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A phylogenetic study of the African catfish family Mochokidae (Osteichthyes, Ostariophysi, Siluriformes), with a key to genera

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ABSTRACT.—A hypothesis of phylogenetic relationships is presented for the African catfish family Mochokidae based on a maximum parsimony analysis of 93 morphological characters in 41 ingroup and 19 outgroup taxa. The analysis reveals that the Mochokidae are a monophyletic group and that *Mochokus* Joannis (1835), *Mochokiella* Howes (1980), *Acanthocleithron* Nichols and Griscom (1917) and *Microsynodontis* Boulenger (1903) are monophyletic and valid as distinct genera within the family. *Synodontis* Cuvier (1816) must include *Hemisynodontis membranacea* and *Brachysynodontis batensoda* to be monophyletic, which are reassigned to *Synodontis* herein. *Chiloglanis* Peters (1868) is rendered paraphyletic by nested placement of *Atopochilus* Sauvage (1879), *Euchilichthys* Boulenger (1900) and *Atopodontus* Friel and Vigliotta (2008), a new genus described separately in this volume. *Euchilichthys* is rendered paraphyletic by nested placement of *Atopochilus savorgnani*. The monophyly of *Atopochilus* could not be tested because only one species was available for study. *Atopodontus* is monophyletic and valid as a distinct genus. Well-supported suprageneric clades within the family include a new tribe, the Atopochilini, with *Atopodontus* as the sister group to a clade composed of *Atopochilus* and *Euchilichthys*. A clade composed of all suckermouthed species, the redefined subfamily Chiloglanidinae, includes tribe Atopochilini nested within *Chiloglanis*. Taxonomic issues related to paraphyly of *Chiloglanis* and *Euchilichthys* require further research on a greater number of taxa before being addressed. Subfamily Chiloglanidinae forms a polytomy with *Synodontis* and *Microsynodontis*. *Acanthocleithron*, followed by *Mochokiella* and then *Mochokus* are recovered as consecutive sister groups to that polytomy. A list of synapomorphies is provided for each major clade recovered, but most clades are left unnamed at this point. A number of the well-supported clades are characterized by changes in the oral jaws and mouth, apparently a key theme in mochokid evolution. Finally, the analysis suggests that the sister group of the Mochokidae is a clade composed of the South American Doradidae plus Auchenipteridae, though support for the relationship is low. Synapomorphies supporting the recovered sister group relationship and possible synapomorphies supporting alternative sister group relationships to the Malapteruridae and Amphiliidae are provided.

New taxon: Atopochilini Vigliotta.

INTRODUCTION

The Mochokidae are a family of African catfishes with nearly 200 species distributed throughout the freshwaters of tropical, sub-Saharan Africa and the Nile River basin. Best known for their presence in the pet trade, mochokids (specifically of the genus *Synodontis*) are commonly known as squeakers or upside-down catfishes. The name ‘squeaker’ is derived from the fact that *Synodontis* are capable of making a squeaking noise by stridulation of the pectoral spine against the pectoral girdle (Jubb, 1967). Stridulation noises are apparent elsewhere in the family in *Mochokiella paynei* and some members of the genus *Atopochilus* (personal observation). The name ‘upside-down catfish’ refers to the peculiar habit of some species of *Synodontis* that are known to swim upside-down. Swimming with an inverted posture is apparently correlated with feeding while upside-down at the water’s surface (Bishai and Abu Gideiri, 1965), but upside-down catfishes will rest and swim in an inverted position on a regular basis. Chapman et al. (1994) showed that an upside-down posture near the surface also facilitates respiration in

poorly oxygenated water.

The greatest diversity of mochokids occurs in the Congo River and its numerous tributaries, but they are also found in the rivers and lakes of western, southern and eastern Africa, including the Nile River basin, Lake Victoria, Lake Tanganyika and Lake Nyasa. Fossil mochokids, of the genus *Synodontis*, have been found in deposits from eastern and northern Africa dating to the early Miocene (Stewart, 2001). Fragments of pectoral spines from *Synodontis* dating from the early Oligocene have been found in Oman, an area where mochokids do not exist today (Otero and Gayet, 2001). Fossil mochokids outside of the genus *Synodontis* are presently unknown.

To date, nearly 250 species of mochokid catfishes have been described, but more than 50 of those are currently considered junior synonyms. With nearly 200 valid species and several undescribed species, the Mochokidae is one of the largest families of catfishes and by far the largest family of African catfishes. Ferraris (2007) provides the most recent list of mochokid species and synonymies (188 valid species). *Synodontis acanthopercra* Friel and Vigliotta (2006), *Chiloglanis productus* Ng and Bailey (2006) and

three species of *Synodontis* from Lake Tanganyika (Wright and Page, 2006) were described too recently to be included in that work; Wright and Page (2006) also resurrect two species of *Synodontis* from synonymy. One new genus and a number of new mochokid species are also described in this volume (Friel and Vigliotta, 2008; Friel and Sullivan, 2008). In all, nearly one third of African catfish species belong to the family Mochokidae.

The family is composed of ten genera according to Ferraris (2007). *Synodontis* Cuvier (1816), with approximately 120 species and a distribution similar to that of the family, was revised by Poll (1971). Poll's revision remains the single largest taxonomic work for the Mochokidae. *Mochokus* Joannis (1835) is limited to two species distributed throughout northern and western Africa, including the Nile River basin. *Brachysynodontis* Bleeker (1862) and *Hemisynodontis* Bleeker (1862) were erected to accommodate certain species of *Synodontis*; both genera are monotypic today. *Hemisynodontis membranacea* and *Brachysynodontis batensoda* are distributed throughout northern and western Africa, including the Nile River basin. The validity of these two genera is questionable at best and some authors have already suggested that the two species belong in the genus *Synodontis* (Günther, 1864; Willoughby, 1994; Paugy and Roberts, 2003), an opinion that is followed here. The reader should assume that references herein to *Synodontis* include these two species, unless specifically indicated. The status of *Hemisynodontis* and *Brachysynodontis* will be effectively settled in this work. *Chiloglanis* Peters (1868) consists of approximately 45 valid species with a distribution similar to that of the family (in lotic systems only, however). *Atopochilus* Sauvage (1879) consists of seven valid species from lotic systems in the Congo River basin, Lower Guinea ichthyofaunal province and eastern Africa. Similarly, *Euchilichthys* Boulenger (1900) consists of five valid species from lotic systems in the Congo River basin, though the distinction between *Euchilichthys* and *Atopochilus* has always been unclear (Pellegrin, 1938; Poll, 1959; 1967). *Microsynodontis* Boulenger (1903) consists of 11 valid species from the Congo River basin, the Lower Guinea ichthyofaunal province and western Africa. *Acanthocheilothron* Nichols and Griscom (1917) is a monotypic genus with a surprisingly large distribution throughout the Congo basin. Finally, *Mochokiella* Howes (1980) is also monotypic with a limited distribution in the coastal drainages of Sierra Leone.

In addition to these, a new genus, *Atopodontus* (Friel and Vigliotta, 2008), is described in this volume. *Atopodontus adriaensi* is a suckermouthed species that shares a number of features with species of *Chiloglanis*, but also with species of *Atopochilus* and *Euchilichthys*. The validity and placement of the genus are tested in this

work. Thus far, *Atopodontus* is known from the Ogôoué and Nyanga Rivers in Gabon.

In his classification of teleostean fishes, Regan (1911) placed mochokid genera (described to date) into their own family for the first time, the Synodontidae. He also noted the fundamental differences between suckermouthed varieties (*Chiloglanis*, *Atopochilus* and *Euchilichthys*) and the other genera (*Synodontis*, *Mochokus*, *Microsynodontis*). Regan made no mention of *Hemisynodontis* or *Brachysynodontis*. Later, Jordan (1923) proposed the family name Mochokidae because the name Synodontidae was preoccupied by a family of marine lizardfishes, though the issue was confused for decades to come. Russell (1987) provides an account of the confusion surrounding this issue.

To date a single subfamily has been proposed within the family. The name Chiloglanidinae (Riehl and Baensch, 1990) is applied to a small number of species of *Chiloglanis* in an aquarist publication, but the name is most appropriate for a group composed of all suckermouthed species. The subfamily name and the term 'chiloglanidin' will be used throughout the text to refer to a group composed of all suckermouthed species in the genera *Chiloglanis*, *Atopodontus*, *Atopochilus* and *Euchilichthys*. The putative monophyly of the suckermouthed mochokids will be tested in this work.

As with African freshwater fishes in general, phylogenetic treatments of African catfishes are rare. Beyond some recent work on the *Synodontis* of Lake Tanganyika (Koblmüller et al., 2006; Day and Wilkinson, 2006), phylogenetic treatment of the Mochokidae is practically non-existent. The application of molecular phylogenetic techniques has resulted in new hypotheses as to the placement of the Mochokidae within the Siluriformes, but relationships within the family are still unknown. A recent molecular phylogeny for the Siluriformes suggests that the Mochokidae are related to several African catfish families and that they are most closely related to the Amphiliidae and Malapteruridae (Sullivan et al., 2006). This is in stark contrast to morphological data, which suggests that the sister group of the Mochokidae is the Doradidae plus Auchenipteridae (Chardon, 1968; Ferraris, 1988; Mo, 1991; Higuchi, 1992; Lundberg, 1993; de Pinna, 1993; de Pinna 1998; Diogo, 2005). In either case, higher-level phylogenies have considered very few mochokid taxa at this point and do not provide a comprehensive picture of the family's diversity or evolutionary history.

The objectives of this research are threefold: (1) to assess the hypothesis of monophyly of known mochokid genera and to determine the phylogenetic relationships between these genera, (2) to assess the hypothesis of monophyly of the Mochokidae and (3) to determine the sister group to the Mochokidae.

MATERIALS AND METHODS

Materials and Preparations

Materials utilized in this study were prepared as cleared and stained specimens, dry skeletons, or fluid specimens. Appendix 1 lists the material examined and denotes the species, catalog number, number of specimens by each preparation type (C&S = cleared and stained, DS = dry skeleton and ALC = alcoholic, fluid specimen), country and abridged locality. Institutional abbreviations follow Leviton et al. (1985) except for the South African Institute of Aquatic Biodiversity (SAIAB).

Specimens were cleared and stained using the techniques outlined by Potthoff (1984). Generally, two specimens from the same lot were cleared and stained in order to account for some variation within a species, to examine sexually dimorphic osteological characters and to rule out anomalous features. External morphological features were examined on fluid specimens and on cleared and stained specimens when appropriate. Fluid specimens and cleared and stained specimens from the same lot were used when possible.

Because material for the genus *Acanthocleithron* is exceedingly rare, other techniques were required to glean osteological information. A paratype specimen of *Acanthocleithron chapini* (AMNH 6575) was sent to the University of Texas at Austin to undergo High-Resolution X-ray Computed Tomography. High-Resolution X-ray CT is a nondestructive technique for visualizing features in the interior of opaque solid objects and for obtaining digital information on their 3-D geometries and properties. Individual slices and video reconstructions of the three-dimensional specimen allowed for visualization of many of the internal features not otherwise accessible in this rare species.

Delimitation of Taxa

Forty-two mochokid species were examined, with at least one species from each genus in the family. The following were considered valid genera herein, with numbers of species examined in parentheses: *Acanthocleithron* (1), *Atopochilus* (1), *Atopodontus* (1), *Chiloglanis* (12), *Euchilichthys* (3), *Microsynodontis* (3), *Mochokiella* (1), *Mochokus* (2), *Synodontis* (17, including *S. membranacea* and *S. batensoda*). The large number of *Synodontis* and *Chiloglanis* species required careful selection in order to maximize the range of intrageneric morphological variation. Type species were examined for all ingroup genera except *Chiloglanis* and *Microsynodontis*. Suitable material for those species was unavailable. A small number of un-

scribed and otherwise unidentifiable species were included in the analyses because of their unique morphologies. They are referred to by an informal name (often a locality) in quotation marks.

Outgroup taxa include members of several families of catfishes, including some putatively basal groups and some hypothesized to be closely related to the Mochokidae. Nineteen species from the following families or genera were examined.

