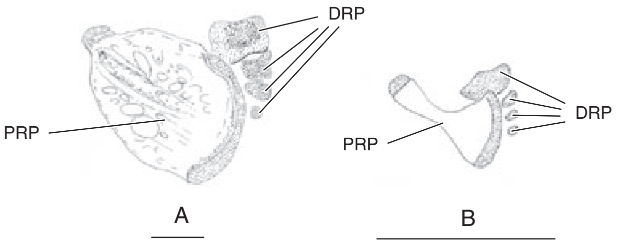

Figure 25. Pectoral-fin radials in *Cetopsis coecutiens*. Ventral views of left side. A, adult condition (MZUSP 38765); B, juvenile condition (LACM 43102-3). Scale bars = 1 mm.

the pectoral girdle (Fig. 25A). As a result of this expansion, the shape of the proximal radial in the derived condition is more rounded than it is in the plesiomorphic state, which is present in most species of the Cetopsidae. Juvenile specimens of *Cetopsis coecutiens* retain the plesiomorphic condition for the radial (Fig. 25B), indicating that the bone expands ontogenetically. That observation provides ontogenetic support for the polarity hypothesized herein for this character.

102. Relative length of coracoid (CI = 100, RI = 100).
State 0: Coracoid extending for nearly entire length of cleithrum.
State 1: Coracoid extending for two-thirds or less of length of cleithrum.

Siluriformes primitively have the coracoid extending medially to approximately the same parasagittal plane as the cleithrum, i.e. to the midline or nearly so, a condition that is also present within the Cetopsidae in the Helogeninae. In the derived condition that is common to all examined members of the Cetopsinae, the ventral limb of the coracoid ends distinctly short of the midsagittal plane and, thus, does not contact its counterpart of the other side. As a consequence, the medial portion of the pectoral girdle is formed exclusively by the cleithrum.

103. Morphology of contact between coracoids (CI = 100, RI = 100).
State 0: Straight, without interdigitations.
State 1: With deep interdigitations.

In most members of the Siluriformes, the coracoids are joined to each other at the midline by way of a deeply interdigitating suture (e.g. Tilak, 1963: figs 1–23; Skelton, 1981: fig. 17A). The condition is attenuated, though still clearly present, in taxa which have a reduced development of the pectoral spine. Within the Siluriformes, interdigitations between the coracoids are absent only in the Diplomystidae, Cetopsidae, Astroblepidae, Nematogenyidae, Siluridae and Trichomycteridae (Mo, 1991). Although this character is irrelevant for the resolution of phylogenetic relationships within the Cetopsidae, it is included to help resolve the position of the family relative to siluriform outgroups.

DORSAL AND ANAL FINS AND ASSOCIATED STRUCTURES

104. Spinous first dorsal-fin ray (spinelet) (CI = 33, RI = 77).
State 0: Present.
State 1: Greatly reduced or absent.

The first dorsal-fin ray in the Siluriformes is typically a small bone in the shape of an inverted ‘V’ that is often referred to as the spinelet. The spinelet is located anterior to the dorsal-fin spine that is the main element of the pungent apparatus of the dorsal fin usually present in siluriforms. The spinelet functions as a lock at the anterior of the base of the dorsal-fin spine and serves to fix that spine in erect position. The presence of a spinelet is plesiomorphic for the Siluriformes, and is present in most members of the order, including the Diplomystidae and the †Hypsidoridae (e.g. Grande & de Pinna, 1998: fig. 5). The spinelet is present only in species of the genus *Cetopsidium* within the Cetopsidae (Fig. 26), although one of the two examined specimens of *Denticetopsis macilenta* has a tiny conical ossification in the position of the spinelet that is present in other members of the Siluriformes. This small ossification may be a vestige of the spinelet which, in this case, is present only in a state of extreme reduction. The absence of the spinelet in members of the Cetopsidae other than *Cetopsidium* is associated with the reduced degree of ossification of the ray that is homologous to the dorsal-fin spine in other catfishes.

A vestigial spinelet was reported for *Paracetopsis* by Royero (1987), based on specimens from southern Venezuela. *Paracetopsis*, however, is limited to the trans Andean portions of Ecuador and northern Peru (Vari

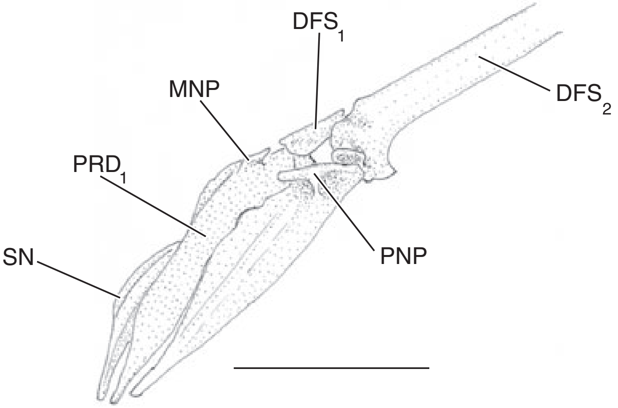

Figure 26. Dorsal-fin spines and skeletal support in *Cetopsidium pemon* (UF 26156). Lateral view. Anterior to left. Scale bar = 1 mm.

et al., 2005), regions far distant from where the specimens examined by Royero originated. Furthermore, the specimens of the two species of *Paracetopsis* examined osteologically in this study lack any vestige of the spinelet. Therefore, the report of the presence of the structure in that genus by Royero (1987) is clearly based on some other misidentified cetopsin, most likely one of the species of *Cetopsidium* that occurs in southern Venezuela or adjoining regions (see Vari *et al*., 2005).

105. Position of dorsal-fin origin (multistate ordered) (CI = 40, RI = 40).
State 0: Located very close to head.
State 1: Located at vertical through posterior margin of pectoral fin.
State 2: Located on posterior half of SL.

The dorsal fin in the Siluriformes is primitively positioned very close to the posterior margin of the head and mechanically linked (often by direct bony contact) with the posterior tip of the supraoccipital process (e.g. Skelton, 1981: fig. 18A). Most species of the Cetopsidae retain the plesiomorphic position of the dorsal fin, with its origin located anterior to the vertical through the posterior margin of the pectoral fin, albeit with the linkage between the dorsal fin and the supraoccipital process limited to soft tissue. In *Cetopsis candiru*, the dorsal fin is moderately displaced posteriorly, such that its origin is located slightly posterior to the vertical through the posterior margin of the pectoral fin (State 1). A more extreme posterior shift characterizes species of the Helogeninae, all of which have the dorsal-fin origin located within the posterior half of the body (State 2).

106. Morphology of second dorsal-fin ray (CI = 33, RI = 85).
State 0: Stiff and forming distinct spine.
State 1: Completely flexible and segmented, not forming stiff spine.

The first and second dorsal-fin rays in siluriforms are usually modified into spine-like structures. The first spine, or spinelet, is discussed above in character 104. The structure of the dorsal-fin spines of most species of the Siluriformes has long been considered as a diagnostic feature of the order (Reed, 1924), and is widely recognized as evidence for the monophyly of the group (Mo, 1991). The second dorsal-fin spine within the Siluriformes is, however, secondarily reduced in several groups, in which the element is soft and flexible and, thus, similar to the other dorsal-fin rays. The absence of a dorsal-fin spine is considered to be an apomorphic condition within the Siluriformes in view of our present understanding of the relationships within the order. Within the Cetopsidae, second dorsal-fin spines are found only in *Cetopsidium* and *Denticetopsis*. In all other genera in the Cetopsinae and, homoplastically, in the Helogeninae, the homologue to the second dorsal-fin spine is flexible and lacks a pungent tip. The secondarily flexible anterior dorsal-fin ray nevertheless almost always retains part of the modification associated with the spine that is typical of other taxa in the Siluriformes, such as a hypertrophy of the articular head and/or fusion between the contralateral halves of the ray on the proximal portion of the ray. The common possession of these attributes demonstrates the homology of the flexible anterior ray with the distinct spine present in most members of the Siluriformes.

107. Degree of development of posterolateral extension of medial nuchal plate (CI = 25, RI = 66).
State 0: Well developed.
State 1: Poorly developed or absent.

The medial nuchal plate in the Siluriformes is an expansion of the distal portion of the first radial element of the dorsal-fin support and is located just beneath the integument. This medial nuchal plate is usually a posteriorly bifurcated structure, the posterior tips of which meet the anterior tips of the posterior nuchal plate. The surface of the medial nuchal plate is often ornamented and exposed on the surface of the body. In the Cetopsidae and a number of other catfish groups this expansion of dorsal-fin radial does not form a surface plate and, instead, it terminates dorsally immediately beneath the integument and lacks an ornamented bony surface. Nevertheless, homologies with the nuchal plates in other groups in the Siluriformes are obvious due to the shape and topological relations of the structures. The median nuchal plate that is present in the Cetopsidae, with the exception of *Helogenes*, *Denticetopsis* and *Cetopsis candiru*, consists of a delicate ossified structure represented primarily by a ring-like arc that is situated anterior to the base of the first dorsal-fin ray. The posterior arms of the ring-shaped structure either barely contact the anterior tips of the posterior nuchal plate, or are connected to these anterior tips only by soft tissue. In the species of *Helogenes* and *Denticetopsis*, and in *Cetopsis candiru*, the radial normally associated with the medial nuchal plate is restricted to its vertical lamina and the structure corresponding to the nuchal plate in other groups in the Siluriformes is absent or reduced to a small undifferentiated flange.

108. First supraneural (CI = 25, RI = 25).
State 0: Present.
State 1: Absent.

The first supraneural in the Siluriformes is a dorsoventrally or obliquely orientated bone that is located in the midsagittal plane anterior to the radial series of the dorsal fin. The dorsal tip of the first supraneural is often expanded into a dorsally convex shield with an ornamented, exposed dorsal surface. That portion of the first supraneural is often referred to as the anterior (or first) nuchal plate. The shape and size of the anterior nuchal plate varies widely across the Siluriformes. In the Cetopsidae, the first supraneural, when present, is deeply embedded within the anterior epaxial trunk musculature and it is adpressed to the anterior margin of the shaft of the first dorsal-fin radial (Fig. 26). The dorsal part of the first supraneural is transversely wider (i.e. more expanded laterally) than the ventral portion of the bone, but lacks shield-like distal elaborations and is not angled relative to the ventral part of the bone. A first supraneural is absent in a subgroup within *Denticetopsis* composed of *D. epa*, *D. macilenta* and *D. praecox* and in *Cetopsis oliveirai*. Such conditions are interpreted herein as independent losses within the final phylogeny, in view of the widespread presence of the first supraneural in outgroups within the Siluriformes and in other species of the Cetopsidae.

109. Transverse radial anterior to anal-fin pterygiophores (CI = 25, RI = 76).
State 0: Absent.
State 1: Present.

In most members of the Cetopsinae, with the exception of the species of *Denticetopsis*, *Cetopsis amphiloxa* and possibly the species of *Paracetopsis* (see below), the radial series of the anal fin is preceded by an unusual median bone that has the shape of either a simple cylinder with slightly expanded ends or an anteriorly curved, double-headed club. The ends of this transversely orientated bone terminate in cartilaginous caps. The main axis of this bone, herein called a transverse radial, is orientated transversely to the sagittal plane of the fin and, thus, stands in stark contrast to the orientation of the bones in the pterygiophore series within the midsagittal plane of the fin (Fig. 27). In lateral view, the transverse radial is aligned with the distal portions of the proximal radial series.

Some variation in the shape of the transverse radial is seen among various genera in the Cetopsidae. In the species of *Cetopsidium*, the main axis of the transverse radial is straight or nearly straight, with the ends of the radial directed laterally and the element being entirely cartilaginous is some species of that genus. In other species of the Cetopsidae this bone may be nearly straight but in most species the element is angled or curved in the middle, such that its extremities are directed anterolaterally (Fig. 27). The most extreme flexure is found in *Cetopsis gobioides*. In *Paracetopsis bleekeri*, there is a small ossified nodule anterior to the anal pterygiophore series in a position comparable with that of the transverse radial. The homologies between the nodule and the transverse radial is uncertain and therefore that species is assigned a missing entry for this character. No similar ossification was found in that area in *P. esmeraldas*. This character may be a source of additional phylogenetic information once it is examined in other species of the family.

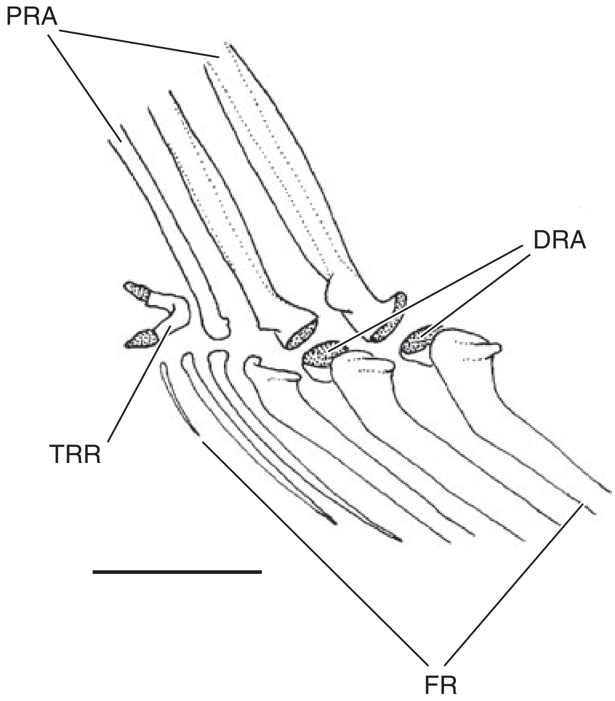

Figure 27. Anterior portion of anal-fin rays and supports in *Cetopsis pearsoni* (MZUSP 27812). Dorsolateral view of left side. Anterior to left. Scale bar = 1 mm.

The homologies of the transverse radial are undetermined. It is a cartilage bone, and in this regard agrees with the developmental pattern of median-fin skeletal supports. Unfortunately, the transverse radial in the examined juvenile specimens is identical in shape and position to that of adults, except for having a lesser degree of ossification and as such is uninformative as to possible homologies. In some specimens of *Cetopsis gobioides*, the transverse radial is associated with a splint-like vertical bone similar in position, shape and orientation to a small proximal anal-fin radial. If that bone is indeed homologous to a proximal radial, its positional relation with the transverse radial suggests that the latter element is homologous to a distal radial. A definitive resolution of this question will have to rely on observations about the early chondrification pattern of the transverse radial in very small juveniles of the Cetopsidae. Such specimens were not available for this study. The only other taxa in the Siluriformes in which a similar structure has been found are the species of the Old World taxa *Austroglanis* (Austroglanididae) and the family Clariidae. A similar bone is also seen in some members of the Bagridae (Mo, 1991: fig. 23, 'crescentic bone'); however, in those instances the bone is located approximately at mid-depth of the shaft of the first fully formed proximal radial, rather than at its distal terminus, such as is the case in the Cetopsinae. The occurrences of these ossifications in these outgroups are all apparently homoplastic to those present in the Cetopsinae, within our present concepts of higher level relationships within the Siluriformes, but more in-depth studies are needed to understand the phylogenetic significance of the transverse radial in the order.