Diplomystidae – The Diplomystidae is the sister group to all other extant catfishes according to many authors (Alexander, 1965; Fink and Fink, 1981; Arratia, 1987; Mo, 1991; de Pinna, 1993). The Diplomystidae was recently established as sister to all siluroid catfishes, with loricarioids as sister to that clade (Sullivan et al., 2006). In either case, because loricarioids are not considered here, the Diplomystidae are sufficiently basal with respect to the Mochokidae and all of the other outgroups. Data for the Diplomystidae were taken from previous studies dealing with higher-level siluriform relationships (Mo, 1991; de Pinna, 1993) and the works of Arratia (1987; 1992) and Arratia and Huaquin (1995).

Ictaluridae – One phylogeny supports a close relationship between the Ictaluridae and the Mochokidae, though support is admittedly weak (Hardman, 2005). The molecular data in that work suggests that the Mochokidae are the sister group of a clade composed of the Ictaluridae plus the Cranoglanididae. *Cranoglanis* was not examined in this study.

Pangasiidae – Some members of the Pangasiidae possess an elastic spring apparatus, an obvious and diagnostic feature in many mochokids. One species of *Pangasius* was included for that reason.

Ariidae – The Ariidae is the basal group of Lundberg's (1993) 'arioid' clade, which included the Mochokidae. In addition, the Ariidae have been firmly established as the sister group to the Anchariidae (Ng and Sparks, 2005; Sullivan et al., 2006), a family endemic to Madagascar, whose members have been included in the Mochokidae (Mo, 1991). Unfortunately, material for the Anchariidae is rare and was not readily available for use in this study.

Auchenipteridae and Doradidae – These families have long been considered a potential sister group of the Mochokidae based on morphology. The affinity of the Mochokidae to these families was hypothesized at least as far back as Cuvier and Valenciennes (1840). Since the advent of cladistic methodology several authors have recovered the Doradidae and Auchenipteridae as sister to the Mochokidae (Chardon, 1968; Ferraris, 1988; Mo, 1991; Higuchi, 1992; Lundberg, 1993; de Pinna, 1993; de Pinna 1998; Diogo, 2005). The Mochokidae, Doradidae and Auchenipteridae have been collectively referred to as

'doradoids' in the recent literature.

Schilbe, Chrysichthys and Parauchenoglanis – These genera represent the families and subfamilies Schilbidae, Claroteinae and Auchenoglanidinae respectively. The 'Big Africa' clade of Sullivan et al. (2006) includes those three groups as well as the Amphiliidae, Malapteruridae and Mochokidae.

Amphiliidae and Malapteruridae – Within the 'Big Africa' clade these families were identified as potential sister groups of the Mochokidae based on molecular data (Sullivan et al., 2006). This relationship had not been previously suggested in a phylogenetic framework, though Diogo (2005) recovered the Malapteruridae as the sister to the 'doradoids.'

Phylogenetic Methodology

The phylogenetic methodology employed in this work was first proposed by Hennig (1950; 1966) and has been modified by several authors subsequently (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981; Rieppel, 1988; Swofford and Olsen, 1990; Wiley et al., 1991). Data were entered into a matrix (Appendix 2) using Mesquite, version 1.11 (Maddison and Maddison, 2006). In the matrix unknown or missing data was entered as '?' and characters that were inapplicable for a given taxon were entered as '-'; both of these were recognized as missing data and treated as such in parsimony analysis. Multistate characters were ordered only when it was reasonable to infer a priori the nature of a transformational series, with the putatively plesiomorphic state coded as state 0. The data were subjected to parsimony analysis in PAUP (Phylogenetic Analysis Using Parsimony), version 4.0b10 (Swofford, 2002).

The analysis includes 41 ingroup taxa and 19 outgroup taxa (refer to matrix, Appendix 2). Given the large number of taxa, the tree bisection-reconnection (TBR) branch-swapping heuristic search algorithm was used to recover a set of trees. Heuristic searches, like TBR, while time-efficient, do not guarantee that the recovered trees are the shortest in all of 'tree space'; they do guarantee the shortest set from the portion of tree space searched. 1,000 starting trees were obtained by random stepwise additions.

Outgroup and ingroup relationships were resolved simultaneously, using global parsimony analysis as outlined by Nixon and Carpenter (1993). The tree was rooted with Diplomystidae placed as the sister to all other extant Siluriformes (Alexander, 1965; Fink and Fink, 1981; Arratia, 1987; Mo, 1991; de Pinna, 1993) or the Siluroidei alone (Sullivan et al., 2006). To test the robustness of the trees recovered, Bremer decay indices were determined for the clades in the consensus tree. Decay indices were cal-

culated using default settings in TreeRot, v.2 (Sorenson, 1999). Calculation of bootstrap values for the TBR search was not time-efficient.

Illustrations and Terminology

Anatomical illustrations were produced digitally using Adobe Photoshop and Adobe Illustrator. Digital photographs were traced with the aid of a pressure-sensitive writing tablet. A few of the objects were traced by hand at first using a Zeiss SV8 stereomicroscope with camera lucida attachment and then converted to a digital tracing. Contour lines and stippling were added to give some effect of three-dimensionality. Solid grey areas represent cartilage in all illustrations.

Osteological terminology generally follows Diogo (2005), with the following exceptions: hyomandibula is used for his hyomandibulo-metapterygoid; metapterygoid is used for his entopterygoid-ectopterygoid; quadrate is used for his quadrato-symplectic. The implicit hypotheses of homology for the elements of the catfish suspensorium, evident in Diogo's terminology, are not widely used at this point.

Anatomical Abbreviations

The following anatomical abbreviations are used in the figures: **a.apa.car.**, anterior autopalatine cartilage; **a.fo.**, anterior fontanelle; **a.n.p.**, anterior nuchal plate; **a.n.p./m.n.p.**, anterior nuchal plate/middle nuchal plate; **a.p.e.**, anterior pterygoid element; **a.prp.c.c.**, anterior parapophysis of the compound centrum; **ahy**, anterohyal or anterior ceratohyal; **al.pr.bpt.**, anterolateral process of the basipterygia; **am.pr.bpt.**, anteromedial process of the basipterygia; **ang-art**, angulo-articular; **apa**, autopalatine; **ar.co.neuro.**, articulating condyle for the neurocranium; **ar.fa.ang-art**, articulating facet for the angulo-articular; **ar.fa.apa.**, articulating facet for the autopalatine; **ar.fa.hyom.**, articulating facet for the hyomandibula; **ar.fa.l.e.**, articulating facet for the lateral ethmoid; **ar.fa.qu.**, articulating facet for the quadrate; **asc.Mck.car.**, ascending Meckel's cartilage; **aux.dn.t.**, auxiliary dentary teeth; **bbr**, basibranchial; **bo**, basioccipital; **car.a.pr.bpt.**, cartilage of the anterior processes of the basipterygia; **cbr**, ceratobranchial; **cl**, cleithrum; **cl.pr.**, postcleithral (humeral) process; **cmk**, coronomeckalian; **cor.pr.**, coronoid process; **d.pr.cl.**, dorsal processes of the cleithrum; **d.pr.r.**, dorsal-fin proximal-middle radial; **d.sp.**, dorsal spine; **d.spt.**, dorsal spinelet; **dhy**, dorsohyal or dorsal hypohyal; **dn**, dentary; **dn.t.**, dentary teeth; **dphbr**, dermopharyngobranchial; **e.s.a.**, elastic spring apparatus; **ebr**, epibranchial; **e-ept**, ento-ectopterygoid; **epo**, epioccipital; **epu**, epural; **esc**,

extrascapular; **exo**, exoccipital; **fr**, frontal; **g.b.**, gas bladder; **h.sp.**, haemal spine; **hbr**, hypobranchial; **hor.Mck.** **car.**, horizontal Meckel's cartilage; **hpu**, hypural; **hpup**, hypurapophysis; **hyom**, hyomandibula; **hyom.pr.**, hyomandibular process; **ihy**, interhyal; **io.1-5**, infraorbitals 1 through 5; **l.e.**, lateral ethmoid; **la.cu.l.e.**, laminar curtain of the lateral ethmoid; **m.n.p.**, middle nuchal plate; **mcor.ar.**, mesocoracoid arch; **me**, mesethmoid; **mpt**, metapterygoid; **mx**, maxilla; **n.sh.**, nuchal shield; **n.sp.**, neural spine; **na**, nasal; **os.sus.**, os suspensorium; **osp**, orbitosphenoid; **p.apa.car.**, posterior autopalatine cartilage; **p.fo.**, posterior fontanelle; **p.lck.for.**, pectoral-locking foramen; **p.n.p.**, posterior nuchal plate; **p.pr.r.**, pectoral-fin proximal radial; **p.prc.c.**, posterior parapophysis of the complex centrum; **p.sp.**, pectoral spine; **pa-so**, parieto-supraoccipital (= supraoccipital); **pa-so.for.**, parieto-supraoccipital foraminal remnant; **pasp**, paraspheonid; **phbr**, pharyngobranchial; **phpu**, parhypural; **phy**, posterothyral or posterior ceratohyal; **plv.spl.**, pelvic splint; **pop**, preopercle; **pro**, prootic; **prp.5**, parapophysis of 5th centrum; **prp.6**, parapophysis of the 6th centrum; **pt**, pterotic; **pt.sp.**, pterotic spine; **pt-scl**, posttemporo-supracleithrum; **ptsp**, pterosphenoid; **pu.c.**, preural centrum; **puhy**, parurohyal; **qu**, quadrate; **r.6**, rib of the 6th centrum; **r.7**, rib of the 7th centrum; **sc-cor**, scapulo-coracoid; **sp**, sphenotic; **tr**, tripus; **urn**, uro-neural; **v.pr.me.**, ventral process of the mesethmoid; **v.pr.tsc.l.**, ventral process of the transcapular ligament; **vhy**, venterohyal or ventral hypohyal; **vo**, vomer.

CHARACTER DESCRIPTIONS

The data matrix (Appendix 2) contains 60 rows for the total number of taxa and 93 columns for as many characters, described below. This section is divided into several subsections that correspond to various osteological and morphological systems.

Each character description starts with a character number that corresponds with the numbers at the top of each column in the matrix. This is followed by a descriptive title for the character. Next, in parentheses, the consistency (CI) and retention (RI) indices are given for each character from the consensus of equally parsimonious trees. The retention index for a character, whose only transformation represents an autapomorphy, is mathematically indeterminate and is signified by 'AUT.'

After the header, each character state (**0**, **1**, **2**, **INAPPLICABLE**, etc.) is listed in a short, telegraphic form, with the distribution for each derived character state following the state itself in most instances. When distributions are complex the reader is referred to the matrix. In most cases, state 0 can be assumed to occur in all taxa not listed for the derived state(s). For derived states, when all

taxa of a higher group (genus or family) share the same state the higher-group name is listed. However, the reader should remember that the states apply to examined materials only and may not apply to all members of a higher group. When most, but not all, taxa within a higher group share the same state, the distribution is listed as 'all HIGHER GROUP except LOWER GROUP.' Each exception to the higher group is followed by a bracketed character state number to indicate which state it does show.

The telegraphic states and corresponding distributions are followed by a paragraph describing the nature of the character in the majority of the outgroup taxa (and sometimes many of the ingroup taxa), as well as the nature of the various derived states. Comments on adaptive nature and the previous use of similar characters are also included. Comments on convergences and reversals are held for the discussion, where they can be placed in the context of the resulting phylogeny.

Neurocranium, Nuchal Shield and Dorsal-fin Radials

1. Presence or absence of ventral process of mesethmoid. (CI = 1.000, RI = 1.000)

0: Mesethmoid without ventral process.

1: Mesethmoid with well-developed ventral process. (*Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, and in most of the taxa examined, the ventral surface of the mesethmoid supports the premaxillae, without any well-developed process between them (Fig. 1A–B). In *Atopodontus*, *Atopochilus* and *Euchilichthys* there is a well-developed, keel-like process on the ventral surface of the mesethmoid that sits between the premaxillae (Fig. 1C). Mo (1991) and Diogo (2005) recognized a similar process in certain loricarioids, but make no mention of this structure in the Mochokidae. A ventral mesethmoid process (in both groups) is most likely functionally correlated with relatively mobile premaxillae for conforming to and clinging to surfaces. A ventral process of the mesethmoid was not observed in any of the smaller suckermouthed mochokids of the genus *Chiloglanis*.