PELVIC FIN AND GIRDLE

110. Posterior cartilaginous processes of basipterygia (CI = 100, RI = 100).
State 0: Contralateral posterior basipterygial cartilages not fused across midline, with independent posterior cartilaginous processes.
State 1: Contralateral posterior basipterygial cartilages fused medially at base, forming single stem for posterior cartilaginous process(es).

The plesiomorphic condition among members of the Siluriformes is to have each basipterygium with a separate posterior cartilage forming an independent posterior process. In several subgroups of the Siluriformes, the posterior cartilages of the basipterygia are fused across the midline, but the processes themselves remain separate. The posterior cartilaginous processes of the basipterygia in the Cetopsinae are among the most highly modified forms of that structure known to occur within the Siluriformes. In the Cetopsinae, the median cartilages of the basipterygia are fused to each other posteriorly well beyond the posterior limit of ossification, so that the posterior cartilaginous processes share a thick common basal stem (Figs 28–31). The distal portions of these basipterygial cartilages remain separate. This basal fusion of the contralateral basipterygial cartilages was proposed as a synapomorphy for the Cetopsinae by de Pinna & Vari (1995: 7), who interpreted the distal bifurcation of the cartilage as a secondary subdivision. Here we correct that interpretation, and consider the distal branches of the basipterygia as remnants of the plesiomorphic condition of separate cartilages. de Pinna & Vari (1995: 9) reported that the bifurcation of the basipterygium was absent in *Cetopsis oliveirai*. We found, however, the feature to be intraspecifically variable once one additional specimen of that species was examined with an incipient bifurcation at the distal end of the cartilage. The condition of this character could not be observed in *Cetopsidium ferreirai*, because the basipterygial cartilages are not preserved in the only specimen of that species available for skeletal examination.

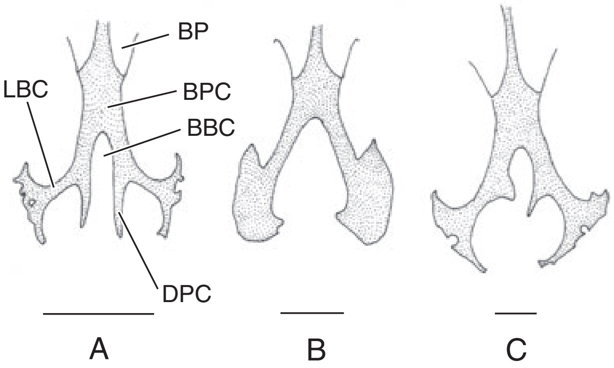

Figure 28. Posterior basipterygial cartilages. Ventral views. Anterior to top. A, *Cetopsidium* sp. (FMNH 45708); B, *Denticetopsis epa* (MZUSP 83228); C, *Paracetopsis bleekeri* (AMNH 97234). Scale bars = 1 mm.

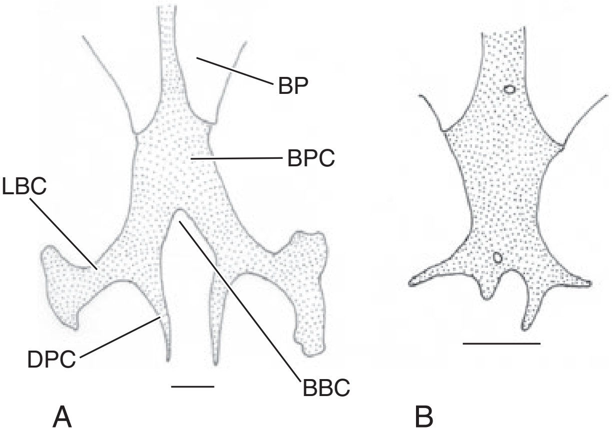

Figure 29. Posterior basipterygial cartilages. Ventral views. Anterior to top. A, *Cetopsis coecutiens* (MZUSP 38765); B, *Cetopsis candiru* (MZUSP 48102). Scale bars = 1 mm.

111. Posteriorly directed process of basipterygial cartilage distal to lateral bifurcation (CI = 100, RI = 100).
State 0: Present.
State 1: Absent.

As discussed under Character 110, the fusion between the posterior basipterygial cartilages seen in the Cetopsinae occurs proximally relative to the basipterygium, with the distal portions of the cartilages remaining separate as two independent branches (Figs 28A, C, 29, 30). These branches are interpreted as remnants of the plesiomorphic unfused condition of the posterior basipterygial cartilage. The posterior branches of the basipterygial cartilages are absent in the species of *Denticetopsis*. Additionally, the lateral processes present in the members of that genus are shifted posteriorly, so that they are longitudinally aligned with the basal portion of the cartilage and

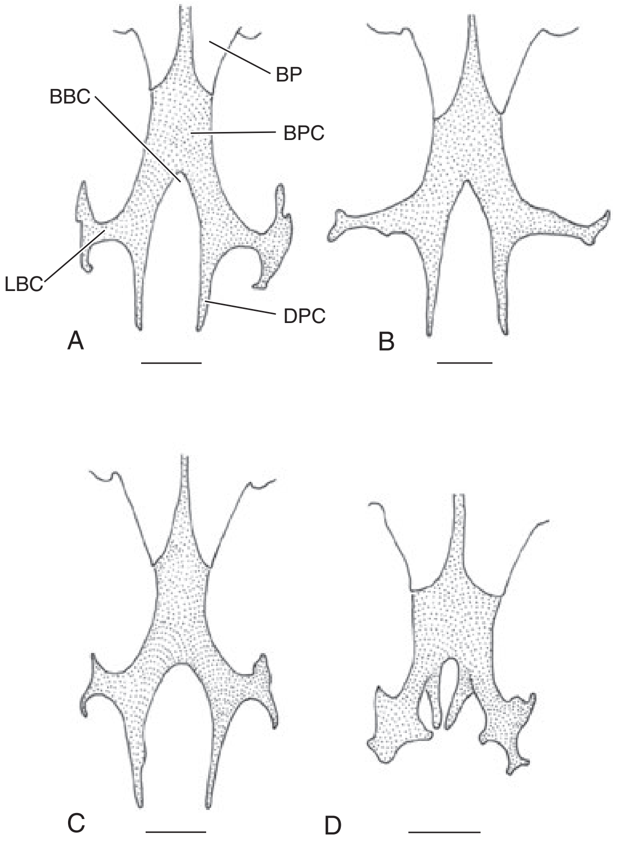

Figure 30. Posterior basipterygial cartilages. Ventral views. Anterior to top. A, *Cetopsis motatanensis* (USNM 121269); B, *Cetopsis othonops* (USNM 76972); C, *Cetopsis fimbriata* (USNM 372826); D – *Cetopsis amphiloxa* (MEPN field number 85–140). Scale bars = 1 mm.

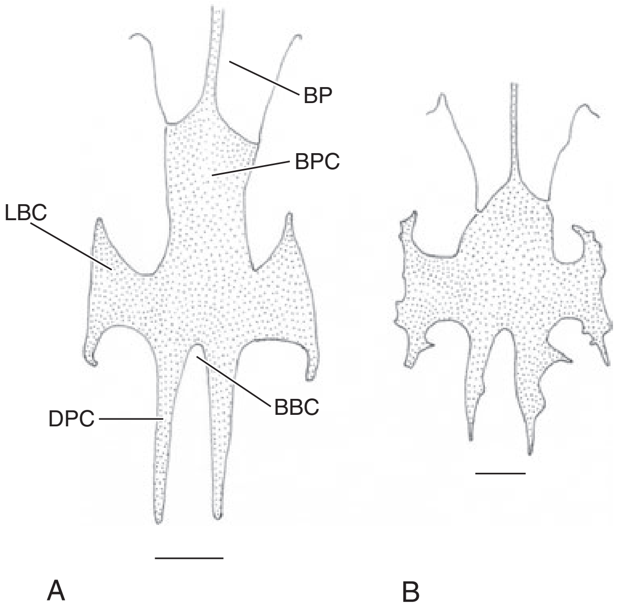

Figure 31. Posterior basipterygial cartilages. Ventral views. Anterior to top. A, *Cetopsis plumbea* (MUSM 4201); B, *C. gobioides* (MZUSP 39599). Scale bars = 1 mm.

positionally replace the primitive distal part of the posterior process (Fig. 28B). The missing entry for *Cetopsidium ferreirai* in the data matrix is a consequence of the poor condition of the cleared and stained specimen of this species available for this study, in which the pelvic-girdle cartilages are degraded.

112. Lateral branch of basal bifurcation of posterior basipterygial cartilage (multistate unordered) (CI = 66, RI = 87).
State 0: Absent.
State 1: Pointed.
State 2: Axe-head shaped.

In most species of the Cetopsinae the posterior basipterygial cartilage has a lateral branch that extends laterally or posterolaterally along the body wall. There is a large degree of variation in the morphology of this process, and properly coding this diversity is complicated due to the absence of this process in outgroups and the scant available ontogenetic information for this feature. For this analysis, we adopted a first approximation and coded the character as three-state unordered, in order to express the main patterns of variation. The absence of the process is considered as State 0. In State 1, present only in *Cetopsis candiru*, the process is a simple pointed process (Fig. 29B). In State 2, present in most species of the Cetopsinae, the process is greatly expanded distally into an axe-shaped structure (Figs 28, 29A, 30). Missing entries in the data matrix for *Cetopsidium ferreirai* and *Paracetopsis esmeraldas* are the result of poorly preserved cleared and stained specimens in which the details of the basipterygial cartilages could not be examined critically. The lateral process of the posterior basipterygial cartilage of *Cetopsis amphiloxa* is roughly tripartite, being continuous with the longitudinal axis of the main cartilage and with the medially directed posterior process (Fig. 30D). This configuration of the posterior basipterygial cartilage is different from that present in all other species of the Cetopsinae that were examined osteologically.

113. Width of lateral branch of posterior process of basipterygial cartilage (CI = 33, RI = 66).
State 0: Approximately same width as main posterior process.
State 1: At least twice width of main posterior process.

One of the variants observed in the lateral branch of the posterior process of the basipterygial cartilage in the species of the Cetopsinae was the width of its base where it arises from the main posterior process of that structure. Two well-defined states of the cartilage width were coded. In one of these (State 0), the process is narrow, being approximately the same width as the main posterior process (Figs 28–30). The other condition (State 1) has a process that is at least twice as wide as the main posterior process (Fig. 31). Taxa that lack a lateral branch of the posterior basipterygial process (species of the Helogeninae, outgroups in the Siluriformes and *Cetopsis oliveirai*) were coded as a missing entry for this character.

114. Relative position of lateral branch of posterior process of basipterygial cartilage (CI = 100, RI = 100).
State 0: Distal to basal bifurcation.
State 1: Partly or completely basal to basal bifurcation.

The lateral branch of the posterior process of basipterygial cartilage, when present, occupies one of two rather distinct positions. In one of them (State 0), its origin is located distally on the posterior basipterygial process and is positioned entirely distal to the split between the two posterior processes (Figs 28–30). In the alternative condition (State 1), the lateral branch is located more basally, either partly (*Cetopsis montana*) or completely (all other species of *Cetopsis* coded as State 1; see Appendix 2) basal to the median split between the two posterior processes (Fig. 31). Taxa lacking the lateral branch of the posterior basipterygial cartilage (species of the Helogeninae, outgroups in the Siluriformes and *Cetopsis oliveirai*) were coded as a missing entry for this character, as was *Cetopsidium ferreirai* because of the incomplete available skeletal preparation of that species. The relative position of the lateral branch was difficult to determine in *Cetopsis candiru* because of the reduced condition of the cartilaginous elements of the pelvic girdle in that species and their intraspecific variability. Therefore, that species was also assigned a missing entry in the matrix.

115. Morphology of base segments of first pelvic-fin ray (multistate ordered) (CI = 50, RI = 88).
State 0: Segments orientated transversely, without laminar expansions.
State 1: Segments orientated obliquely, without laminar expansions.
State 2: Segments orientated obliquely, with distinct laminar expansion.

The pelvic-fin segments in the Siluriformes primitively appear in lateral view as simple rectangles of bone that form a linear arrangement along the length of the ray and have basal and distal margins perpendicular to the axis of the ray. Within the Cetopsinae, the ray segments in *Cetopsidium morenoi*, *Cetopsis coecutiens*, *C. oliveirai* and *C. candiru* contact each other by way of an oblique articulation (State 1). In all other species of the Cetopsinae, the lateral margins of each segment are also expanded into a laminar expansion, forming a nearly continuous shelf along the lateral margins of the fin ray (State 2).

116. Width of base of unbranched ray of pelvic fin (CI = 100, RI = 100).
State 0: As wide as, or only slightly wider than, base of branched fin rays.
State 1: Approximately twice as wide as base of branched fin rays.

The base of the first pelvic-fin ray, which is unbranched in all groups within the Siluriformes except for the Chacidae (Brown & Ferraris, 1988), is usually as wide and thick as, or slightly wider and thicker than, the corresponding portions of the other rays in the fin. In all species of *Denticetopsis* the first ray is markedly enlarged along its proximal portion, being at least twice as wide as the corresponding portions of the other pelvic-fin rays. This apomorphic enlargement extends to the base of the first ray, where the contrast in width relative to the other rays is particularly obvious.

117. Association of pelvic fin to wall of abdomen (multistate ordered) (CI = 40, RI = 85).
State 0: Lacking medial membrane joining abdomen.
State 1: With medial membrane joining abdomen, membrane extending for one-quarter to one-third of distance along base of medial ray.
State 2: With medial membrane joining abdomen, membrane extending one-half to two-thirds of distance along base of medial ray.

The inner most ray of the pelvic fin in the Siluriformes is primitively not connected by membrane to the body surface, a condition seen in the outgroups examined in this study and within the Cetopsidae in the species of the Helogeninae. In all species of the Cetopsinae, except *Cetopsis candiru*, the pelvic fin is attached medially to the wall of the abdomen by a membrane of integument. This union can take the form of an attachment along the basal one-quarter to one-third of the ray (State 1, species of *Denticetopsis*) or along the basal one-half to two-thirds of the ray (State 2, species of *Cetopsidium* and *Paracetopsis* and all species of *Cetopsis*, except *C. candiru*).

MISCELLANEOUS

118. Number of principal caudal-fin rays (CI = 50, RI = 0).
State 0: 18.
State 1: 17 or fewer.

Members of the Siluriformes primitively have 18 principal caudal-fin rays, a count exclusive to the Diplomystidae within the order (Lundberg & Baskin, 1969; Grande, 1987). In most other groups in the Siluriformes, these rays are 17 or fewer. This character is included in the analysis to resolve relationships among the outgroup portion of the tree, but is uninformative as to intrafamilial relationships of the Cetopsidae.

119. Membranous connection between posterior-most anal-fin ray and caudal peduncle (multistate ordered) (CI = 28, RI = 64).
State 0: Little or no membranous connection between posterior-most anal-fin ray and caudal peduncle.
State 1: Membranous connection between posterior-most anal-fin ray and caudal peduncle extending along basal half of ray.
State 2: Membranous connection between posterior-most anal-fin ray and caudal peduncle extending along entire length of ray.

In most taxa in the Siluriformes, the last anal-fin ray is not connected, or at most connected only basally, to the ventral margin of the caudal peduncle by a short sheet of membranous integument. In many species of the Cetopsinae (Appendix 2), the membrane extends from the caudal peduncle up the basal one-half, or slightly more, of the last fin ray (State 1). In the most extreme condition, found in *Denticetopsis sauli* (State 2), the connective tissue sheet continues to the distal tip of the posterior-most anal-fin ray and forms a continuous connection with the ventral margin of the caudal fin. That extreme condition is also found in *D. royeroi* (Ferraris, 1996), the putative closest relative to *D. sauli*, but a species not included in this analysis.

120. Distinct filament on first ray of dorsal fin (multistate ordered) (CI = 33/40, RI = 73/80).
State 0: Absent in both sexes.
State 1: Present only in, or proportionally longer in, males.
State 2: Present and approximately equally proportionally long in both males and females.

A filamentous distal extension of the unbranched dorsal-fin ray is a sexually dimorphic feature found in most adult males of the species of the Cetopsinae. Generally, but not always, this elaboration of the dorsal fin is accompanied by a comparable extension of the first pectoral-fin ray. Females and immature males have either no distal extension of the dorsal-fin ray tip, or the extension, when present, is proportionally much shorter than that in mature males of the species. In *Cetopsis coecutiens* (Fig. 39) and *C. oliveirai* (Fig. 40), specimens of both sexes exhibit filamentous extensions of the first dorsal and pectoral-fin rays, without any discernible difference in the proportional length of the filament between the sexes (State 2). Species of *Denticetopsis* exhibit the more common siluriform feature of the absence of filamentous extensions of the first dorsal-fin ray in both sexes (Fig. 36), a condition also found in *Cetopsidium ferreirai*.

121. Sexual dimorphism of anal-fin form (CI = 25, RI = 78).
State 0: Absent.
State 1: Males with broadly convex fin margin and females with straight fin margin.

The distal margin of the anal fin is a sexually dimorphic feature in many members of the Cetopsinae (Vari *et al.*, 2005). In those species exhibiting such dimorphism, the length of the anal-fin rays in females and immature males decreases in length at a uniform rate from the first branched fin-ray to the posterior-most fin ray, resulting in the distal margin of the fin being approximately straight (see Vari *et al.*, 2005: fig. 40). In mature males of these species, in contrast, the middle rays of the anal fin are progressively longer than those more anteriorly and more posteriorly, thereby making the margin convex (see Vari *et al.*, 2005: fig. 39). A few species within the Cetopsinae (*Cetopsis amphiloxa*, *C. oliveirai* and the species of *Denticetopsis*) exhibit no discernible sexual dimorphism in the anal-fin margin, and instead all specimens have a straight fin margin. Such observations are based on widely different numbers of specimens across the Cetopsinae, and are therefore not equally corroborated at this time. Whereas the lack of anal-fin sexual dimorphism in *C. oliveirai* (Fig. 40) and in species of *Denticetopsis* is consistent across often extensive series, observations for *C. amphiloxa* were limited to eight specimens, and an examination of additional specimens of the latter species is necessary in order to confirm its lack of sexual dimorphism. The anal-fin margin in the species of *Helogenes* is slightly convex (see Vari & Ortega, 1986) but dimorphism in the shape of the fin was not observed by Vari & Ortega (1986) or in this study.

122. Adipose fin in adults (CI = 50, RI = 83).
State 0: Present.
State 1: Absent.

An adipose fin is present in most members of the Siluriformes and, in fact, in most of the lower Euteleostei. Within the Cetopsidae, an adipose fin is present in adult specimens only in *Helogenes*, and even in that genus, some populations of *H. marmoratus* and *H. castaneus* lack that structure or have it significantly reduced in size (Vari & Ortega, 1986: 4–5). The absence of an adipose fin in adults was proposed as a potential additional synapomorphy for Cetopsinae by de Pinna & Vari (1995: 16). The same authors observed that juvenile specimens of *Cetopsis coecutiens* have an adipose fin, which presumably recedes and then disappears during ontogeny. How widespread the presence of an adipose fin is among juveniles of species of the Cetopsinae requires additional data on early ontogenetic stages of other members of the subfamily.

123. Size of opercular opening (multistate ordered) (CI = 100, RI = 100).
State 0: Wide and mostly free from isthmus.
State 1: Narrow, with membranes broadly joined to isthmus, but with dorsal portion of opening extending dorsal to pectoral-fin base.

State 2: Very narrow, with membranes broadly joined to isthmus and none of opercular opening extending dorsal to pectoral-fin base.

The branchial openings in the Siluriformes are primitively wide, which is the result of the lack, or near lack, of attachment of the branchial membranes to the isthmus. Within the Cetopsidae, that putatively plesiomorphic condition (State 0) is found in all species of *Helogenes*, *Cetopsidium*, *Denticetopsis* and *Paracetopsis*. In species of *Cetopsis* the branchial membranes are joined to the isthmus to a pronounced degree, so that the ventral part of the primitive branchial opening is closed along the entire isthmus. The dorsal part of the opening, however, remains and extends dorsally beyond the base of the pectoral fin (State 1). A more extreme reduction of the branchial opening is seen in *C. candiru*, in which there is also a restriction of the opening dorsally with the result that the opening is reduced to a small area immediately anterior to the base of the pectoral fin (State 2).

124. Form and position of posterior narial opening (CI = 50, RI = 0).
State 0: Opening small and oval; located on anterior section of dorsolateral portion of head and remote from contralateral narial opening.
State 1: Opening large, elipsoid; medial end of opening near to midline of body and close to contralateral narial opening.

The nares in the Siluriformes are usually rounded and located on the anterior region of the dorsolateral portion of the head. In the Cetopsidae the posterior nares are located between the eyes and are usually closer to the eye of their respective side of the head than they are to their contralateral nares. In *Cetopsis coecutiens* and *C. oliveirai*, the nares are proportionally wider and ellipsoidal in shape. Furthermore, in the former species the contralateral nares are much closer to each other than either is to the proximate eye. A comparison of that characteristic is impossible in *C. oliveirai* as a consequence of its lack of eyes (see Character 125). However, the posterior nares in that species are very close to each other relative to the head width, and we conclude that the relative position of the nares is comparable with that occurring in *C. coecutiens*.

125. Relative size of eye (multistate ordered) (CI = 100, RI = 100).
State 0: Moderately to well developed.
State 1: Very small, barely visible.
State 2: Absent.

The eye of most species of the Cetopsidae is relatively small when compared with that of other families of the Siluriformes. Although subtle variations of eye size are difficult to quantify objectively, instances of extreme differences in eye size can be coded as discrete characters. In State 1, which is found in *Cetopsis coecutiens* and *C. candiru*, the eye is small and sunken into the head integument making it inconspicuous from an external view of the fish. In *C. coecutiens*, HL is on the average 21.6 times eye diameter (Oliveira, 1988: table 2), while in *C. candiru* that figure is 20.8 (Oliveira, 1988: table 7), representing State 1. In all other species of the Cetopsidae except *C. oliveirai* (below), the proportional values for this feature vary between 8.3 and 15.6 (Oliveira, 1988: tables 1–22), which is coded as state 0. The ultimate reduction in eye size occurs in *C. oliveirai*, in which the eye is absent, a unique case within the Cetopsidae. A reduction and sometimes a loss of eyes has occurred repeatedly in freshwater fish groups living in deep river channels, the habitat occupied by *C. oliveirai* (Lundberg & Rapp Py-Daniel, 1994: 387–388). The level of light penetration in that environment is probably equivalent to that typical of the deep parts of caves, a habitat in which there are many cases of eye reduction in fishes and other animals (Trajano, 2003).

126. Shape of chromatophores on body (CI = 100, RI = 100).
State 0: Rounded or symmetrically stellate.
State 1: Horizontally elongated over most of body surface.

The chromatophores in most members of the Cetopsinae, in particular, and across the Siluriformes, in general, have a circular dendritic pattern, with irregular ramifications extending in all directions from the cell centre. In the species of *Denticetopsis*, with the exception of *D. sauli* (and its putative closest relative, *D. royeroi*, which was not included in this analysis), the chromatophore ramifications are bilaterally orientated, with half of its branches directed anteriorly and half posteriorly (Vari *et al.*, 2005). This modification results in an hourglass-shaped expanded chromatophore. This peculiar morphology of the chromatophores was first described and illustrated by Eigenmann (1912a: 211, pl. 23, fig. 1) in *Denticetopsis macilenta*.

127. Posterior extent of lateral line (multistate ordered) (CI = 28, RI = 72).
State 0: Extending to base of caudal fin.
State 1: Extending onto caudal peduncle, but falling short of base of caudal fin.
State 2: Not reaching past vertical through posterior terminus of anal-fin base.

The lateral line in the Siluriformes, and ostariophysans in general, normally extends posteriorly across the caudal peduncle to a point somewhat beyond the posterior margin of the hypural complex (State 0). This form of the lateral line also occurs in the Helogeninae within the Cetopsidae. Members of

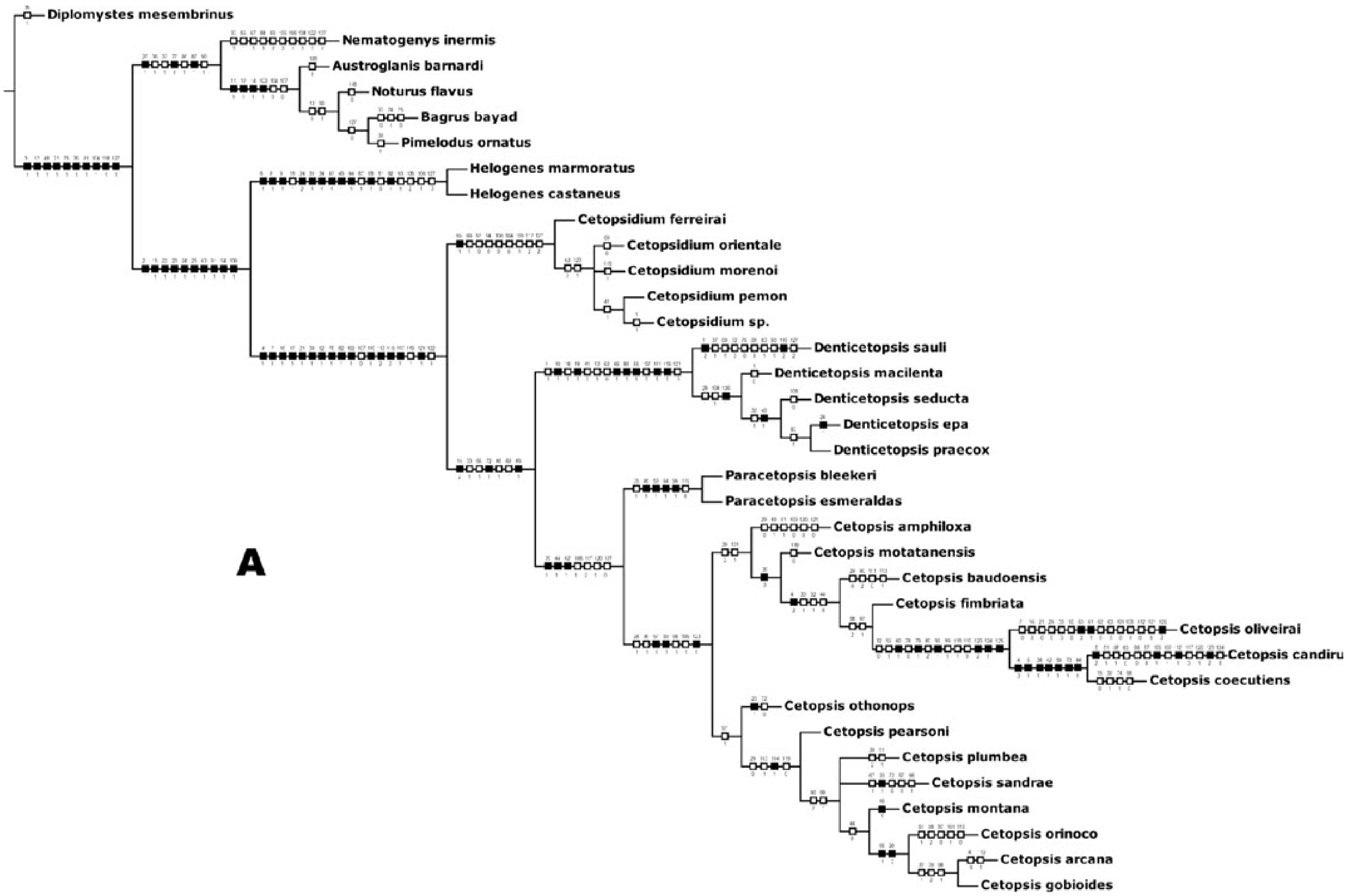

Figure 32. Two most parsimonious trees, A and B (L = 272, CI = 54, RI = 83) of relationships among Cetopsidae and outgroups, based on matrix in Appendix 2. Note in particular alternative topologies within *Cetopsidium*.