2. Degree of development of anterolateral cornua of mesethmoid (ORDERED). (CI = 0.333, RI = 0.879)

0: Mesethmoid with well-developed anterolateral cornua.

1: Mesethmoid with poorly developed anterolateral cornua. (*Doumea*; *Phractura*; *Doradidae*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*)

2: Mesethmoid lacking anterolateral cornua. (*Zaireichthys*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, as in the Diplostomatidae (Arratia, 1987), the anterior portion of the mes-

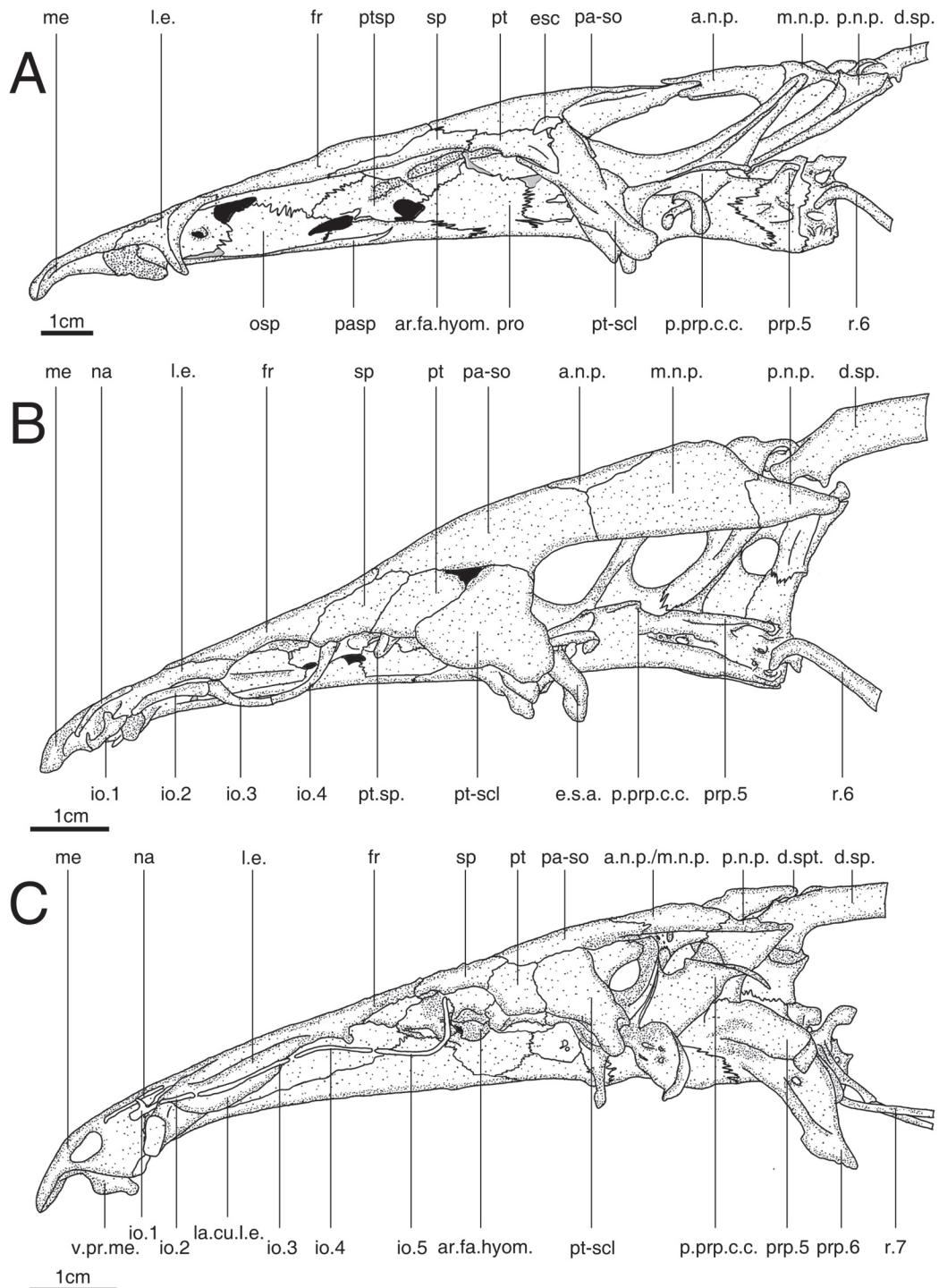


Fig. 1. Lateral view of neurocranium of A) *Ictalurus punctatus*; CU 79403, B) *Synodontis acanthomias*; CU 91613 and C) *Euchilichthys royauxi*; CU 91614. Dorsal spinelet shown in C only.

ethmoid consists of two well-developed, laterally directed cornua that can be nearly double the width of the more posterior portion of the bone (Fig. 2A). *Mochokus* and *Mochokiella* are the only mochokids with well-developed anterolateral cornua. In remaining mochokids the anterolateral cornua are reduced to various degrees. In *Acanthocleithron*, *Microsynodontis* and *Synodontis* and some outgroup taxa the cornua are poorly developed, with the anterior portion of the mesethmoid being only slightly wider than the rest of the bone (Fig. 2B); note that in the Doradidae the development of the anterolateral cornua is actually much more variable (from absent to well-developed) than reported for the taxa examined (pers. comm., Mark Sabaj Pérez). In all chiloglanidins, as well as *Zaireichthys*, the mesethmoid lacks anterolateral cornua altogether (Fig. 2C). Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

3. Relative width of dorsal and ventral portions of mesethmoid. (CI = 0.250, RI = 0.885)

0: Dorsal portion of mesethmoid as wide as ventral portion.

1: Dorsal portion of mesethmoid narrower than ventral portion. (Amphiliiidae; Malapteruridae; *Mochokus*; *Mochokiella*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

In a large number outgroup taxa, as well as some mochokids, the dorsal portion of the mesethmoid, where it fuses with the frontals posteriorly, is as wide as the ventral portion, where it joins to the lateral ethmoids synchondrally (Fig. 2A–B). Alternatively, in *Mochokus*, *Mochokiella* and all chiloglanidins, as well as the Amphiliiidae and Malapteruridae, the dorsal portion of the mesethmoid is considerably narrower than the ventral portion, which flares out to form a base to the nasal cavity (Fig. 2C).

4. Shape of lateral ethmoids. (CI = 0.250, RI = 0.800)

0: Lateral ethmoids short and wide, with transverse suture to frontals.

1: Lateral ethmoids elongate and narrow, with longitudinal suture to frontals. (*Parauchenoglanis*; Amphiliiidae; *Centroadoras*; *Microsynodontis*; *Synodontis*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, as in the Diplomystidae (Arratia, 1987), the lateral ethmoids are short and wide, with lateral expansions forming a significant portion of the orbit and almost transversely sutured to the frontals (Fig. 2A). In all mochokids except *Mochokus*, *Mochokiella* and *Acanthocleithron*, as well as a number of outgroup taxa, the lateral ethmoids are more elongate, without lateral expansions forming a large portion of the orbit, and with longitudinal sutures at the lateral margins

of the frontals (Fig. 2B–C).

5. Orientation of anterolateral margin of lateral ethmoid. (CI = 1.000, RI = 1.000)

0: Anterolateral margin of lateral ethmoid horizontal.

1: Anterolateral margin of lateral ethmoid vertical. (*Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the anterolateral margin of the lateral ethmoid is roughly horizontal, without any obvious downward bend in this region (Figs. 1A–B, 3A–B). In *Atopodontus*, *Atopochilus* and *Euchilichthys* the lateral ethmoid turns downward to a vertical position at the anterolateral margin, forming a thin, hanging, laminar curtain (Figs. 1C, 3C; labeled la.cu.l.e.). The muscle extensor tentaculi is surrounded by the modified lateral ethmoid, running medial to the hanging, laminar curtain and ventral to the main body of the element (De Puyseleir, 2006). This curtain provides attachment for muscle and may enhance muscular control of the oral disc.

6. Development of posterior cranial fontanelle (ORDERED). (CI = 0.222, RI = 0.588)

0: Posterior cranial fontanelle well developed; bounded by frontals anteriorly and cutting well into parieto-supraoccipital posteriorly.

1: Posterior cranial fontanelle modestly developed; bounded by frontals anteriorly and just reaching parieto-supraoccipital posteriorly. (*Mochokus niloticus*; *Acanthocleithron*; *Synodontis acanthopercra*)

2: Posterior cranial fontanelle entirely absent. (*Paruchenoglanis*; *Chrysichthys*; *Schilbe*; Malapteruridae; *Tetrapamphilus*; *Zaireichthys*; Ariidae; Auchenipteridae; Doradidae; all Mochokidae except *Mochokus niloticus* [1], *Acanthocleithron* [1] and *Synodontis acanthopercra* [1])

Plesiomorphically, among catfishes, including the Diplomystidae (Arratia, 1987), the posterior cranial fontanelle forms a single longitudinal aperture that begins anteriorly between the posterior portions of the frontals (posterior to epiphyseal bar) and finishes posteriorly in the anterior half of the parieto-supraoccipital (Figs. 2A, 4B). Among the mochokids examined a well developed posterior cranial fontanelle is found in *Chiloglanis batesii* only (Fig. 4B). In *Acanthocleithron*, *Mochokus niloticus* and *Synodontis acanthopercra* the posterior cranial fontanelle is much smaller, only just reaching the parieto-supraoccipital (Fig. 4A). In remaining mochokids and a large number outgroup taxa the posterior cranial fontanelle is entirely absent, occluded by bone (Fig. 2C). A greatly shortened, rounded opening confined to the frontals was variably present in some *Synodontis* species (Fig. 2B), but when present, the openings were always variable in size and the modal condition in adult specimens was total

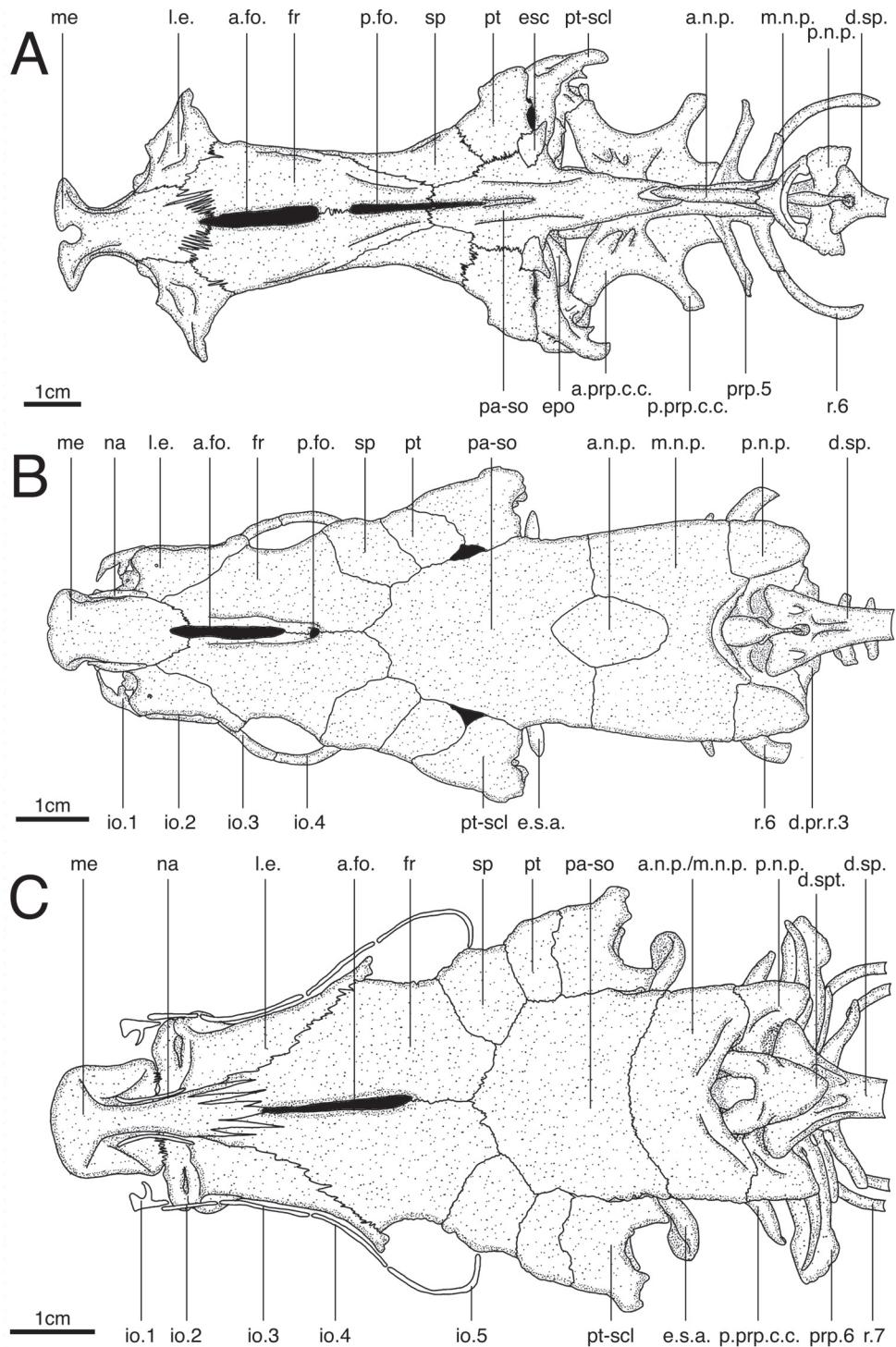


Fig. 2. Dorsal view of neurocranium of A) *Ictalurus punctatus*; CU 79403, B) *Synodontis acanthomias*; CU 91613 and C) *Euchilichthys royauxi*; CU 91614. Dorsal spinelet shown in C only.