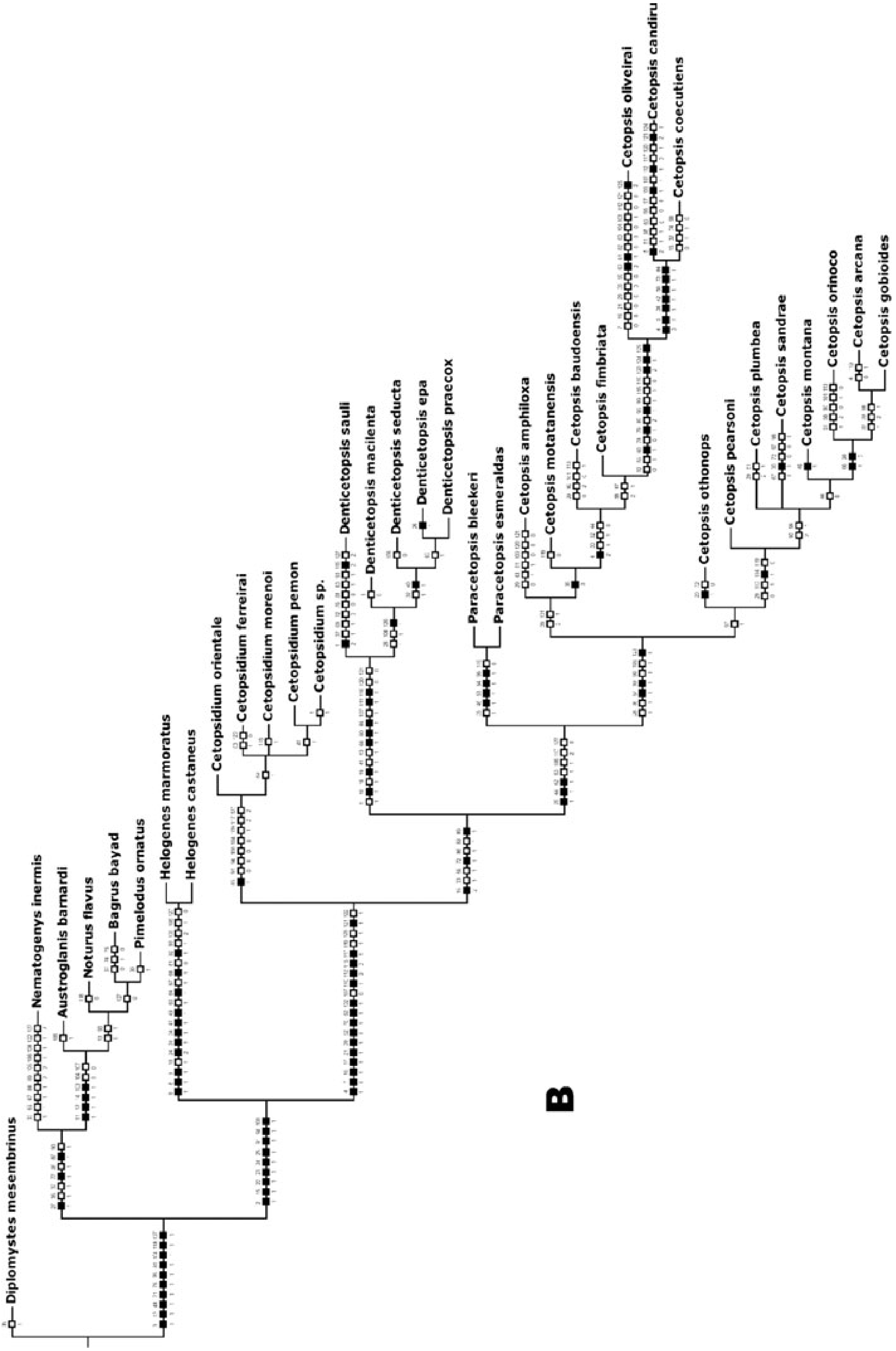

Figure 32. *Continued*

the Cetopsinae have differing degrees of reduction of the length of the pored portion of the lateral line (Vari *et al.*, 2005). In the first condition (State 1, in all examined species of *Denticetopsis*, except *D. sauli*), the lateral line extends onto the caudal peduncle, but ends short of the base of the caudal fin. In a more extreme reduction (State 2, in *Cetopsidium* and *Denticetopsis sauli*) the lateral line does not extend posteriorly onto the caudal peduncle. In *D. sauli* (and in its closest relative, *D. royeroi*, which was not examined during this study) the lateral line does not extend beyond the abdominal cavity (Ferraris, 1996).

Reductions of the sensory canal system are common events in miniaturized species, and a well-known indicator of paedomorphosis in fishes (Weitzman & Vari, 1988). In the Cetopsidae, lateral-line reductions occur only in species with small body sizes, which strongly indicates that such reductions in the family are associated with paedomorphic processes.

PHYLOGENETIC ANALYSIS

The characters described in the previous section were analysed by strict parsimony, which resulted in two equally parsimonious trees with NONA (using the WINCLADA interface, mult* with 5000 replicates, hold five trees per replicate (L = 272, CI = 54, RI = 83). Heuristic searches with Hennig86 (using the TreeGardener interface, and algorithms mh* bb*) resulted in six trees with the same statistics as the NONA results. The additional trees found with Hennig86 are resolutions resulting from alternative interpretations for zero-length branches (Coddington & Scharff, 1994). All four additional trees are topologies resulting from specific optimizations of ambiguous state-distributions. Successively collapsing all unsupported nodes in the six Hennig86 trees, under both ACCTRAN and DELTRAN optimizations, results in the same two trees found with NONA. Those two trees, shown in Figure 32 (with ambiguous characters ACCTRAN-optimized) are those resulting from unambiguous changes only. Strict consensus trees are identical in the analyses with the two programs (Fig. 33). Conflicting resolution is confined to the portion of the tree corresponding to the genus *Cetopsidium*.

Jackknife and Bootstrap values (Fig. 33) were calculated with NONA using the WINCLADA interface. Bremer support values were estimated directly with NONA. Statistics mostly agree on the strongest clades: Cetopsidae, Helogeninae, Cetopsinae, *Cetopsidium*, *Denticetopsis*, *Paracetopsis* and *Cetopsis*, all with Bremer support 3 or higher, bootstrap and Jackknife values 70% or higher. The clade formed by *Cetopsis oliveirai*, *C. coecutiens* and *C. candiru*, and that formed by *C. gobioides* and *C. arcana* also has moderately strong support. Other clades within *Cetopsis* are weakly supported, with Bremer supports of 1 and less than 50% bootstrap and Jackknife. Those support estimates played a role in nomenclatural decisions explained in the following section.

NEW CLASSIFICATORY SCHEME

As is the case with many groups of organisms, the elucidation of phylogenetic relationships in the Cetopsidae revealed inadequacies of previous, non-phylogenetic classificatory schemes. The tendency to equate degree of morphological divergence with taxonomic differentiation resulted in the recognition, or maintenance, of separate genera for externally aberrant forms. This was the case with many of the better known forms in the Cetopsidae, such as *Cetopsis*, *Hemicetopsis*, *Paracetopsis* and *Bathycetopsis*, all of which were monotypic under previous concepts of taxonomy in the Cetopsidae. As a corollary of the practice of recognizing distinctive forms at the generic level, the genus *Pseudocetopsis* had become a waste basket for 'generalized' species of the Cetopsinae. Some of species previously assigned to *Pseudocetopsis* were found to be widely disjunct phylogenetically in our analysis. For example, a close examination of the species herein placed in *Cetopsidium* revealed many characteristics which placed them firmly as the sister group to all other species of the Cetopsinae. Nonetheless, these species were formerly included in the broadly defined genus *Pseudocetopsis* because of their lack of autapomorphies diagnostic of the larger and more conspicuous species assigned to *Cetopsis*, *Bathycetopsis* or *Hemicetopsis* under previous classificatory schemes.

Our decision to markedly expand the previously monotypic genus *Cetopsis* is a significant departure from the traditional taxonomy of the Cetopsidae, but is the only reasonable solution in view of the structure of the cladogram and the present nomenclatural situation within that family. Restrictions on nomenclatural alternatives are imposed mostly as a result of the paraphyletic nature of a subset of species formerly included in *Pseudocetopsis*. In the most parsimonious tree many species that were formerly assigned to *Pseudocetopsis* form a succession of sister groups to a well-diagnosed clade consisting of species previously placed in the genera *Bathycetopsis*, *Hemicetopsis* and *Cetopsis*. Retention of the genera *Hemicetopsis* and *Bathycetopsis* would have required generic names for each of the sister branches at the progressively more inclusive levels within the phylogeny. While *Pseudocetopsis* is an available name for one of those branches, it would have been necessary to propose several additional generic names for the unnamed clades. Although an increase in the number of generic names is not a priori undesirable, practical considerations

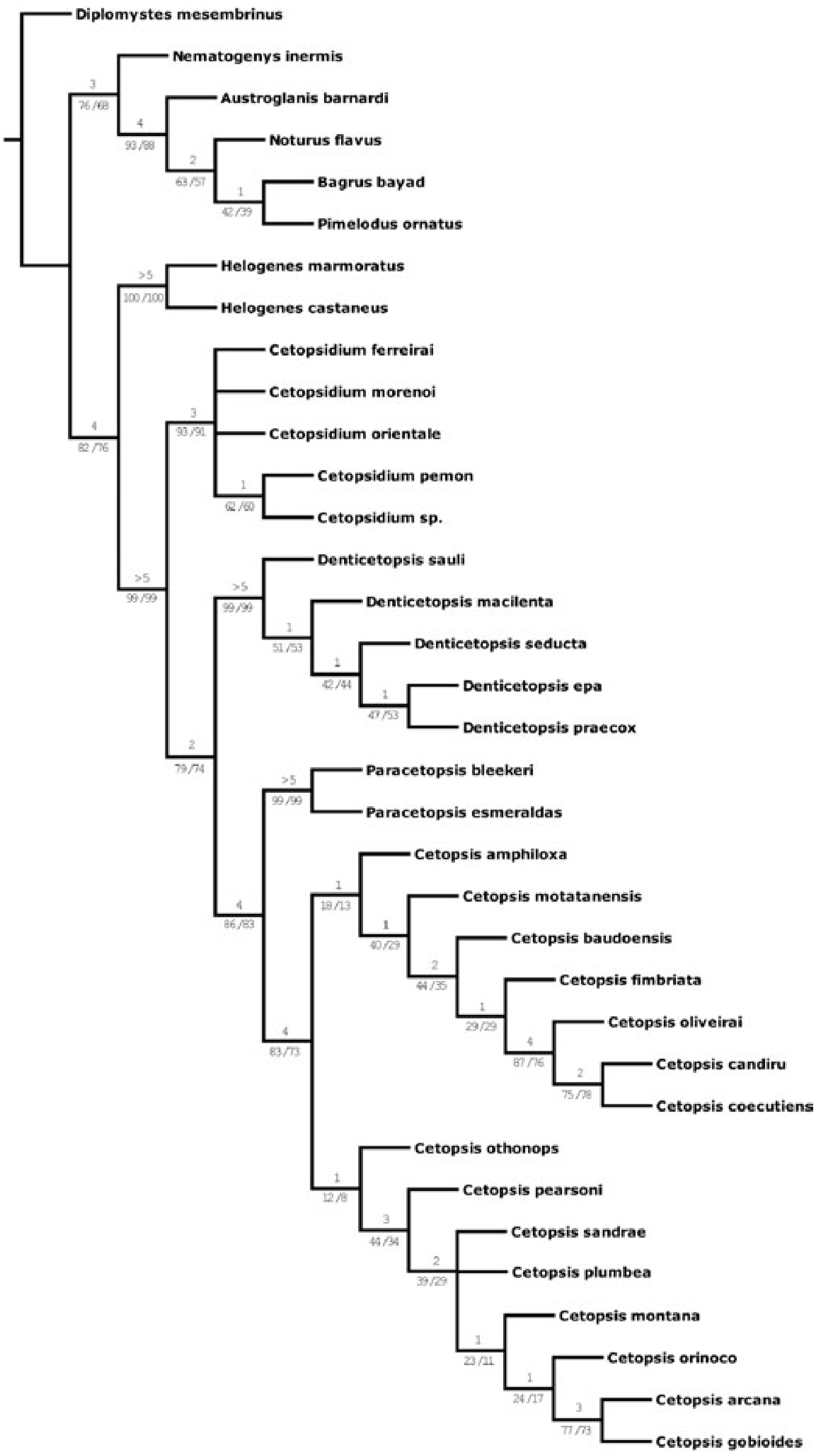

Figure 33. Strict consensus tree of two equally parsimonious trees in Figure 28, with branch support. For each clade, Bremer support is shown above the branch, Jackknife and Bootstrap values, separated by a slash, are below.

argue against that course of action. A separate genus for each of the sister groups to the *Cetopsis*/*Hemicetopsis*/*Bathycetopsis* clade would necessitate the proposal of new generic names for species which can distinguished externally only with some difficulty. Additionally, the phylogenetic diagnoses of those genera would rely on a few characters that are, for the most part, homoplastic at various levels of the cladogram. In view of the importance that generic identification has in fish taxonomy, that situation would have been indefensible. Additionally, resolution within the *Cetopsis* clade is for the most part weakly supported, with Bremer supports of 1 and Jackknife and bootstrap values below 50%. This means that taxonomic names hinged on those clades would not likely contribute to nomenclatural stability.

Rather than propose new genera, given the limitations noted above, we assigned generic names only to clades that were strongly supported and practical to diagnose, such as the lineage that forms the sister group to *Paracetopsis*. This clade is clearly diagnosable on the basis of both external and internal characters. It is also well corroborated in the analysis, with strong character support (see above) and is characterized by several homoplasy-free synapomorphies. Of course, placing *Bathycetopsis* and *Hemicetopsis* in the synonymy of *Cetopsis* eliminates two well-diagnosed names which were recognized in full accordance with previous standards of taxonomy of the Cetopsidae and which have been widely utilized since originally proposed. This is an unfortunate but necessary cost for adopting a phylogenetic classification for the Cetopsidae.

The genus *Denticetopsis*, originally proposed to include two highly modified miniaturized species (*D. sauli* and *D. royeroi*) from the Upper Orinoco and Negro Rivers (Ferraris, 1996), is herein expanded to include various other small-sized species related to *D. macilenta* (formerly known as *Hemicetopsis macilentus* or *Pseudocetopsis macilentus*). *Denticetopsis macilenta* has been suggested as pertaining to a separate genus on two occasions, but a putative new genus was never formally described for that species. Oliveira (1988) included the species as sole member of a monotypic genus (named but not validly described because that study is an unpublished dissertation). Milani de Arnal (1991), in turn, united forms related to *D. macilenta*, *Cetopsidium morenoi* and *C. minutum* in an unnamed genus. Although both studies have merit in recognizing the challenges posed by some species of the Cetopsinae to traditional generic limits in Cetopsidae, neither author suggested a group corresponding to a monophyletic *Denticetopsis* as recognized in this paper. There is strong character support for the clade that unites *D. macilenta* and its close relatives with the two species originally assigned to *Denticetopsis*. On that basis, *Denticetopsis* was expanded by Vari *et al*. (2005) and, in its expanded sense, is easily diagnosed by various characteristics unique within the Cetopsidae, such as the lateralmost one or two premaxillary teeth being larger than the other teeth on that bone, with their longitudinal axis approximately parallel to the plane of the premaxilla (Character 10); the ventral surface of the vomer with a median protuberance (Character 41); and the base of the unbranched (first) ray of the pelvic fin approximately twice as wide as the bases of the branched rays (Character 116). All species in *Denticetopsis* also share a very similar morphology of the posterior basipterygial cartilage, not seen elsewhere in the Cetopsidae or in other taxa on the Siluriformes (Fig. 28B; compare with fig. 5 of Ferraris, 1996).