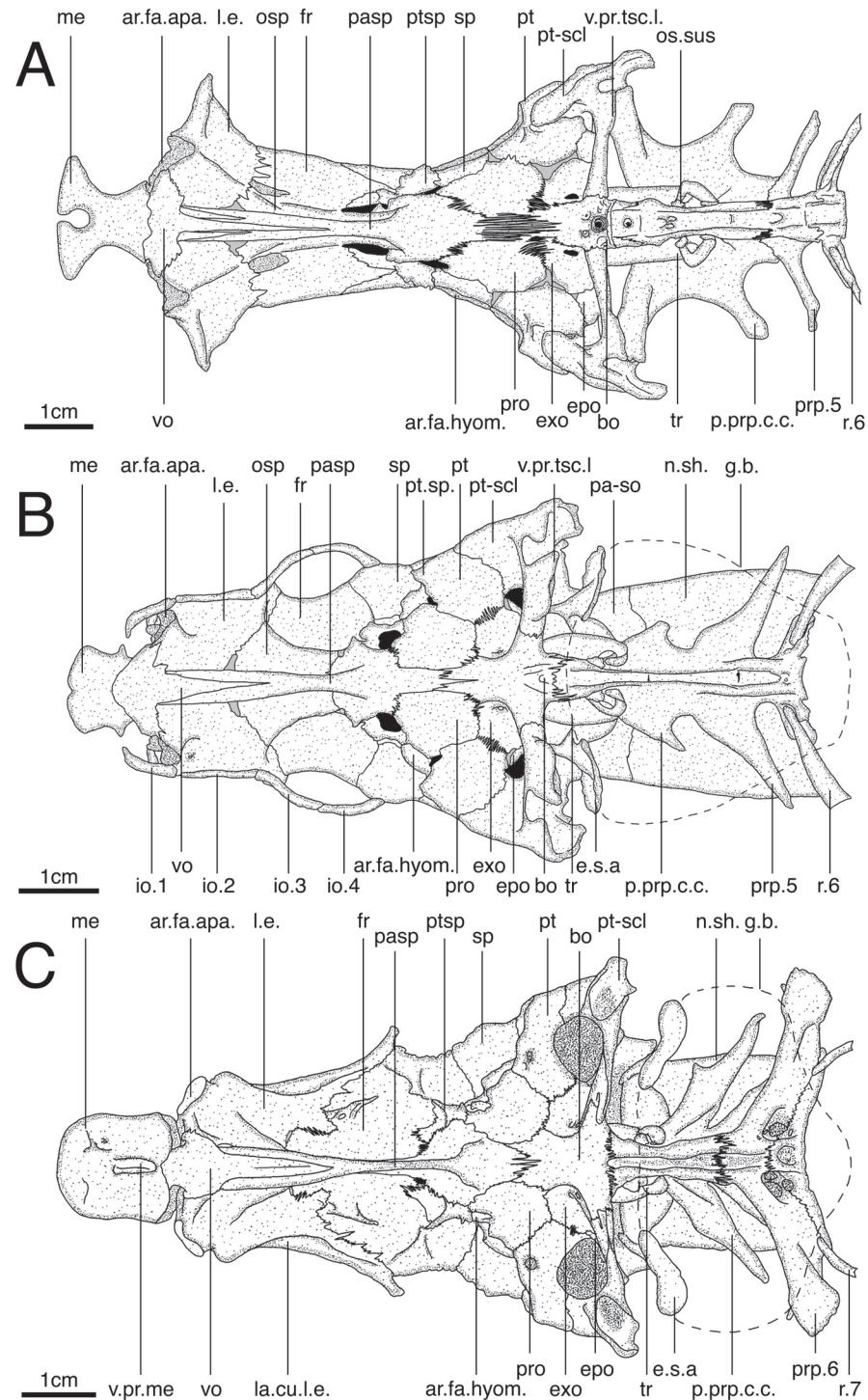


Fig. 3. Ventral view of neurocranium of A) *Ictalurus punctatus*; CU 79403, B) *Synodontis acanthomias*; CU 91613 and C) *Euchilichthys royauxi*; CU 91614. Dashed lines represent the boundary of the gas bladder.

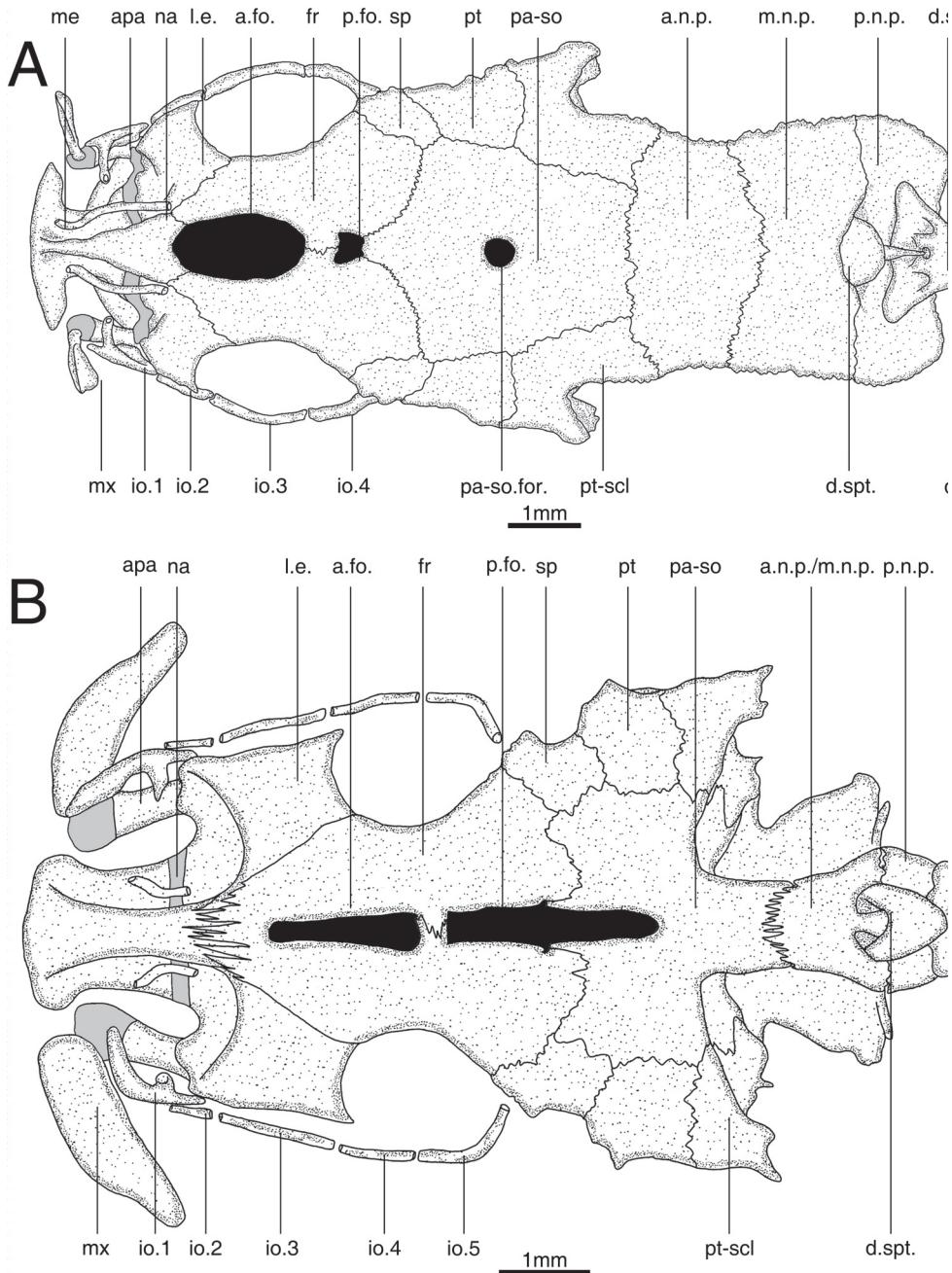


Fig. 4. Dorsal view of neurocranium of A) *Mochokus niloticus*; CU 91386 and B) *Chiloglanis batesii*; CU 91434. Dorsal spinelet shown in B only.

occlusion. Furthermore, the opening never reached the parieto-supraoccipital posteriorly. Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

7. Presence or absence of foraminal remnant of posterior cranial fontanelle. (CI = 0.167, RI = 0.444)

0: Foraminal remnant of posterior cranial fontanelle present.

1: Foraminal remnant of posterior cranial fontanelle absent.

Inapplicable: In all of those taxa possessing state 0 for character 6 because the posterior cranial fontanelle is well developed and extends to the middle of the parieto-supraoccipital, where the foraminal remnant is otherwise present (Figs. 2A, 4B).

Among catfishes, when the posterior cranial fontanelle is only modestly formed or altogether absent, there is sometimes a small circular foraminal remnant at the center of the parieto-supraoccipital, even in adults (Lundberg and McDade, 1986); within the Mochokidae, a foraminal remnant is present in *Mochokus niloticus*, *Acanthocheilichthys*, *Microsynodus*, *Synodontis acanthoperca*, *Chiloglanis macropterus*, *C. occidentalis*, *C. congicus* and *C. polypogon* (Fig. 4A). In all remaining mochokids, and several out-

group taxa, the foraminal remnant is absent (Fig. 2B–C). Refer to the matrix for a more exact distribution of states.

8. Formation of posterolateral corner of neurocranium. (CI = 1.000, RI = 1.000)

0: Posterolateral corner of neurocranium formed by exoccipital, epioccipital, pterotic and posttemporo-supracleithrum.