Our recognition of most other genera and suprageneric taxa in the new classification of the Cetopsidae also relies on the degree of character support, with names assigned to relatively robust clades. The proposed classification of the Cetopsidae, which is sequenced for the tribes of Cetopsinae and subordinated otherwise, is as follows:

Family Cetopsidae Bleeker, 1858
  Subfamily Helogeninae Regan, 1911
    Genus *Helogenes* Günther, 1863
  Subfamily Cetopsinae Bleeker, 1858
    Tribe Cetopsidiini New Tribe
      Genus *Cetopsidium* Vari, Ferraris & de Pinna, 2005
    Tribe Denticetopsini New Tribe
      Genus *Denticetopsis* Ferraris, 1996
    Tribe Cetopsini Bleeker, 1858
      Genus *Paracetopsis* Bleeker, 1862
      Genus *Cetopsis* Spix & Agassiz, 1829

SYNAPOMORPHY SCHEME AND SUMMARY OF RECOGNIZED TAXA

The named clades recognized in the new classification of Cetopsidae are diagnosed herein according to the character transitions hypothesized to be synapomorphic in the analysis. For each of the clades below, a list of apomorphic transitions is provided, numbered according to the respective list of characters in the character analysis section. Unless otherwise indicated, transitions are from State 0 to State 1. Only non-ambiguous changes are listed. The only exception is character 117, which certainly undergoes a transition at the Cetopsinae branch, but whose specific path is uncertain (either 0–1 or 0–2). Reference to homoplastic occurrences, when ambiguous, follows ACCTRAN optimization. Bremer support (Br), Jackknife (jk) and Bootstrap (bs) values are also provided for each taxon. Intrageneric relationships are presented in Figure 32, and character transitions at those levels can be traced therein.

FAMILY CETOPSIDAE BLEEKER, 1858

Diagnosis (Br: 4, jk: 82, bs: 76):

Maxilla with a single articular head (2);

Anterior and medial palatine cartilages continuous (15, reversed to state 0 in *C. coecutiens*);

Opercle and interopercle overlapping, forming a lap suture (22);

Point of attachment of interoperculo-mandibular ligament on the dorsal margin of the interopercle (23);

Interopercle with reduction of its anteroposterior axis, so that it is as deep as, or slightly deeper than, long (24);

Metapterygoid rectangular (25).

Included subfamilies: Helogeninae, Cetopsinae.

SUBFAMILY HELOGENINAE REGAN, 1911

Diagnosis (Br: > 5, jk: 100,bs: 100):

Teeth in anterior portion of outer row of dentary much larger and more widely spaced apart than other teeth of jaw (6);

Coronoid bone shifted laterally, visible in lateral view of lower jaw (8);

Coronoid process of lower jaw composed mostly of unossified ascending process of Meckel's cartilage (9);

Hyoid branch of hyoideomandibular nerve on hyomandibula trespassing hyomandibula and running exposed on its lateral surface (convergent with Denticetopsini) (18);

Interopercle extremely reduced anteroposteriorly, restructured into vertically elongated bone (24, State 2);

Frontals with large paired fontanels (31);

Sphenotic not contacting supraoccipital (34);

Posterior process of vomer reduced or absent (47);

Medial portion of mesethmoid unossified (49);

Lateral margins of second basibranchial expanded and forming convex lateral shelf (63, convergent with *Cetopsidium ferreirai*, and Cetopsini with a subsequent reversal in *Cetopsis oliveirai*).

Posterior portion of third basibranchial and associated cartilage greatly expanded posteriorly (64);

Second hypobranchial entirely cartilaginous (67, convergent in *Cetopsis sandrae*);

Second hypobranchial with well-defined concavity anteriorly (68);

Association of branchiostegal rays with opercle without strong ligamentous connection (81, State 0, convergent in *Denticetopsis sauli*);

Distal portion of neural arches of fifth to eighth vertebrae with trabeculae (92);

Four or five pleural ribs (93, convergent in *Denticetopsis sauli*);

Dorsal fin located on posterior half of SL (105, State 2);

Second dorsal-fin ray completely flexible and segmented, not forming spine (106, convergent with Cetopsini).

Included genus: *Helogenes*.

Genus *Helogenes* Günther, 1863
Helogenes Günther, 1863 (type species: *Helogenes marmoratus* Günther 1863)
Leyvaichthys Dahl, 1960 (type species: *Leyvaichthys castaneus* Dahl 1960).

Diagnosis: see Helogeninae.

Included species: *Helogenes castaneus* (Dahl), *H. gouldingi* Vari and Ortega, *H. marmoratus* Günther (Fig. 34), *H. uruyensis* Fernández-Yépez.

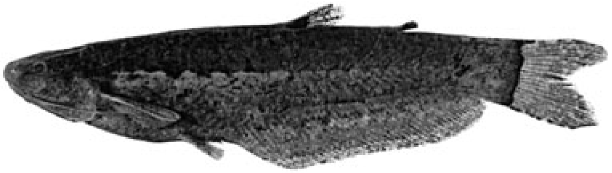

Figure 34. *Helogenes marmoratus*, USNM 273057, 63.5 mm SL; Guyana, Potaro River.

SUBFAMILY CETOPSINAE BLEEKER, 1858

Type genus: *Cetopsis* Spix and Agassiz, 1829

Diagnosis (Br: > 5, jk: 99, bs: 99):

Single row of dentary teeth, or more than one row of teeth present only along approximately one-half of length of tooth-bearing surface, plus some additional teeth located near symphysis (4);

Adductor mandibulae muscle hypertrophied, extending dorsally to midline of neurocranium (7);

Levator arcus palatini muscle very developed and clearly visible in dorsal view (reversed in *Cetopsis oliveirai*) (16);

Dorsal portion of hyomandibula with distinct anterior process forming long, direct articulation with ventrolateral margin of neurocranium (17);

Metapterygoid extending posteromedial of entopterygoid (21);

Vomerine teeth disposed in one row (39);

Rigid layer of fibrous cartilage associated with anterolateral margins of mesethmoid, forming protective wall surrounding anteromedial portions of olfactory capsule (52);

Distal portion of posterior ceratohyal broadened (78, reversed in *Denticetopsis sauli*);

Third and fourth branchiostegal rays distinctly shorter than other rays (82);

Coracoids extending for two-thirds or less of length of cleithrum (102);

Contralateral posterior basipterygial cartilages fused medially at base, forming single stem for posterior cartilaginous process(es) (110);

Lateral branch of basal bifurcation of posterior basipterygial cartilage ax-head shaped (112, State 2, reversed to state 0 in *Cetopsis oliveirai*);

First pelvic-fin ray base segments orientated obliquely, with distinct laminar expansion (115, State 2, reversed to State 1 in *Cetopsidium morenoi*);

Pelvic fins with medial membrane joining contralateral medial rays and abdomen (117, State 1 or 2, reversed to State 0 in *Cetopsis candiru*);

Last anal-fin ray and caudal peduncle united by membranous connection extending at least to basal one-half of ray and may extend along entire length of ray (119, reversed to State 0 in species of *Paracetopsis*, *Cetopsis motatanensis*, the clade formed by *Cetopsis oliveirai*, *C. coecutiens* and *C. candiru*, and in the clade formed by *C. pearsoni*, *C. plumbea*, *C. sandrae*, *C. montana*, *C. orinoco*, *C. gobioides* and *C. arcana*, with a subsequent transition to State 1 in the latter species);

Adipose fin absent in adults (122, convergent in the outgroup species *Nematogenys inermis*).

TRIBE CETOPSIDIINI, NEW TRIBE

Type genus: *Cetopsidium* Vari, Ferraris & de Pinna, 2005

Diagnosis (Br: 3, jk: 93,bs: 91):

Uncinate process of first hypobranchial longer than free anterior margin of bone (65);

Third hypobranchial with long axis oblique relative to basibranchial series (69, reversed in *Cetopsidium orientale* and convergent in *Denticetopsis sauli*)

Presence of transverse radial anterior to anal-fin pterygiophores (109, convergent with *Cetopsis* and subsequently reversed in *C. amphiloxa*);

Lateral line not reaching past vertical through posterior terminus of anal-fin base (127, State 2, convergent with *Denticetopsis sauli* and the outgroup species *Nematogenys inermis*);

Included genera: *Cetopsidium* Vari, Ferraris and de Pinna, 2005

Genus *Cetopsidium* Vari, Ferraris and de Pinna, 2005

Cetopsidium Vari, Ferraris and de Pinna, 2005 (type species: *Pseudocetopsis orientale* Vari, Ferraris and Keith, 2003).

Diagnosis: As for the tribe.

Included species: *Cetopsidium ferreirai* Vari, Ferraris, and de Pinna, *C. minutum* (Eigenmann) (Fig. 35), *C. morenoi* (Fernández-Yépez), *C. orientale* (Vari, Ferraris, and Keith), *C. pemon* Vari, Ferraris, and de Pinna, and *C. roae* Vari, Ferraris, and de Pinna.

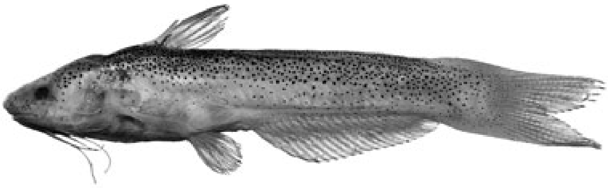

Figure 35. *Cetopsidium minutum*, ANSP 175839, 21 mm SL; Guyana, Essequibo River.

TRIBE DENTICETOPSINI, NEW TRIBE

Type genus: *Denticetopsis* Ferraris, 1996

Diagnosis (Br: > 5, jk: 99,bs: 99)

Lateral-most one or two premaxillary teeth larger than remaining premaxillary teeth, with their longitudinal axis parallel, or nearly parallel, to longitudinal plane of premaxilla (10);

Hyoid branch of hyoideomandibular nerve on hyomandibula trespassing hyomandibula and running exposed on its lateral surface (18, convergent with Helogeninae);

Passage for trigeminal nerve narrow and constricted by dorsal lamina of metapterygoid (19);

Vomer with median protuberance anteriorly on ventral surface (41, convergent with clade formed by *Cetopsidium pemon* and *Cetopsidium* sp.);

Dorsal surface of shaft of mesethmoid strongly concave (43, convergent with *Cetopsis amphiloxa*);

First hypobranchial with posteromedial concavity, strongly arched (66);

Interhyal distinctly elongate, with length approximately six or more times its length (80);

Posterior process of posterior ceratohyal long and well defined, extending posteriorly or posterodorsally along posterior margin of interhyal (85);

Posteriorly directed process of basipterygial cartilage distal to lateral bifurcation absent (111);

Base of unbranched ray of pelvic fin approximately twice as wide as base of branched fin rays (116).

Included genera: *Denticetopsis* Ferraris, 1996

Genus *Denticetopsis* Ferraris, 1996

Denticetopsis Ferraris, 1996 (type species: *Denticetopsis sauli* Ferraris, 1996).

Diagnosis: As for tribe.

Included species: *Denticetopsis epa* Vari, Ferraris, and de Pinna, *D. iwokrama* Vari, Ferraris, and de Pinna (Fig. 36), *D. macilenta* (Eigenmann), *D. praecox* (Ferraris and Brown), *D. royeroi* Ferraris, *D. sauli* Ferraris.

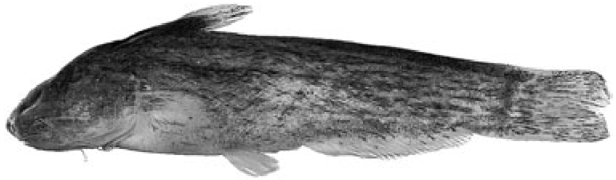

Figure 36. *Denticetopsis iwokrama*, ANSP 177215, 43 mm SL; Guyana, Essequibo, Essequibo River basin, Siparuni River.

TRIBE CETOPSINI BLEEKER, 1858

Diagnosis (Br: 4, jk: 86,bs: 83):

Anterior process of vomer expanding anteriorly and terminating in broad truncate margin (44, reversed in clade formed by *Cetopsis baudoensis*, *C. fimbriata*, *C. oliveirai*, *C. candiru* and *C. coecutiens* and in the clade formed by *C. montana*, *C. orinoco*, *C. arcana* and *C. gobioides*);

Developed anteriorly and extending to transverse line through anterior bony margin of first hypobranchial (62, reversed in *Cetopsis oliveirai*);

Lateral margins of second basibranchial expanded and forming convex lateral shelf (63, convergent in Helogeninae and *Cetopsidium ferreirai*, reversed in *Cetopsis oliveirai*);

Second dorsal-fin ray completely flexible and segmented, not forming spine (106, convergent in the Helogeninae and the outgroup *Nematogenys inermis*).

Included genera: *Cetopsis* and *Paracetopsis*.

Genus *Paracetopsis* Bleeker, 1862

Paracetopsis Bleeker, 1862 (type species: *Paracetopsis bleekeri* Bleeker 1862)

Paracetopsis Eigenmann & Bean, 1907 (type species: *Cetopsis occidentalis* Steindachner, 1880).

Cetopsogiton Eigenmann and Bean, 1910 (type species: *Cetopsis occidentalis* Steindachner, 1880).

Diagnosis (Br: > 5, bs: 100, jk: 100):

Supraoccipital spine with only vertical blade, lacking horizontal component (35, convergent in the outgroup *Olivaichthys mesembrinus*);

Lateral wings of vomer narrow, less than one-half width of premaxilla (46);

Anterior part of mesethmoid cornua with vertical ventral laminae (53);

Anterior margin of anterior process of vomer with jagged anterior margin (54);

Anterior ventral prezygapophysis of complex centrum thickened and with jagged distal margin (96);

Little or no membranous connection between posterior-most anal-fin ray and caudal peduncle (119, a reversal to State 0, three similar reversals occur in various subclades of *Cetopsis*).

Included species: *Paracetopsis atahualpa* Vari, Ferraris, and de Pinna, *P. bleekeri* Bleeker, *P. esmeraldas* Vari, Ferraris, and de Pinna (Fig. 37).

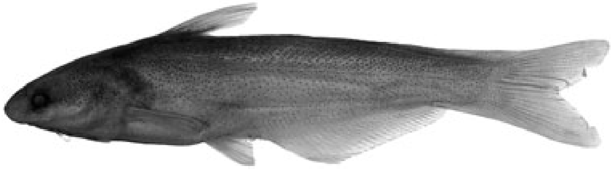

Figure 37. *Paracetopsis esmeraldas*, MCZ 48768, 68 mm SL; Ecuador, Esmeraldas, Río Esmeraldas basin, Río Blanco.

Genus *Cetopsis* Spix and Agassiz, 1829

Cetopsis Spix and Agassiz, 1829 (type species: *Silurus coecutiens* Lichtenstein, 1819).

Hemicetopsis Bleeker, 1862 (type species: *Cetopsis candiru* Spix and Agassiz, 1829).

Pseudocetopsis Bleeker, 1862 (type species: *Cetopsis gobioides* Kner, 1857).

Bathycetopsis Lundberg and Rapp Py-Daniel, 1994 (type species: *Bathycetopsis oliveirai* Lundberg and Rapp Py-Daniel, 1994).

Diagnosis (Br: 4, jk: 83,bs: 73):

Anterior cranial fontanel reduced or absent in adults (28, convergent with a subclade of *Denticetopsis* including all species in the genus except *D. sauli*);

Tip of supraoccipital spine bifurcated (36, convergent with a clade formed by all outgroups except *Olivaichthys mesembrinus*);

Posterior process on ventral limb of supracleithrum present and well-defined (57);

Contralateral parietal branches of laterosensory canal system converging posteromedially to midline and then running adpressed dorsally in soft tissue and adpressed to each other (59, reversed in *Cetopsis oliveirai*);

Anterior ventral transverse process of complex centrum present and relatively short, not or only barely extending laterally past lateral limit of tripus (90, convergent with an outgroup clade formed by *Austroglanis barnardi*, *Bagrus bayad*, *Noturus flavus* and *Pimelodus ornatus*);

Opercular opening reduced, with membranes broadly joined to isthmus, but with dorsal portion of opening extending dorsal to pectoral-fin base (123).

Included species: *Cetopsis amphiloxa* (Eigenmann), *Cetopsis arcana* Vari, Ferraris, and de Pinna, *Cetopsis baudoensis* (Dahl), *Cetopsis caiapo* Vari, Ferraris, and de Pinna, *Cetopsis candiru* Spix and Agassiz (Fig. 38), *Cetopsis coecutiens* (Lichtenstein) (Fig. 39), *Cetopsis fimbriata* Vari, Ferraris, and de Pinna, *Cetopsis gobio-*

ides Kner, *Cetopsis jurubidae* (Fowler), *Cetopsis montana* Vari, Ferraris, and de Pinna, *Cetopsis motatanensis* (Schultz), *Cetopsis oliveirai* (Lundberg and Rapp Py-Daniel) (Fig. 40), *Cetopsis orinoco* (Schultz), *Cetopsis othonops* (Eigenmann), *Cetopsis parma* Oliveira, Vari and Ferraris, *Cetopsis pearsoni* Vari, Ferraris, and de Pinna, *Cetopsis plumbea* Steindachner, *Cetopsis sandrae* Vari, Ferraris, and de Pinna (Fig. 41), *Cetopsis sarcodes* Vari, Ferraris, and de Pinna, *Cetopsis starnesi* Vari, Ferraris, and de Pinna, and *Cetopsis umbrosa* Vari, Ferraris, and de Pinna.

PHYLOGENETIC POSITION OF THE CETOPSIDAE

One of the by-products of this analysis is a proposal about the phylogenetic position of Cetopsidae within the Siluriformes. It has been previously suggested that the Cetopsidae (the Cetopsidae and Helogenidae of authors prior to de Pinna & Vari, 1995) may occupy a rather basal position within its order (Mo, 1991; de Pinna, 1993; Diogo *et al*., 2005; Diogo, 2005). While those previous hypotheses have not been challenged, each involves problematic aspects. Mo's hypothesis (1991) was associated with other results considered as rather unlikely (e.g. the non-monophyly of the Cetopsidae in Mo, 1991; the Cetopsinae herein), a situation that makes the overall results difficult to interpret. Diogo (2005) proposed a novel scheme that placed the loricarioid families as the sister group to all catfishes other than the Diplomystidae, and with the Cetopsidae as the sister to all remaining non-loricarioid families. Regardless, the possibility of a basal, or near basal placement for the Cetopsidae within the Siluriformes contrasts sharply with previous concepts of the family as a highly specialized group of catfishes (e.g. Chardon, 1968). In most of the literature, this degree of specialization was interpreted as evidence of a deeply internested, distal position of the family within the Siluriformes. While there is little question that the Cetopsidae has had an extensive history of phylogenetic divergence and is a long branch within the evolution of catfishes, neither of these facts has bearing on the phylogenetic position of the family within the Siluriformes.

Character variation informative at the relevant levels of universality, on the other hand, reveals several characters in which the Cetopsidae are primitive relative to nearly all other Recent groups in the Siluriformes. Such characters include the large foramen between the lateral ethmoid and the orbitosphenoid (Character 27), the presence of a double row of gill rakers on the first ceratobranchial (Character 77), the presence of a normal intervertebral disc between the fifth centrum and the complex centrum (Character 87), and the lack of interdigitating sutures between the contralateral coracoids (Character 103). All of these four conditions are plesiomorphic within the Otophysi. Within the Siluriformes, these features are otherwise also present in the Diplomystidae and in very few, or no, other taxa across the Siluriformes. Additionally, most of those few other cases of occurrence of these features outside the Cetopsidae and Diplomystidae probably represent reversals in that they occur in taxa deeply internested within other clearly monophyletic subgroups of the Siluriformes. Another putatively primitive, albeit less exclusive, character state has been noticed in the past to be present within the Cetopsidae in the Cetopsinae. The presence of six hypurals in the caudal skeleton of the Cetopsinae

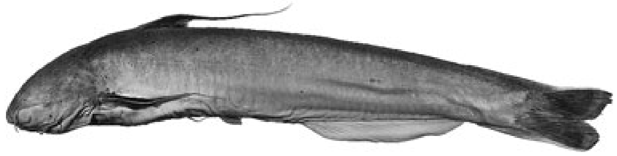

Figure 38. *Cetopsis candiru*, FMNH 112635, mature male, 194 mm SL; Peru, Loreto, Río Pastaza basin.

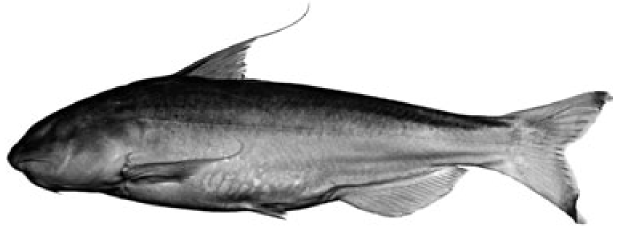

Figure 39. *Cetopsis coecutiens*, MCNG 5262, 216 mm SL; Venezuela, Apure, Río Sarare.

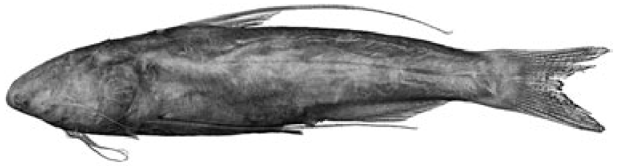

Figure 40. *Cetopsis oliveirai*, MUSM 9033, 30.6 mm SL; Peru, Madre de Dios, Palma Real.

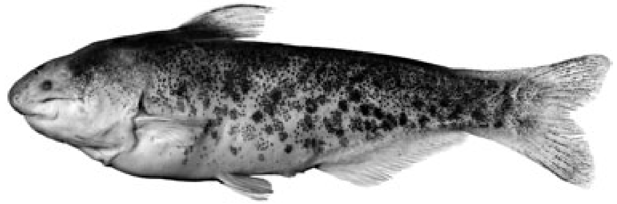

Figure 41. *Cetopsis sandrae*, MZUSP 83227, female, 75 mm SL; Brazil, Mato Grosso, Nova Mutum.

(Lundberg & Baskin, 1969: 13, 42) is the only such case among Neotropical components of the Siluriformes other than for the Diplomystidae. That character may also provide indirect support for the basal position of the Cetopsidae in the Siluriformes.

The Cetopsidae share other synapomorphies with the clade composed of other non-diplomystid catfishes, such as the lack of maxillary teeth (Character 3), the lack of cartilaginous tips at the uncinate processes of epibranchials 3 and 4 (Character 71), the lack of a second pharyngobranchial (Character 76) and the presence of 17 or fewer principal caudal-fin rays (Character 118; see other characters in Fig. 32). Those characters corroborate the widely accepted position of Diplomystidae as the sister group to all other members of the Siluriformes.

The sum of the evidence analysed herein supports the Cetopsidae as the sister group to all Recent non-diplomystid catfishes. As such, the Cetopsidae is relevant in assessing conditions primitive for the Siluriformes and, thus, particularly important in resolving relationships of the order. Also, the position of the fossil and possibly basal †Hypsidoridae (Grande, 1987) needs to be scrutinized in the context of the additional characters utilized in this and other recent analyses.

PHYLOGENETIC BIOGEOGRAPHY OF THE CETOPSIDAE

Our ability to propose a comprehensive hypothesis involving the historical biogeography of the Cetopsidae is limited by two factors: the incomplete species-level coverage in the phylogeny due to the unavailability of cleared and stained specimens of various species, and the incomplete resolution of the intrageneric phylogenies of *Cetopsidium* and *Cetopsis*. These limitations notwithstanding, the phylogenetic hypothesis of relationships within the Cetopsidae generated in this study does yield insights as to minimum ages for the major intrafamilial cladogenic events.

All species of the Helogeninae (Vari & Ortega, 1986) along with *Cetopsidium* and *Denticetopsis*, the sequentially basal genera in the Cetopsinae (Fig. 32), are limited to Cis-Andean drainage systems. The sister group to *Denticetopsis*, the clade consisting of *Cetopsis* and *Paracetopsis*, alternatively includes both Cis- and Trans-Andean species. Species of *Paracetopsis* are endemic to Pacific Ocean versant drainages from northern Peru to northern Ecuador (Vari *et al.*, 2005: fig. 55). *Cetopsis*, although a predominantly Cis-Andean genus with 15 species in that region, also encompasses six Trans-Andean endemic species that inhabit Caribbean or Pacific versant drainages from northern Ecuador to northern Colombia (Vari *et al.*, 2005: figs 12, 19, 25, 33). Each of the two major clades within *Cetopsis* (Fig. 32) includes some Trans-Andean species. In the first of these clades, *Cetopsis othonops* of the Trans-Andean Río Magdalena basin is the sister species to seven species with distributions in various portions of Cis-Andean South America. The second clade within *Cetopsis* consists of eight species, with the basal five species (*C. amphiloxa*, *C. motatanensis*, *C. baudoensis* and *C. fimbriata*) inhabiting Trans-Andean basins and the remaining species being all Cis-Andean.

Members of both the Helogeninae and the Cetopsinae are inhabitants of lowland drainages and less commonly of mid-elevation upland rivers. As such, the uplift of the Andean Cordilleras is the likely vicariant event dividing the ancestral components of the Cetopsidae into Cis- and Trans-Andean components. Given that both major clades within *Cetopsis* include taxa on each side of the Andes, this distribution pattern indicates that each of these intrageneric clades was in existence prior to the major uplift of that mountain chain and the resultant separation of the lowland ichthyofaunas to each side of the cordilleras. It follows directly that clades arising at progressively more inclusive nodes within the phylogeny of the Cetopsidae (the ancestors of, respectively: *Cetopsis*, the clade consisting of *Cetopsis* and *Paracetopsis*, *Paracetopsis*, *Cetopsidium*, *Denticetopsis*, the Cetopsinae, and the Cetopsidae) of necessity also evolved prior to this isolation of the components of the Cetopsidae to each side of the uplifting Cordilleras.

The specific geological event associated with final vicariance into Cis- and Trans-Andean components of the Cetopsidae cannot be identified, but the minimum age for that event would be the closure of the Maracaibo-Falcon outlet of the Río Orinoco approximately eight million years ago during the final uplift sequence of the northern portions of the Andean Cordilleras (Lundberg *et al.*, 1998: 40, fig. 20). With the exception of *Cetopsis motatanensis*, an endemic to the Lago Maracaibo basin, all Trans-Andean species in the Cetopsidae occur, however, in drainages that lie west of the central and western Cordilleras, all of which were uplifted prior to the closure of the Maracaibo-Falcon outlet. The most recent and, thus, pertinent of those major uplift events involved the Sierra de Perija that lies between the Lago Maracaibo basins and the rivers positioned further to the west. These uplands formed approximately 11.8 million years ago as evidenced by the westward shifts of the palaeocurrents within what is now the Río Magdalena valley (Lundberg *et al.*, 1998: 37). As such, the formation of the Sierra de Perija 11.8 million years ago represents a minimum age for the Cetopsidae, the ancestors of the Helogeninae, the Cetopsinae, *Cetopsidium*, *Denticetopsis*, the clade consisting of *Cetopsis* and *Paracetopsis*, *Paracetopsis*, *Cetopsis*, and the two major clades within *Cetopsis*.

Although a few species deeply interested within the phylogeny of *Cetopsis* demonstrate pronounced differences in overall morphology relative to their congeners (e.g. *C. candiru*, *C. coecutiens*, *C. oliveirai*), the other species of the genus to the two sides of the Andes share very similar bauplans (see figures in Vari *et al*., 2005). These biogeographical conclusions indicate that the basic bauplan of the Cetopsidae that typifies most members of *Cetopsis* extends back at a minimum 11.8 million years. Hypotheses of comparable long-term morphological stasis for other groups of South American freshwater fishes have been proposed either on the basis of fossil evidence (e.g. the characiform genus *Colossoma*; Lundberg, Machado-Allison & Kay, 1986) or the present distribution of extant taxa to the two sides of the Cordilleras (e.g. Prochilodontidae; Castro & Vari, 2004: 68). Such morphological stasis may be general for multiple components of the Neotropical freshwater ichthyofauna.

The age of separation for the Cetopsidae from the remainder of the Siluriformes with the exception of the Diplomystidae, however, may vastly exceed the 11.8 million years proposed as the minimum age for that family. A much older time of separation of those lineages is suggested by the hypothesized position of the Cetopsidae as the sister group to all other members of the Siluriformes except the Diplomystidae (see Phylogenetic Position of the Cetopsidae, above). That phylogenetic position implies that the vicariant event that separated the Cetopsidae from their sister group must have preceded the differentiation of nearly all other families of the Siluriformes. There are few catfish clades which are correlated with benchmark geological events that may provide a temporal estimate for that vicariant event. Perhaps the best component available for this purpose is the separation between the African Mochokidae and Neotropical Doradoidea (Doradidae and Auchenipteridae, the latter including Ageneiosidae and Centromochlidae of some previous authors), a division that is commonly regarded as correlated with the separation of and drifting apart of Africa and South America. This places the separation of these taxa at a minimum 112 million years ago (Lundberg *et al*., 1998: 52, 60).