1: Posterolateral corner of neurocranium formed largely by prootic, exoccipital, pterotic and sphenotic. (*Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, elements of the posterolateral corner of the neurocranium that surround the brain include the exoccipital, epioccipital and pterotic. In addition, the posttemporo-supracleithrum is generally tightly joined at this corner of the neurocranium, inserting between the epioccipital posteriorly and pterotic anteriorly (Fig. 3A). In all chiloglanidins the epioccipital contributes little to the posterolateral corner of the neurocranium. Instead, the epioccipital is continuous with the ossified transcapular ligament and forms a nearly complete wall between the neurocranium and the post-cranial skeleton. In addition, the posterior border of the pterotic has shifted anteriorly, creating a large cavity below the posttemporo-supracleithrum. In these taxa, elements of the posterolateral

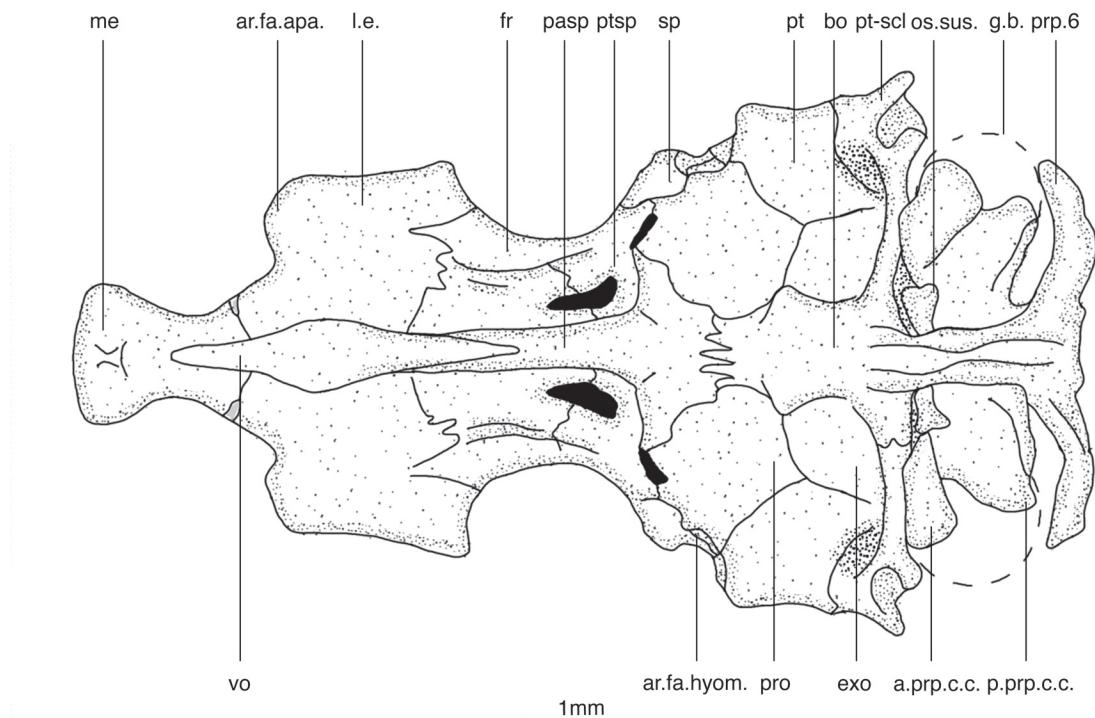


Fig. 5. Ventral view of neurocranium of *Chiloglanis batesii*; CU 91434. Dashed lines represent the boundary of the gas bladder.

corner of the neurocranium that surround the brain include the prootic, exoccipital, pterotic and sphenotic (Figs. 3C, 5).

9. Size of epioccipital. (CI = 1.000, RI = 1.000)

0: Epioccipital not reduced.

1: Epioccipital greatly reduced. (all *Synodontis* except *S. acanthoperca* [0])

Inapplicable: In *Chiloglanis*, *Atopodontus*, *Atopochilus*

and *Euchilichthys* because the epioccipital plays such a drastically different role in these taxa.

Plesiomorphically, among catfishes, as in the Diplostomatidae (Arratia, 1987), the epioccipital is present as a substantial element in the posterolateral corner of the neurocranium, with only modest amounts of cartilage between that element and adjoining elements (Fig. 6A). In all *Synodontis* except *S. acanthoperca* the epioccipital is greatly reduced and the posterolateral corner of the neurocranium

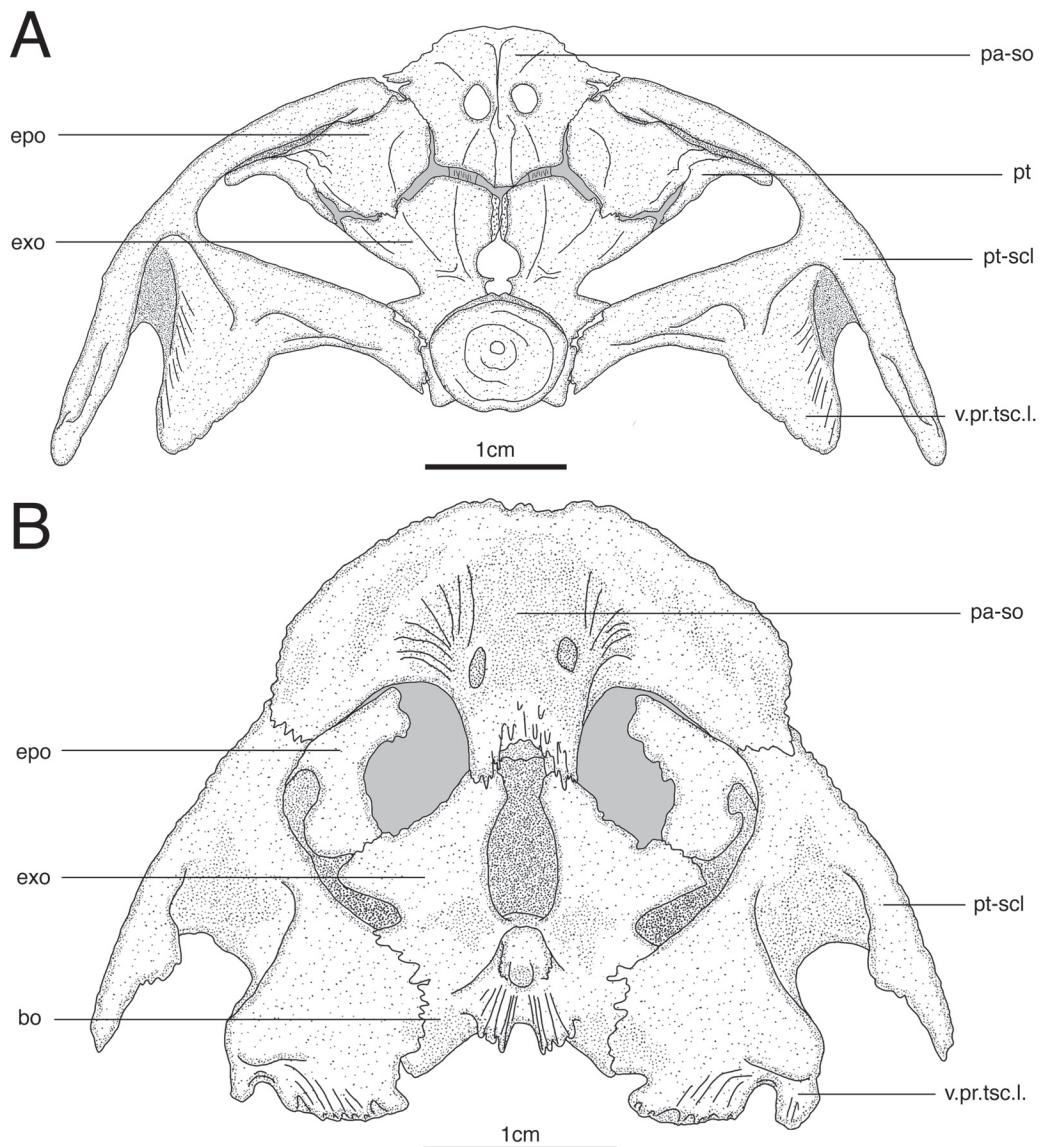


Fig. 6. Posterior view of neurocranium of A) *Ictalurus punctatus*; CU 79412 and B) *Synodontis geledensis*; UMMZ 241265.

is formed by cartilage that joins the crescent shaped and delicate ossification to adjoining elements (Fig. 6B).

10. Position of articulating facet for hyomandibula. (CI = 0.333, RI = 0.900)

0: Facet for hyomandibula insertion along border between the sphenotic and prootic.

(Diplomystidae; all Mochokidae except *Mochokus* [1] and *Acanthocleithron* [1])

1: Facet for hyomandibula insertion on sphenotic, excluded from prootic. (All taxa not showing state 0)

Among some putatively basal catfishes (Diplomystidae, loricarioids), the hyomandibula inserts on the underside of the neurocranium between the sphenotic and prootic. The facet for the hyomandibula often extends to the faces of the pterotic and pteryosphenoid (Arratia, 1987; Mo, 1991). This apparently plesiomorphic state is also found in all mochokids (Fig. 3B–C), except *Acanthocleithron* and *Mochokus*. Mo (1991) did not recognize that the prootic plays a role in this articulation in most members of the Mochokidae. Alternatively, in most siluroid catfishes, as in *Acanthocleithron* and *Mochokus*, the main portion of the facet for the hyomandibula is on the sphenotic only and is entirely excluded from the prootic; here, the facet may also extend to the pterotic and pteryosphenoid (Fig. 3A). The plesiomorphic nature of this character within the Mochokidae, and its distribution among catfishes in general, is intriguing because mochokids are highly derived catfishes in most respects.

11. Presence or absence of pterotic spine. (CI = 0.500, RI = 0.957)

0: Pterotic spine absent.

1: Pterotic spine present. (*Mochokiella*; *Acanthocleithron*; *Microsynodus*; *Synodontis*; *Chiloglanis macropterus*; *Chiloglanis* sp. ‘burundi’)

Plesiomorphically, among catfishes, the ventral face of the pterotic is generally unornamented, without well-formed anteroventrally directed spinous projections (Fig. 1A, 1C). However, in many mochokids there is a spinous projection on the ventral surface of the pterotic that accepts and envelopes the posterolateral edge of the hyomandibula (Fig. 1B; labeled pt.sp.). Among mochokids the pterotic spine is absent in *Mochokus* and all chiloglanidins except *Chiloglanis macropterus* and *Chiloglanis* sp. ‘burundi’.

12. Presence or absence of basioccipital pit. (CI = 0.500, RI = 0.889)

0: Basioccipital pit present.

1: Basioccipital pit absent. (*Tetracamphilius*; *Zaireichthys*; Ariidae; Auchenipteridae; Doradidae; Mochokidae)

In several outgroup taxa (state unclear in the Diplo-

mystidae) there is a small pit on the ventral surface of the basioccipital along the midline and just anterior to the connection with the first centrum (Fig. 3A). In smaller specimens and in certain taxa this pit is filled by a small plug of cartilage. In other instances the pit is filled by a small bony plug, but is still distinguishable as a pit. In the Mochokidae, as well as the Ariidae, Auchenipteridae, Doradidae, *Zaireichthys* and *Tetracamphilius*, there is no evidence of a pit on the ventral surface of the basioccipital, even in smaller specimens (Fig. 3B–C). The small bony plug may be totally fused with the surrounding bone or it may be replaced by bone of the basioccipital itself.

13. Presence or absence of lateral expansions of basioccipital. (CI = 0.500, RI = 0.909)

0: Basioccipital without distinct lateral expansions.

1: Basioccipital with distinct lateral expansions. (*Zaireichthys*; Ariidae; Auchenipteridae; Doradidae; Mochokidae)

Among basal catfishes, including the Diplomystidae (Arratia, 1987), the basioccipital is without distinct lateral expansions and is not much wider than the anterior centra (Fig. 3A). In the Mochokidae, as well as the Ariidae, Auchenipteridae, Doradidae and *Zaireichthys*, the basioccipital has distinct lateral expansions (arms) that join the ossified transcapular ligaments. In these taxa the lateral expansions make the basioccipital considerably wider than the anterior centra (Fig. 3B–C). Lundberg (1993) suggested that a basioccipital with ossified lateral expansions was a synapomorphy for a group called the ‘arioids’, which included the Ariidae, Doradidae, Auchenipteridae, Mochokidae and the fossil ‘titanoglanis’.

14. Presence or absence of distinct extrascapular. (CI = 0.500, RI = 0.889)

0: Presence of distinct extrascapular.

1: Absence of distinct extrascapular. (Amphiliidae; Auchenipteridae; Doradidae; Mochokidae)

Plesiomorphically, among catfishes, there is a distinct and separate extrascapular near the posterolateral corner of the neurocranium (Fig. 2A). In the Mochokidae, as well as the Amphiliidae, Auchenipteridae and Doradidae, the extrascapular is not present as a separate element (Mo, 1991; Diogo, 2005). It is either lost or wholly fused to the elements surrounding it (Figs. 2B–C, 4B). It is important to note that at least one specimen of *Mochokus niloticus* shows an autonomous element (on each side) where you might expect to find the extrascapular. The nature of this element in *Mochokus* is of particular interest given the other odd morphological features found in the genus. However, absence of a discrete epioccipital is the modal condition for *M. niloticus* and is coded as such (state 1).