Interestingly, none of the currently known fossils clearly assignable to the Siluriformes approaches that age. The oldest catfish remains are from the late Cretaceous (Maastrichthian) that were deposited maximally 73 million years ago (Gayet & Meunier, 1998: 97–100). Particularly striking, however, is the fact that some of the oldest catfish fossils belong to relatively distal clades within the Siluriformes. *Corydoras revelatus*, a fossil taxon deeply nested within the phylogeny of the Neotropical Loricarioidea and the family Callichthyidae (Reis, 1998: 352), comes from Palaeocene deposits laid down 58.5 million years ago (Lundberg *et al*., 1998: 61; Reis, 1998: 357). Other Cretaceous catfish remains also demonstrate well-defined diagnostic characters either for the entire Siluriformes or for major subgroups thereof (Lundberg *et al*., 1998: 59). Catfishes also clearly demonstrate the large gaps that exist in the fossil record, particularly for freshwater fishes. For example, although the Diplomystidae are hypothesized to be the sister group to a clade consisting of all other catfishes, both living and fossil, that family is not known from any convincing fossil occurrences. All such data point to an age of differentiation for the deep catfish lineages that is much older than indicated by the age of the currently dated fossils assignable to the order.

Geographical distribution also agrees with the presumed antiquity of basal branches within the Siluriformes. The clade composed of all members of that order with the exception of the Cetopsidae and Diplomystidae is virtually cosmopolitan. A Pangean distribution consequently seems probable for the group unless we assume major transoceanic dispersal, an apparently unlikely event for a group of largely freshwater fishes. This would push the age of the Siluriformes and its basal cladogenic events (Diplomystidae and Cetopsidae vs. the remainder of the order) into the middle Jurassic, 180 million years ago (Golonka & Bocharova, 2000: 53–54; Golonka & Ford, 2000: 24). Although such dates are far older than the earliest known occurrence of the Siluriformes in the fossil record, they do seem reasonable in view of the degree of differentiation and phylogenetic position within the order of the oldest known catfish fossils from the late Cretaceous and early Palaeocene.

MINIATURIZATION, GIGANTISM, AND PHYLOGENETIC SIGNAL

The hypothesis of the monophyly of the clade composed of *Cetopsis coecutiens*, *C. candiru* and *C. oliveirai* is among the most interesting results of this study given that the each of these species is autapomorphy-rich, a situation that resulted in each being previously assigned to its own monotypic genus (*Cetopsis*, *Hemicetopsis* and *Bathycetopsis*, respectively). Additionally, the clade is striking because it includes two of the largest known species of the Cetopsidae (*C. coecutiens* and *C. candiru*) and one of the smallest (*C. oliveirai*). Notwithstanding the pronounced degree of autapomorphic and phenetic divergence in each of these species, the monophyly of the clade formed by *C. candiru* (Fig. 38), *Cetopsis coecutiens* (Fig. 39) and *C. oliveirai* (Fig. 40) is well corroborated within this analysis (Fig. 33).

Cetopsis oliveirai is judged to be a paedomorphic species as attested to by its small size and thinly ossified bones, traits that are often present in paedomorphic species of various groups of fishes (Weitzman & Vari, 1988). The similarity in general aspect between adults specimens of *C. oliveirai* (Fig. 40) and juveniles of *C. coecutiens* is striking (see below). However, juveniles of *C. candiru* of a comparable small body size are, unfortunately, unknown. Such a sister group relationship between a miniaturized species and forms of large body size is a most unusual situation in fishes. More typically in bony fishes, miniaturization and gigantism are gradual events that progressively develop across a phylogeny, with each extreme being the end result of a long series of lineages that gradually increase or decrease in body size (de Pinna, 1996). The case with *C. coecutiens*, *C. candiru* and *C. oliveirai* seems rather to involve a phylogenetically abrupt event of miniaturization in *C. oliveirai* combined, to a degree, with the occurrence of gigantism in *C. coecutiens* and *C. candiru*. It is, however, possible that the apparent dramatic shift in body sizes between these species reflects a temporal sampling artefact. The pronounced morphological divergence among these three species is presumably indicative of a long history of phylogenetic differentiation which was unlikely to have occurred in the absence of cladistic diversification. Extinction probably eliminated the relevant intermediate lineages and resulted in apparent abrupt changes in body size that characterize the Recent representatives of the clade consisting of *C. coecutiens*, *C. candiru* and *C. oliveirai*.

Examination of a juvenile specimen of *C. coecutiens* reveals various similarities with *C. oliveirai* that are not evident in adults of the former species. Most revealing among those is the structure of the suspension of the upper jaw. Adult specimens of *C. oliveirai* (Fig. 42) and juveniles of *C. coecutiens* (Fig. 43) have a unique degree of development of the ventral lamina of the mesethmoid; a process which forms a large horizontal platform anterior to, and continuous with, the premaxillae. This structure disappears entirely in adults of *C. coecutiens* in which the mesethmoid is restricted to its median component and furthermore completely lacks the cornua and ventral lamina. These restructurings of the mesethmoid in adults of *C. coecutiens* are similar to those that are present in adults of *C. candiru*, and are considered to be synapomorphies for these two species (Character 50 above). The peculiar dental specializations of *C. coecutiens* and *C. candiru* are entirely absent in juveniles of *C. coecutiens*, which have simple conical teeth that are identical to those of adults of *C. oliveirai*.

While the monophyly of the group composed of *Cetopsis oliveirai*, *C. coecutiens* and *C. candiru* is well corroborated in this study, the hypothesized sister-group relationship between *C. coecutiens* and *C. candiru* may be artefactual, being the result of comparison among widely divergent semaphoronts resulting from the pronounced paedomorphosis in *C. oliveirai*. Many of the synapomorphies observed between *C. coecutiens* and *C. candiru* are absent in juveniles of *C. coecutiens* of a size comparable with the adult body size of *C. oliveirai*. Only a detailed anatom-

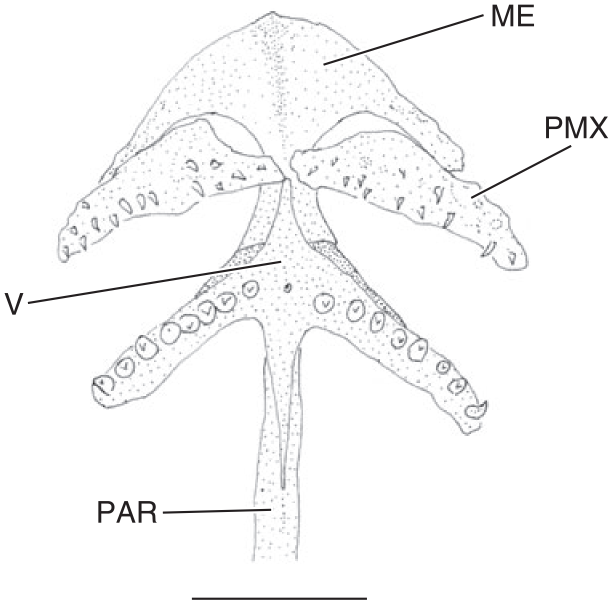

Figure 42. Ethmoid region and associated structures in *Cetopsis oliveirai* (MZUSP 79338). Ventral view. Anterior to top. Scale bar = 1 mm.

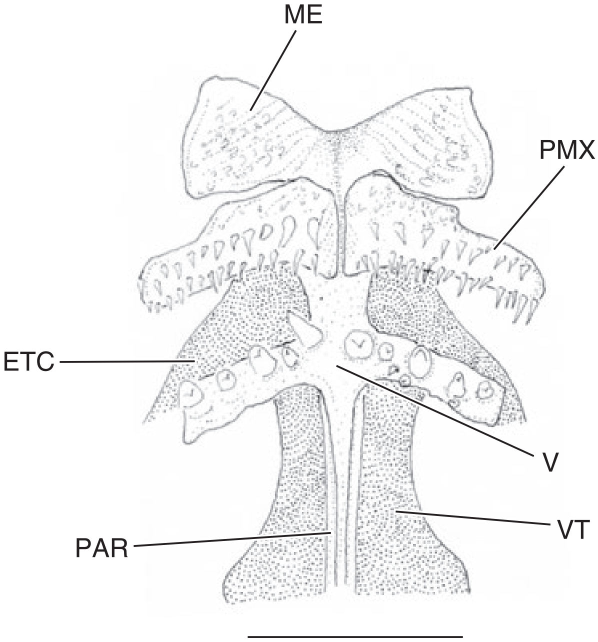

Figure 43. Ethmoid region and associated structures in juvenile specimen of *Cetopsis coecutiens* (LACM 43102-3). Ventral view. Anterior to top. Scale bar = 1 mm.

ical comparison among similar-sized specimens of the three species can resolve this question. That exercise is currently impossible because small juveniles of *C. candiru* have not been located in museum collections.

In order to examine the effect that different semaphoronts can have in our phylogenetic hypothesis with the data at hand, we performed an analysis in which *Cetopsis coecutiens* was represented by data from a juvenile specimen rather than an adult individual as was the case in the overall phylogenetic analysis. This juvenile of *C. coecutiens* is of a body size similar to that of adult specimens of *C. oliveirai*. After recoding of all characters, parsimony analysis places *C. coecutiens* and *C. oliveirai* as sister groups, rather than resulting in a sister group relationship between *C. candiru* and *C. coecutiens*. Most, but not all, of the changes in coding were derived from attributes of jaw and vomerine dentition, since juveniles of *C. coecutiens* lack the highly specialized cutting dentition characteristic of adults of that species, a specialization that is shared with adults of *C. candiru*. While these results do not prove that *C. coecutiens* and *C. oliveirai* are sister groups, they do show that most, perhaps all, of the support for the monophyly of the clade consisting of *C. coecutiens* plus *C. candiru* is sensitive to paedomorphosis. Once the effects of divergent heterochronic parameters are rescaled, it is possible that *C. coecutiens* and *C. oliveirai* will be demonstrated to be sister species.

ACKNOWLEDGEMENTS

Research associated with this project was funded by the Neotropical Lowlands Research Program of the Smithsonian Institution (to R.P.V.), the Herbert R. and Evelyn Axelrod Chair in Systematic Ichthyology in the Division of Fishes, Smithsonian Institution (to R.P.V.), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #301082 and 3057i3/2003-5 to M.C.C.d.P.), the Fundação de Amparo à Pesquisa no Estado de São Paulo (FAPESP #99/09781-6 to M.C.C.d.P.) and National Science Foundation (DEB-9903533 to M.C.C.d.P.; DEB-0315963 to C.J.F.). We thank the following individuals and institutions for the loan of specimens, hospitality of various forms during visits, and diverse other assistance: M. L. J. Stiassny, B. Brown and S. A. Schaefer (AMNH); W. Saul (ANSP), D. Catania (CAS); M. A. Rogers (FMNH); L. Rapp Py-Daniel (INPA); J. A. Siegel (LACM); R. Barriga (MEPN); H. Ortega and F. Chang (MUSM); S. O. Kullander and E. Åhlander (NRM), and G. H. Burgess (UF). C. Moreira (MZUSP) provided assistance with phylogenetic software and graphics programs during the final stage of manuscript preparation, including the preparation of Figures 32 and 33. Special thanks go to S. J. Raredon (NMNH) who prepared digital versions of, edited and labelled the anatomical illustrations. The initial phases of the present study were facilitated by specimens prepared by J. Maia whose study of the Cetopsinae was terminated due to non-scientific reasons. This paper benefitted from the comments of L. Grande (FMNH) and an anonymous reviewer.

NOTE ADDED IN PROOF

Recent work based on molecular data (Sullivan, Lundberg & Hardman, 2006) has challenged the position of Diplomystidae as sister group to remaining siluriforms. In that study, such position is occupied by the suborder Loricarioidei, with diplomystids as the next sister group to remaining siluriforms. That proposal diverges from nearly all previous work on catfish relationships, and still needs independent evaluation. If confirmed, it will result in a different rooting assumption for the present study (it would be in *Nematogenys*, only loricarioid representative included). Such different rooting, however, would not imply changes in relationships here inferred for the ingroup.

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APPENDIX 1: MATERIAL EXAMINED

The number following the catalogue number indicates the number of cleared and stained specimens in the lot, a number which is typically less than the total number of specimens in the series. Parenthetical information indicates whether the specimen(s) forms part of the type series of the species, the nature of the skeletal preparation and the range of standard lengths of that material. Specimens cleared and stained only for bone are indicated by B, those cleared and counterstained for cartilage and bone are indicated by C&B, and dry skeletons are labelled as S. The final component under each entry is the locality information for each lot.

CETOPSIDAE

CETOPSINAE

Cetopsidium ferreirai Vari, Ferraris, and de Pinna, INPA 6501, 1 (paratype, C&B, 37 mm); Brazil, Pará, Rio Trombetas, Cachoeira Porteira.

Cetopsidium morenoi (Fernández-Yépez) INHS 69416, 1 (C&B). Venezuela, Río San Bartolo (8°03′N, 66°42′W).

Cetopsidium orientale (Vari, Ferraris, and Keith), USNM 226147, 2 (C&B, 21–21 mm), and MZUSP 79285, 1 (C&B, 22 mm); Suriname, Nickerie District, stream near Camp Anjoemara.

Cetopsidium pemon Vari, Ferraris, and de Pinna, UF 26156, 2 (C&B, 25–27 mm); Colombia, Meta, Río Yucao, 13.5 km from Puerto Gaitan.

Cetopsidium sp. FMNH 45708, 1 (C&B, 27 mm); Venezuela, Bolivar, Chimanta-Tepui, Río Abacapa, camp 1, altitude 1300 m.

Cetopsis amphiloxa (Eigenmann), MEPN 85-140, 1 (C&B, 80 mm); Ecuador, Esmeraldas, Estero Sabalera, tributary to Río Bogota, Río Santiago basin.

Cetopsis arcana Vari, Ferraris, and de Pinna, MZUSP 55965, 1 (paratype, C&B, 85 mm), Brazil, Goiás, sumidoro of Rio da Lapa, Parque Estadual de Terra Ronca. MZUSP 41492, 2 (C&B, 35–43 mm); Brazil, Mato Grosso, upper Rio Araguaia, Córrego do Mato, fazenda Córrego do Mato.

Cetopsis baudoensis (Dahl), NRM 31747, 1 (C&B, 77 mm), Colombia, Choco, Río Baudó drainage, Boca de Pepé, various tributaries and river close to village (5°04′N, 77°03′W).

Cetopsis candiru Spix and Agassiz, MZUSP 6272, 1 (B, approximately 120 mm); Brazil, Amazonas, Rio Solimões, above Ilha Iauara. MZUSP 24688, 1 (B, approximately 185 mm); Brazil, Amazonas, Tapuru, Rio Purus. MZUSP 48102, 3 (C&B, 82–130 mm); Brazil, unspecified locality.