15. Attachment of posttemporo-supracleithrum. (CI = 0.500, RI = 0.857)

0: Posttemporo-supracleithrum set loosely in neurocranium.

1: Posttemporo-supracleithrum sutured tightly to neurocranium. (Amphiliidae; Ariidae; Auchenipteridae; Doradidae; Mochokidae)

In many putatively basal catfishes, including the Diplomystidae (Arratia, 1987; Mo, 1991), the posttemporo-supracleithrum is set loosely between the extrascapular anteriorly and the epioccipital posteriorly (Fig. 2A). In all mochokids and several outgroup taxa the posttemporo-supracleithrum is tightly sutured to the posterolateral corner of the neurocranium (Figs. 2B–C, 4B). This derived condition can be correlated with increased stabilization of the pectoral girdle through increased ossification, fusion and tighter articulations.

16. Shape of ventral process of ossified transcapular ligament. (CI = 0.333, RI = 0.857)

0: Ventral process of ossified transcapular ligament simple, without medial expansion.

1: Ventral process of ossified transcapular ligament complex, with notable medial expansion. (*Microsynodontis* sp. ‘odzala’; all *Synodontis* except *S. acanthoperca* [0], *S. nigriventralis* [0] and *S. contracta* [0])

Plesiomorphically, among catfishes, the ventral extremities of the ossified transcapular ligament are simple, extending laterally to accept the upper arm of the cleithrum and without complex ornamentations or processes ventromedially (Fig. 6A). Alternatively, in many species of *Synodontis* and one species of *Microsynodontis* the ventral extremities of the transcapular ligament are complex, with ventrally-expansive ornamentations and processes directed medially, as well as laterally (Fig. 6B).

17. Development of nuchal shield (ORDERED). (CI = 0.400, RI = 0.889)

0: Nuchal shield poorly formed.

1: Nuchal shield moderately formed. (Pangasiidae; *Chrysichthys*; Ariidae; *Chiloglanis* sp. ‘igamba’; *C. occidentalis*; *C. batesii*; *C. polypogon*; *Chiloglanis* sp. ‘chambeshi’)

2: Nuchal shield well formed. (Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Chiloglanis disneyi*; *C. macropterus*; *C. conicus*; *C. carnosus*; *Chiloglanis* sp. ‘kalungwishi’; *Chiloglanis* sp. ‘ntumbachushi’; *Chiloglanis* sp. ‘burundi’; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Inapplicable: In the Malapteruridae, because most dorsal-fin elements are totally absent in the family.

The nuchal shield is considered herein to be composed of the anterior, middle and posterior (paired) nuchal

plates (dermal bones) which are superficial expansions associated with the supraneural, first and second pterygiophores (endochondral bones), respectively. Primitively in actinopterygians each pterygiophore has three separate radials: proximal, middle and distal. In most catfishes each pterygiophore is composed of fused bony proximal and middle radials, otherwise referred to as ‘proximal-middle radials’ (Johnson and Patterson, 1993), and the distal radial remains separate and cartilaginous. Plesiomorphically, among catfishes, as in the Diplomystidae (Arratia, 1987), the nuchal shield is very narrow and barely joins the dorsal-fin elements to the neurocranium, if at all (Fig. 2A). In certain species of *Chiloglanis* and some outgroup taxa the nuchal plates are slightly more developed, creating a solid bridge between the dorsal-fin elements and the supraoccipital spine. However, in these taxa, the supraoccipital spine and nuchal shield are not nearly as wide as the main body of the parieto-supraoccipital (Fig. 4B). Finally, in the Auchenipteridae, Doradidae and the great majority of the Mochokidae the nuchal shield is extremely well developed and is as wide as or wider than the main body of the parieto-supraoccipital (Figs. 2B–C, 4A). Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

18. Dorsal suture between posttemporo-supracleithrum and nuchal plates. (CI = 0.667, RI = 0.750)

0: Posttemporo-supracleithrum not joined to any nuchal plates.

1: Posttemporo-supracleithrum joined to middle nuchal plate obliquely. (Doradidae)

2: Posttemporo-supracleithrum joined to anterior nuchal plate transversely. (*Mochokus*, *Mochokiella*)

Inapplicable: In the Malapteruridae, because most dorsal-fin elements are totally absent in the family.

In a large majority of taxa considered the posttemporo-supracleithrum does not extend posteriorly to contact the nuchal plates and is generally excluded from them by the parieto-supraoccipital (Figs. 2A–C, 4B). However, in the Doradidae the dorsal surfaces of the posttemporo-supracleithrum and middle nuchal plates are sometimes joined obliquely (Lundberg, 1993; Fig. 8.10.). Lundberg (1993) suggested that this derived state was a synapomorphy for a group composed of the ‘doradoids’ (including mochokids) and the fossil ‘titanoglanis’. However, the state observed in most mochokids is notably different, nonhomologous and independently derived. For example, in *Mochokus* and *Mochokiella*, the posttemporo-supracleithrum and anterior nuchal plates (as opposed to middle) are joined transversely (Fig. 4A). NOTE: In *Mochokus brevis* a very small portion of the bridge-shaped middle nuchal plate sutures with the posttemporo-supracleithrum (see character 20), but it is

largely excluded from contact by the anterior nuchal plate. The nature of this character in *Mochokus brevis*, being a transverse suture largely between the posttemporo-supracleithrum and anterior nuchal plate, is most similar to that seen in *Mochokus niloticus* and *Mochokiella* and is coded as such (state 2).

19. Presence or absence of separate anterior and middle nuchal plates. (CI = 0.333, RI = 0.895)

0: Anterior nuchal plate and middle nuchal plate separate.
1: Anterior nuchal plate and middle nuchal plate not separate. (*Synodontis nigriventris*; *S. batesii*; *S. contracta*; *Chiloglanis*; *Atopodontus*; *Euchilichthys*)

Inapplicable: In the Malapteruridae, because most dorsal-fin elements are totally absent in the family.

In all outgroup taxa and many of the ingroup taxa the two anteriormost elements of the nuchal shield are present as separate elements (Figs. 2A–B, 4A). In *Chiloglanis*, *Atopodontus*, *Euchilichthys* and some species of *Synodontis* the two anteriormost elements of the nuchal shield are not visible as separate elements dorsally; the suture between these elements is not visible and the elements may be entirely fused or one may be lost, most likely the anterior nuchal plate (Figs. 2C, 4B). Notably, among all chiloglanidins considered, *Atopochilus savorgnani* is the only species with obviously separate anterior and middle nuchal plates. *Synodontis nigrita* is polymorphic for this character, with both states commonly occurring; when the nuchal plates are obviously distinct in this species, the anterior nuchal plate is present as a small scale-shaped plate bounded by the parieto-supraoccipital anteriorly and the middle nuchal plate posteriorly and laterally, as seen in many other species of *Synodontis* (e.g., *Synodontis acanthomias*; Fig. 2B).

20. Presence or absence of suture between middle nuchal plate and parieto-supraoccipital. (CI = 0.333, RI = 0.882)

0: Middle nuchal plate not sutured to parieto-supraoccipital.
1: Middle nuchal plate sutured to parieto-supraoccipital. (Auchenipteridae; Doradidae; *Mochokus brevis*; all *Synodontis* except *S. acanthoperca* [0] and those listed in ‘Inapplicable’ below)

Inapplicable: In the Malapteruridae, because most dorsal-fin elements are totally absent in the family. In *Synodontis nigriventris*, *S. contracta*, *S. batesii*, *Chiloglanis*, *Atopodontus* and *Euchilichthys*, because in these taxa the anterior nuchal plate and middle nuchal plate are not readily distinguishable.

Plesiomorphically, among catfishes, the middle nuchal plate is fully posterior to the anterior nuchal plate

and does not extend forward on each side to join the parieto-supraoccipital (Figs. 2A, 4A). In the Auchenipteridae, the Doradidae, *Mochokus brevis* and most *Synodontis* the middle nuchal plate is bridge-shaped, wherein it surrounds the anterior nuchal plate laterally to join the parieto-supraoccipital anteriorly (Fig. 2B) and sometimes other elements of the neurocranium. In *Mochokus brevis* the bridge-shaped middle nuchal plate also joins the posttemporo-supracleithrum by a small margin anterolaterally (see character 18). Note that the middle nuchal plate is not sutured to the parieto-supraoccipital in all doradids, but sometimes excluded by the anterior nuchal plate (pers. comm. Mark Sabaj Pérez).

21. Expansion of dorsal portion of dorsal-fin proximal-middle radials. (CI = 0.143, RI = 0.769)

0: Dorsal-fin proximal-middle radials slightly expanded laterally or not at all, near dorsal tip.
1: Dorsal-fin proximal-middle radials greatly expanded laterally, near dorsal tip. (Pangasiidae; Schilbidae; Ariidae; all Doradidae except *Agamyxis* [0]; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Synodontis*)

Inapplicable: In the Malapteruridae, because most dorsal-fin elements are totally absent in the family.

Plesiomorphically, among catfishes, as in the Diplomystidae (Arratia, 1987), the dorsal-fin proximal-middle radials, beyond the second (which lies below the posterior nuchal plate), are without conspicuous dorso-lateral expansion, but may be slightly expanded in some instances (Figs. 2A, 2C, 4B). Alternatively, in *Mochokus*, *Mochokiella*, *Acanthocleithron* and *Synodontis*, as well as a number of outgroup taxa, some or all of the dorsal-fin proximal-middle radials are greatly expanded dorsolaterally, though the size of these expansions decreases moving posteriorly (Figs. 2B, 4A).

22. Attachment of third dorsal-fin proximal-middle radial to posterior nuchal plate. (CI = 0.333, RI = 0.882)

0: Third proximal-middle radial not joined to posterior margin of posterior nuchal plate.
1: Third proximal-middle radial joined to posterior margin of posterior nuchal plate. (*Bagre*; *Mochokiella*; all *Synodontis* except *S. acanthoperca* [0])

Inapplicable: In the Malapteruridae, because most dorsal-fin elements are totally absent in the family.

Among catfishes, including the majority of those considered here, there is typically a gap between the posterior margin of the posterior nuchal plate (underlain by the second dorsal-fin proximal-middle radial) and the dorsal portion of the third dorsal-fin proximal-middle radial (Fig. 4A), which may or may not be expanded laterally as detailed in character 21. Alternatively, in some ariids

and some mochokids the dorsal portion of the third dorsal-fin proximal-middle radial is tightly joined to the posterior margin of the posterior nuchal plate (Fig. 2B).

23. Number of Infraorbitals (ORDERED). (CI = 0.500, RI = 0.900)

0: Six or more infraorbitals. (Diplomystidae; Ictaluridae; Pangasiidae)

1: Five infraorbitals. (*Chrysichthys*; Schilbidae; *Amphilinus*; *Doumea*; Malapteruridae; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

2: Four infraorbitals. (*Parauchenoglanis*; *Tetracamphilius*; *Zaireichthys*; Ariidae; Auchenipteridae; *Agamyxis*; *Platydoras*; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*)

3: Three infraorbitals. (*Centrodonas*)

The number of infraorbitals herein includes the lacrimal (with any succeeding elements fused to the lacrimal) as the first infraorbital. In putatively basal catfishes there are at least six infraorbitals and sometimes upwards of eight, as in the Diplomystidae (Arratia, 1987). In various groups considered here, the number of infraorbitals has been greatly reduced to as few as three (Figs. 2, 4). Within the Mochokidae the count is always five (all chiloglanidins) or four (all other mochokids). The first two elements may be fused in mochokids with only four infraorbitals and separate in those with five. Alternatively, one element may be lost in those with four infraorbitals. As a count of discrete elements, this character allowed for the hypothesis of a transformational series and is treated as ordered in the analyses.

Splanchnocranium

24. Presence or absence of ascending Meckel's cartilage. (CI = 0.333, RI = 0.857)

0: Ascending branch of Meckel's cartilage present.

1: Ascending branch of Meckel's cartilage absent. (*Amphilinus*; *Doumea*; *Phractura*; Malapteruridae; Mochokidae)

Plesiomorphically, among catfishes, the Meckel's cartilage is composed of two branches, an ascending branch running vertically, just lateral to the coronomeckalian and medial to the dentary and a horizontal branch running along the medial side of the dentary (Fig. 7A). In *Amphilinus*, *Doumea*, *Phractura*, the Malapteruridae and the Mochokidae the ascending branch is absent and Meckel's cartilage is limited to a horizontal sheath (Fig. 7B).

25. Length of horizontal Meckel's cartilage. (CI = 0.500, RI = 0.923)

0: Horizontal branch of Meckel's cartilage elongate.

1: Horizontal branch of Meckel's cartilage short. (Amphiliidae; Mochokidae)

Plesiomorphically, among catfishes, the horizontal branch of Meckel's cartilage is many times longer than it is thick (Mo, 1991; de Pinna, 1993; Diogo, 2005). In general, the cartilage sits medial to the dentary running from the dentary anteriorly/medially to the angulo-articular posteriorly/laterally (Fig. 7A). In the Amphiliidae and Mochokidae the horizontal branch of Meckel's cartilage is only slightly longer than it is thick. Here, the cartilage is formed as a cylinder joining flat faces of both the angulo-articular and the dentary, but does not lie against the dentary for any part of its length (Fig. 7B).

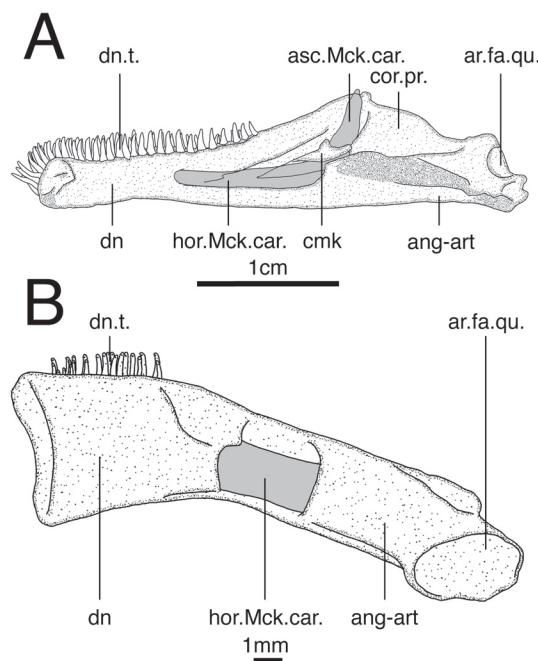


Fig. 7. Posteromedial view of right half of mandible of A) *Ictalurus punctatus*; CU 79403 and B) *Synodontis acanthomias*; CU 91613.

26. Presence or absence of coronomeckalian. (CI = 0.500, RI = 0.941)

0: Coronomeckalian present.

1: Coronomeckalian greatly reduced or absent. (Malapteruridae; Mochokidae)

Among catfishes the coronomeckalian is generally present as a small, but obvious block-like element tight against the medial side of the dentary (Fig. 7A). In the Malapteruridae and Mochokidae the coronomeckalian is greatly reduced or absent (Fig. 7B). It should be noted

that, in fact, some species of *Synodontis* do exhibit what may be a greatly reduced coronomeckalian that floats freely within the horizontal portion of Meckel's cartilage; previous authors have indicated that the coronomeckalian was altogether absent in the Mochokidae (Mo, 1991; de Pinna, 1993; Diogo, 2005). The highly reduced nature of the element is somewhat variable and, as such, was not utilized as a separate character state.

27. Development of coronoid process. (CI = 1.000, RI = 1.000)

0: Coronoid process well formed.

1: Coronoid process absent or very poorly formed. (Mochokidae)

Plesiomorphically, among catfishes, there is a well-formed dorsally directed coronoid process on the lower jaw where the dentary joins the angulo-articular (Fig. 7A). In the Mochokidae the coronoid process is poorly formed and often entirely absent (Fig. 7B).

28. Size of intermandibular angle. (CI = 0.500, RI = 0.957)

0: Intermandibular angle near 90 degrees.

1: Intermandibular angle obtuse, between 135 and 180 degrees. (*Microsynodontis*; all *Synodontis* except *S. membranacea* [0]; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Herein the angle formed by the two points at the articulations of the mandible with the quadrate and a point at the symphysis of the lower jaw (the vertex) is referred to as the intermandibular angle. Plesiomorphically, among catfishes, the intermandibular angle is about 90 degrees (Fig. 8A). In all mochokids except *Mochokus*, *Mochokiella*, *Acanthocleithron* and *Synodontis membranacea* these points form an obtuse angle between 135 and 180 degrees (Fig. 8B).

29. Shape of angulo-articular facet for quadrate. (CI = 1.000, RI = 1.000)

0: Angulo-articular facet for quadrate saddle-shaped.

1: Angulo-articular facet for quadrate cup-shaped. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the angulo-articular facet for the quadrate is saddle-shaped (a hyperbolic paraboloid) (Figs. 7A, 8A). In all mochokids except *Mochokus* this facet is shaped as a cup with a raised rim along the entire edge (Figs. 7B, 8B). A precursor of the derived condition might be present in *Mochokus*, where the facet is bordered by an extension of the angulo-articular laterally; however, the facet is still shaped as a saddle and has no rim along the medial edge. The shape of the articular surface at

the anterior end of the quadrate is directly correlated to this character. Taxa with the plesiomorphically saddle-shaped facet on the angulo-articular have a similar facet on the quadrate that is rotated by roughly 90 degrees; the two saddles slide across each other when the jaw opens and closes. The articular surface of the quadrate in most mochokids is ball-shaped for articulation with the cup-shaped facet of the angulo-articular.

30. Presence or absence of dentary tooth cup. (CI = 1.000, RI = 1.000)

0: Dentary tooth cup absent.

1: Dentary tooth cup present. (*Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Among putatively basal siluroid catfishes, as in the Diplomystidae (Arratia, 1987), the dentary is dorsoventrally compressed towards the symphysis and relatively flat for supporting dentary teeth (Figs. 7A, 8A). In many mochokids, as in various loricarioid catfishes (de Pinna, 1993; Diogo, 2005), the dentary is not very compressed and the anterior face of the dentary has a deep depression that supports teeth, herein referred to as the tooth cup (Fig. 9A–B).

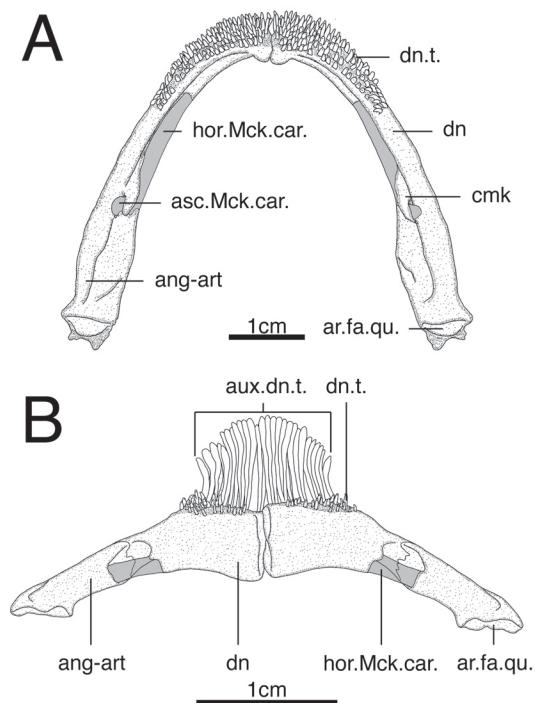


Fig. 8. Dorsal view of mandible of A) *Ictalurus punctatus*; CU 79403 and B) *Synodontis acanthomias*; CU 91613.

31. Presence or absence of primary dentary teeth. (CI = 0.286, RI = 0.848)

- 0:** Primary dentary teeth in single patch across symphysis.
1: Primary dentary teeth in separate patches, divided at symphysis. (*Phractura*; *Microsynodontis*; all *Synodontis* except *S. contracta* [2], *S. katangae* [2], *S. longirostris* [2], *S. sorex* [2], *S. clarias* [2], *S. pleurops* [2], *S. congica* [2])
2: Primary dentary teeth altogether absent. (*Acanthocleithron*; *Synodontis contracta*; *S. katangae*; *S. longirostris*; *S. sorex*; *S. clarias*; *S. pleurops*; *S. congica*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

In most catfishes, including nearly all outgroup taxa examined, the dorsal surface of the dentary supports gently recurved, conical, **primary** dentary teeth in a continuous patch across the symphysis (Figs. 7A, 8A); *Mochokus* and *Mochokiella* show this state. In contrast, the most visible (and perhaps most functional) dentary teeth in most mochokids are **auxiliary** dentary teeth, coming from the anteriorly directed tooth cup (S-shaped in all cases except *Acanthocleithron*). However, several species (including *Microsynodontis* and many *Synodontis*) have more typical conical and gently recurved teeth on the dorsal surface of the aforementioned tooth cup (Figs. 7B, 8B, 9A). Based on position and shape, those teeth are interpreted as homologs of the primary teeth on the dorsal surface of the dentary in other catfishes. Further, the auxiliary teeth in most mochokids are considered a separate synapomorphy for the taxa that exhibit them. That being the case, in some mochokids and some amphiliids the dentary does support

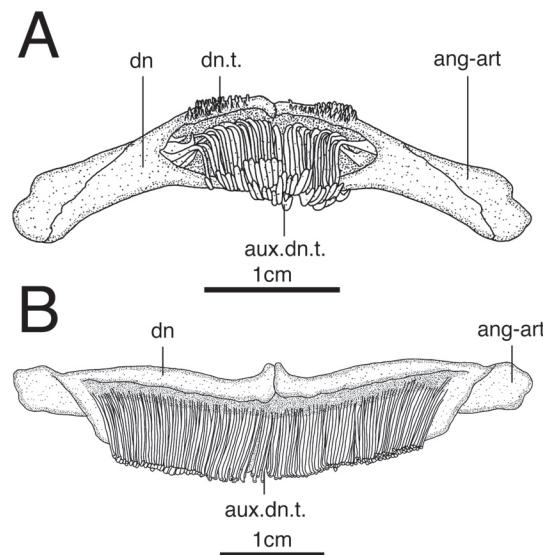


Fig. 9. Anterior view of mandible of A) *Synodontis acanthomias*; CU 91613 and B) *Euchilichthys royauxi*; CU 91614.

primary dentary teeth on its dorsal surface, but they are in separate patches on each side of the symphysis (Figs. 7B, 8B, 9A). In the remaining mochokids there are no primary teeth on the dorsal surface of the dentary, only auxiliary teeth within the tooth cup (Fig. 9B).

32. Presence or absence of auxiliary dentary teeth. (CI = 1.000, RI = 1.000)

- 0:** Auxiliary dentary teeth not present.
1: S-shaped auxiliary dentary teeth present, tips pointed. (*Microsynodontis*; *Synodontis*; *Chiloglanis*)
2: S-shaped auxiliary dentary teeth present, tips spatulate. (*Atopochilus*; *Euchilichthys dybowskii*)
3: S-shaped auxiliary dentary teeth present, tips trowel-shaped. (*Atopodontus*; all *Euchilichthys* except *E. dybowskii* [2])
4: Gently recurved and robust auxiliary dentary teeth present, tips spatulate. (*Acanthocleithron*)

In all outgroup taxa, teeth of the lower jaw are restricted to the relatively flat dorsal surface of the dentary. In most mochokids the lower jaw also holds auxiliary dentary teeth of various sorts in the tooth cup. The teeth in these taxa exist in at least four general forms, differing in shape of the tooth shaft and the tooth tip. In the great majority of these the teeth are S-shaped (Fig. 10A, C–F). In the *Microsynodontis*, *Synodontis* and *Chiloglanis* examined the tips of S-shaped auxiliary dentary teeth are pointed (Fig. 10D–F). In *Atopochilus* and *Euchilichthys dybowskii* the tips of the S-shaped auxiliary dentary teeth are spatulate (Fig. 10C). In remaining *Euchilichthys*, as well as *Atopodontus*, the tips of the S-shaped auxiliary dentary teeth are trowel-shaped, with a keel along the midline (Fig. 10A). *Acanthocleithron* is the only mochokid that possesses auxiliary dentary teeth that are not distinctly S-shaped; they are recurved, robust and have spatulate tips (Fig. 10B).