Cetopsis coecutiens (Lichtenstein), LACM 43102-3, 1 (C&B, 21 mm); Venezuela, Río Orinoco, bottom of river channel near Islote de Fajardo. MZUSP 23354, 1 (B, 113 mm); Brazil, Amazonas, Fonte Boa, igarapé in Jacaré, near Fonte Boa. MZUSP 23975, 1 (B, 145 mm); Brazil, Pará, Engenho de Santo Antônio, Furo de Panaquera. MZUSP 24177, 1 (B, disarticulated); Brazil, Pará, Rio Tocantins, in front of Tucuruí. MZUSP 38765, 2 (C&B, 107–128 mm); Brazil, Amazonas, Rio Negro, near mouth of Rio Cuieras. MZUSP 83336, 3 (22–25 mm); Brazil, Amazonas, Rio Amazonas, 29.8 km downstream from mouth of Rio Madeira.

Cetopsis fimbriata Vari, Ferraris, and de Pinna, USNM 257763, 1 (C&B, 84 mm); Colombia, quebrada tributary of upper Río Nercua. USNM 372826, 2 (paratypes (C&B, 73–87 mm); Colombia, Choco, upper Río Nercua, Río Truando system.

Cetopsis gobioides (Kner), MZUSP 22762, 1 (C&B, 106 mm); Brazil, Minas Gerais, Alfenas, Rio Cabo Verde. MZUSP 22945, 1 (B, 77 mm); Brazil, São Paulo, Pirassununga, Rio Mogi-Guaçu, Emas. MZUSP 23091, 1 (B, 61 mm); Brazil, São Paulo, Ilha Solteira, Rio Paraná. MZUSP 24455, 1 (B, 41 mm); Brazil, Mato Grosso do Sul, Ilha Solteira, Rio Paraná, Ilha Solteira. MZUSP 38808, 1 (B, 85 mm); Brazil, São Paulo, Rio Turvo, tributary of Rio Grande, near São José do Rio Preto. MZUSP 39599, 1 (C&B, 98 mm) and MZUSP 40217, 1 (C&B, 78 mm); Brazil, Minas Gerais, Córrego Água Limpa, tributary of Rio Abaeté along highway between Quirinos and Major Porto. MZUSP 38564, 1 (C&B, 71 mm); Brazil, Mato Grosso, Rio Araguari, Salto de Nova Ponte, Município de Nova Ponte.

Cetopsis montana Vari, Ferraris, and de Pinna, LACM 41735-1, 1 (C&B, 21 mm); Peru, Amazonas, Río Santiago, Pinglo. LACM 41736–1, 2 (1 C&B); Peru, Amazonas, Río Marañon at El Pongo.

Cetopsis motatanensis (Schultz), USNM 121269, 1 (paratype, C&B, 77 mm); Venezuela, Lago Maracaibo basin, Río Motatan, near bridge 22 km N of Motatan.

Cetopsis oliveirai (Lundberg and Rapp Py-Daniel), MZUSP 79338, 1 (C&B 33 mm); Brazil, Amazonas, Rio Solimões, 5.4 km below Paraná de Javarimirim; MZUSP 79337, 1 (C&B, 33 mm). Brazil, Amazonas, Rio Solimões, 17.8 km below Lago Amori.

Cetopsis orinoco (Schultz), MCNG 5375, 1 (C&B, 69 mm); Venezuela, Río Mitiado-seco.

Cetopsis othonops (Eigenmann), USNM 76972, 1 (C&B, 82 mm); Colombia, Apulo [now Rafael Reyes].

Cetopsis pearsoni Vari, Ferraris, and de Pinna, MZUSP 27812, 1 (paratype, C&B, 59 mm); Bolivia, Beni, Río Mamoré, Chapare, Villa Tunari.

Cetopsis plumbea Steindachner, MUSM 4201, 1 (C&B, 71 mm); Peru, Madre de Dios, Manu, Parque Nacional Manu, Pakitza, Quebrada Pachiya.

Cetopsis sandrae Vari, Ferraris, and de Pinna, MZUSP 61051, 1 (paratype, C&B, 46 mm); Brazil, Mato Grosso, Nova Mutum, unnamed córrego, Fazenda Buriti, approximately 1.5 km S of Fazenda.

Denticetopsis epa Vari, Ferraris, and de Pinna, MZUSP 83228, 4 (1 paratype, B, 45 mm and 3 paratypes B & C, 27–44 mm); Brazil, Pará, Baião, Igarapé do Limão, Rio Tocantins. MZUSP 24183, 2 (paratypes, 1B, 34 mm, and 1C&B, 35 mm); igarapé #5, km 5 on road from Tucurí to Mato Grosso.

Denticetopsis macilenta (Eigenmann), AMNH 55332 SW, 2 (C&B, approximately 29–32 mm); Guyana, Kartabo (6°23′N, 58°41′W).

Denticetopsis praecox (Ferraris and Brown), AMNH 74449, 1 (paratype, C&B, 43 mm); Venezuela, Amazonas, Río Baria basin, tributary of Río Mawarinuma at Neblina base camp.

Denticetopsis sauli Ferraris, ANSP 161432, 2 (paratypes, 1 B, 21 mm, and 1 C&B, 20 mm); Venezuela, Amazonas, outflow stream from series of morichales, *c*. 5.0 km from mouth of Río Pamoni (2°48′N, 65°53′W).

Denticetopsis seducta Vari, Ferraris, and de Pinna, MZUSP 37813, 5 (2 B, 36–38 mm, and 3 C&B, 27–34 mm); Brazil, Mato Grosso, Aripuanã, Igarapé Ingazeiro, 20 km above mouth of Canumã on Rio Aripuanã, below Dardanelos.

Paracetopsis bleekeri Bleeker, AMNH 97234, 1 (C&B, 94 mm); no locality data.

Paracetopsis esmeraldas Vari, Ferraris, and de Pinna, MZUSP 22328, 1 (B, 58 mm); Ecuador, Esmeraldas, Río Esmeraldas basin, Río Blanco, 4 km above its confluence with Río Quinindé.

HELOGENINAE

Helogenes castaneus (Dahl), MZUSP 63091, 2 (C&B, 35–37 mm); Colombia, Meta, Caño Emma, Finca El Viento, *c*. 33.5 km NE of Puerto Lopez (4°08′ ”N 72°39′W).

Helogenes marmoratus Günther, AMNH 7113 SW, 1 (B, 37 mm); Guyana, Holmia. AMNH 13332 SW, 1 (B); Guyana, Rockstone. MZUSP 23858, 2 (C&B, 31–40 mm); Brazil, Pará, Igarapé Caranandéua, Rio Capim. MZUSP 40235, 1 (B, 58 mm); Brazil, unspecified locality.

AUSTROGLANIDIDAE

Austroglanis barnardi (Skelton), MZUSP 62630, 1 (C&B, 54 mm); South Africa, Western Cape, Noordhoeks River.

BAGRIDAE

Bagrus bayad (Forsskål), USNM 229884, 1 (C&B, 111 mm); Nigeria, Sokoto-Rima floodplain at Sokoto.

DIPLOMYSTIDAE

Olivaichthys mesembrinus (Ringuelet), MZUSP 62595, 1 (C&B, 150 mm); Argentina, Chubut, Los Altares, Río Chubut.

ICTALURIDAE

Noturus flavus Rafinesque, MZUSP 62603, 1 (C&B, 102 mm); USA, Michigan, Washtenaw, Huron River.

MALAPTERURIDAE

Malapterurus sp. MZUSP 62600, 3 (1 C&B, 102 mm); Cameroon, upper Ndian River bordering Korup.

NEMATOGENYIDAE

Nematogenys inermis (Guichenot), CAS 12692, 1 (C&B, 164 mm); Chile, Santiago market.

PIMELODIDAE

Pimelodus ornatus Kner, MZUSP 79770, 2 (C&B, 102–125 mm); no data.

APPENDIX 2: CHARACTER STATE MATRIX

Character matrix for 127 characters for the examined species of the Cetopsidae and outgroups. Character numbers correspond to those in the text.

	Character												
										1	1111111111	1111111111	1111111
	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001	1111111112	2222222
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Outgroups													
Olivaichthys mesembrinus	0000000000	0000000000	0000000000	0000100000	00000?0000	0000000000	0000000000	0000000000	0000000000	00000?0?00	0000001000	00??000000	0000000
Austroglanis barnardi	0010000000	1111000000	0000001000	0000011??0	0000000100	0000000000	0000000000	1000111000	1000011001	0000?0?000	0010000010	00??000100	0000001
Bagrus bayad	0010000000	1101000000	0000001000	00000100?0	0000000100	0000000000	0000000000	1001011000	1000011001	0000000100	0010000000	00??000100	0000000
Nematogenys inermis	0010000000	0010000000	0000001000	0010??1??0	00000?0100	00001000?0	0000001000	1000111000	10000?112?	?00?????00	0001211100	00??000100	0100002
Noturus flavus	0010000000	1101000000	0000001000	0000??1??0	0000000100	0000000000	0000000000	1000111000	1000011001	0000000100	0010000000	00??000000	0000001
Pimelodus ornatus	0010000000	1101000000	00000010?1	0000011??0	0000000100	000000000?	0000000000	1000111000	1000011001	000?000?00	0010000000	?0??000100	0000000
Cetopsidae													
Helogenes marmoratus	0110010110	0010100100	0112100000	1001000000	0000001110	?000000000	0011001100	1000110000	0000000000	?111000001	0001211000	00??000100	0000000
Helogenes castaneus	0110010110	0010100100	0112100000	1001000000	0000001110	?000000000	0011001100	1000110000	0000000000	1111000001	0001211000	00??000100	0000000
Cetopsidium ferreirai	0?11001000	0010111000	1111100000	0000000010	0000000100	0100000000	0010100010	10001101??	?1?0000000	0000000000	010000001?	??0?202110	?100002
Cetopsidium morenoi	0111001000	0010111000	1111100000	0000000010	0000000100	0100000000	0??0100010	1000110100	1100000000	0000000000	0100000011	0200102111	1100002
Cetopsidium orientale	0111001000	0010111000	1111100000	0000000010	0000000100	0100000000	0000100000	1000110100	1100000000	0000000000	0100000011	0200202111	1100002
Cetopsidium pemon	0111001000	0010111000	1111100000	0000000010	1000000100	0100000000	0000100010	1000110100	1100000000	0000000000	0100000011	0200202111	1100002
Cetopsidium sp.	1111001000	0010111000	1111100000	0000000010	1000000100	0100000000	0000100010	1000110100	1100000000	0000000000	0100000011	0200202111	1100002
Denticetopsis epa	1111001001	0010211110	1111110100	0110000011	1010000100	0100000100	0000010000	1100110101	1110110110	1001000001	0101001101	1200211110	0100011
Denticetopsis macilenta	0111001001	0010211110	1111100100	0010000010	1010000100	0100000100	0000010000	1100110101	1100110110	1001000001	0101001101	1200211110	0100011
Denticetopsis praecox	1?11001001	0010211110	1111100100	0110000011	1010000100	0100000100	0000010000	1100110101	1110010110	1001000001	0101001101	1200211110	0100011
Denticetopsis sauli	2111001001	0010211110	11111?0000	0010001???	1010000100	01000001?0	0000010010	1000110001	0110110110	1011000001	0101001001	1200211120	0100002
Denticetopsis seducta	1111001001	0010211110	1111100100	0110000011	1010000100	0100000100	0000010000	1100110101	1100010110	1001000001	0101001001	1200211110	0100011
Paracetopsis bleekeri	0111001000	0010211000	1111100010	0010100010	0001010100	0111000100	0110000000	1100110100	1100010110	1001010001	01010100?1	0200202101	1100000
Paracetopsis esmeraldas	0?11001000	0010211000	1111100010	0010100010	0001010100	0111000100	0110000000	1100110100	?100010110	1001010001	0101010001	0?0020210?	?100000
Cetopsis amphiloxa	0111001000	0010211000	1111100100	0010010020	0011000100	1100001110	0110000000	1100110100	1100010111	1001000001	1101010001	0200202110	0110000
Cetopsis arcana	0110001000	0010211000	1111100100	0110010020	0000000100	01000?1110	0110000000	1100110100	1100010113	1001001111	0101010011	0211202111	1110000
Cetopsis baudoensis	0112001000	0010211000	1111100101	0110010030	0000000100	0100001110	0110000000	1100110100	1100010112	1001000001	0101010011	0210202111	1110000
Cetopsis candiru	0113201000	0010211000	1111100111	0010010130	0100000101	1100101110	0110000000	1110110010	1101010121	1001000011	1101111011	010?100101	1120100
Cetopsis coecutiens	0113101000	0010011000	1111100111	0110010130	0100000101	0100101211	?110000000	1111110010	1101010121	1001101001	1101010011	0200102102	1111100
Cetopsis fimbriata	0112001000	0010211000	1111100111	0110010030	0000000100	0100001210	0110000000	1100110100	1100010111	1001001001	1101010011	0200202111	1110000
Cetopsis gobioides	0111001000	0010211000	1111100100	0110010020	0000000100	0100011110	0110000000	1100110100	1100010113	1001001111	0101010011	0211202101	1110000
Cetopsis montana	0111001000	0010211000	11111001?0	0010010010	0000100100	0100001110	0110000000	1100110100	1100010112	1001001011	0101010011	0211202101	1110000
Cetopsis motatanensis	0111001000	0010211000	1111100110	0010010030	0001000100	0100001110	0110000000	1100110100	1100010111	1001000001	1101010011	0200202101	1110000
Cetopsis oliveirai	0112000000	0010201000	0111100100	0010010030	0000000100	0100101202	1000000000	1100110010	110001012?	1001101011	0101010111	00??102102	0111200
Cetopsis orinoco	0111001000	0010211000	1111100100	0010010010	0000000100	11000?1210	0110000000	1100110100	1100010113	1001000011	1101010011	0201202101	1110000
Cetopsis othonops	0?11001000	0010211001	1111100110	0010010010	0001000100	0100001110	0110000000	1000110100	?100010111	1001001001	0101010011	0200202111	1110000
Cetopsis pearsoni	0?11001000	0010211000	1111100100	0010010010	0001000100	0100001110	0110000000	1100110100	1100010111	1001001001	0101010011	0211202101	1110000
Cetopsis plumbea	0111001000	0010211000	1111100100	0010010020	0001000100	1100001110	0110000000	1100110100	1100010112	1001001011	0101010011	0211202101	1110000
Cetopsis sandrae	0111001000	0010211000	1111100100	0010010010	0001000100	0100001110	0?10001001	1000110100	1100010112	1001000111	0101010011	0211202101	1110000