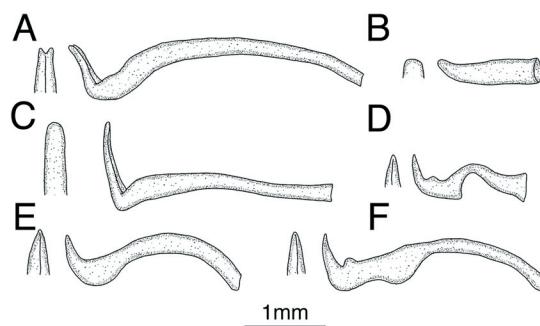


Fig. 10. Mochkid auxiliary dentary teeth in lateral view, tips shown in anterior view; A) *Euchilichthys*, B) *Acanthocleithron*, C) *Atopochilus*, D) *Microsynodontis*, E) *Chiloglanis* and F) *Synodontis*.

33. Size of maxilla. (CI = 0.500, RI = 0.944)**0:** Maxilla small.**1:** Maxilla large. (*Zaireichthys*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the maxilla is a small element supporting the elastin cartilage of the maxillary barbel. In most of the taxa examined the maxilla is about as long as the mesethmoid is wide and quite often substantially shorter (Fig. 4A). In *Zaireichthys* and all chiloglanidins the maxilla is massive and longer than the mesethmoid is wide (Fig. 4B).

34. Presence or absence of laminar expansions of maxilla. (CI = 1.000, RI = 1.000)**0:** Maxilla without laminar expansions proximally.**1:** Maxilla with laminar expansions proximally. (*Chiloglanis* sp. 'igamba'; *C. disneyi*; *C. occidentalis*; *C. batesii*; *C. polypogon*; *Chiloglanis* sp. 'chambeshi'; *Chiloglanis* sp. 'ntumbachushi')

Plesiomorphically, among catfishes, the proximal portion of the maxilla is composed of two bulbous heads (dorsal and ventral) that articulate with the anterior autopatine cartilage. Unlike all outgroup taxa and most ingroup taxa, in several species of *Chiloglanis* the dorsal head of the maxilla is continuous with a large horizontal lamina along the anterior side of the element (Fig. 4B).

35. Shape of premaxillae. (CI = 1.000, RI = 1.000)**0:** Premaxillae flat, with ventrally directed tooth-bearing face only.**1:** Premaxillae block-like and solid, with posterior and ventral tooth-bearing faces. (*Microsynodontis*; *Synodontis*)**2:** Premaxillae block-like, with posterior and ventral tooth-bearing faces joined by swath of porous bone. (*Chiloglanis disneyi*; *C. macropterus*; *C. congicus*; *C. carnosus*; *Chiloglanis* sp. 'kalungwishi'; *Chiloglanis* sp. 'burundi'; *Atopodontus*; *Atopochilus*; *Euchilichthys*)**3:** Premaxillae claw-shaped, with posterior and ventral

tooth-bearing faces joined near symphysis only. (*Chiloglanis* sp. 'igamba'; *C. occidentalis*; *C. batesii*; *C. polypogon*; *Chiloglanis* sp. 'chambeshi'; *Chiloglanis* sp. 'ntumbachushi')

Plesiomorphically, among catfishes, the premaxillae are plate-like and laterally expansive, being a good deal wider than they are deep and supporting teeth in a single patch on the ventral surface (Fig. 11). In most mochokids however, there are multiple faces for the support of premaxillary teeth and the premaxillae are more block-like in shape. In each case the premaxillae support teeth on a vertical posterior face in addition to the anterior ventral face. In *Microsynodontis* and *Synodontis* the premaxillae are generally rectangular and support teeth on both the ventral and posterior faces of a single solid element (Fig. 12). In *Atopodontus*, *Atopochilus*, *Euchilichthys* and some *Chiloglanis* the faces of a block-like element are joined to each other by a transverse swath of porous bone (Fig. 13). In the remaining species of *Chiloglanis* the two faces are even more disjunct, being attached to each other only near the symphysis; in this instance the premaxillae are claw-shaped (Fig. 14).

36. Differentiation of premaxillary teeth. (CI = 1.000, RI = 1.000)**0:** Teeth uniform or only gradually differentiated by size.**1:** Teeth abruptly differentiated by size. (*Microsynodontis*; *Synodontis*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the premaxillae hold teeth in a single patch; the teeth may gradually decrease in size from front to back, but do not occur in discrete patches separated by shape or drastic changes in size (Fig. 11). In all mochokids except *Mochokus*, *Mochokiella* and *Acanthocleithron* the premaxillae have teeth of at least two distinct sizes separated into discrete patches, the most posterior of these with small and often needle-like teeth (Figs. 12, 13, 14).

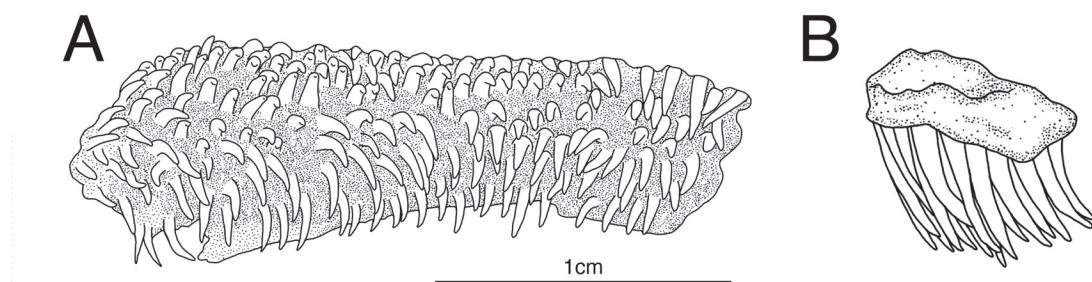


Fig. 11. Ventral (A) and medial (B) views of premaxilla of *Ictalurus punctatus*; CU 79378, right side.

37. Shape of premaxillary tooth shaft. (CI = 1.000, RI = 1.000)

0: Premaxillary teeth cylindrical and gently recurved.
1: Premaxillary teeth cylindrical and S-shaped. (*Microsynodus*; *Synodontis*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Shape of the premaxillary teeth in catfishes is fairly conserved. In the Diplomystidae and the Ictaluridae, as in many others, the premaxillary teeth are gently recurved and cylindrical (Fig. 15C). In all mochokids except *Mochokus*, *Mochokiella* and *Acanthocleithron* the premaxillary teeth are cylindrical, but are obviously S-shaped. The shaft of the tooth bends anteriorly before bending posteriorly at its tip (Fig. 15A–B). The distribution of the states for this character is similar to that of the preceding character and they are most likely phylogenetically correlated. However, the characters are probably independent because it is unlikely that the distribution of the derived states is entirely

congruent throughout the Mochokidae. It is possible that some unexamined mochokids have gently recurved teeth differentiated by size. Alternatively, some mochokids may have S-shaped teeth that are not differentiated by size.

38. Shape of premaxillary tooth tips. (CI = 0.333, RI = 0.600)

0: Tips of premaxillary teeth conical and pointed.
1: Tips of premaxillary teeth spatulate. (*Acanthocleithron*; *Chiloglanis disneyi*; *C. batesii*; *C. congicus*; *C. carnosus*;

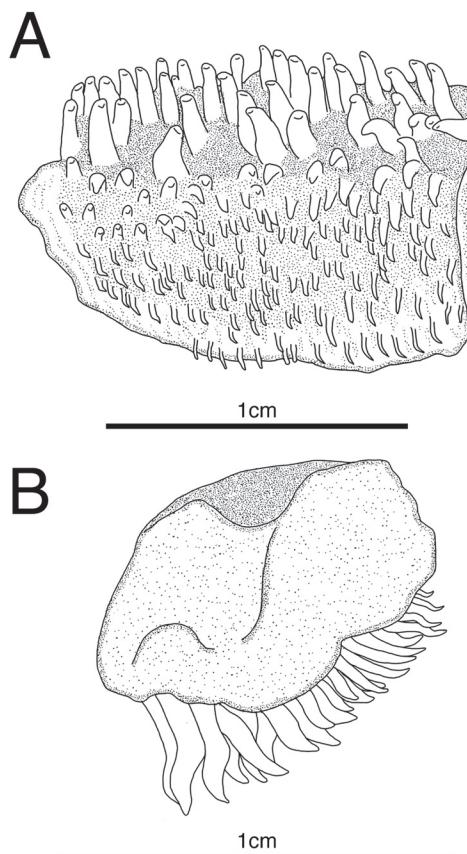


Fig. 12. Ventral (A) and medial (B) views of premaxilla of *Synodontis acanthomias*; CU 89763, right side.

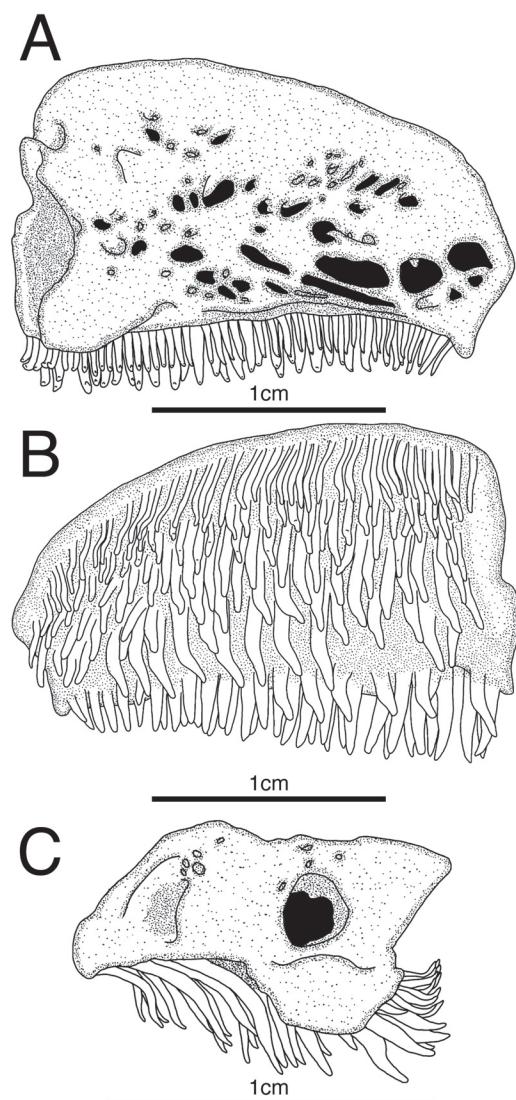


Fig. 13. Dorsal (A), ventral (B) and medial (C) views of premaxilla of *Euchilichthys royauxi*; CU 91614, right side.

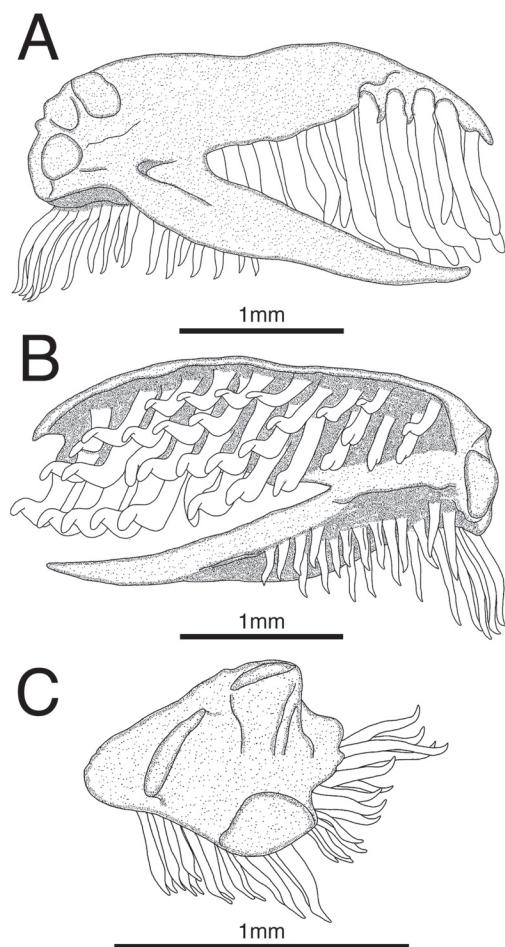


Fig. 14. Dorsal (A), ventral (B) and medial (C) views of premaxilla of *Chiloglanis batesii*; CU 91434, right side.

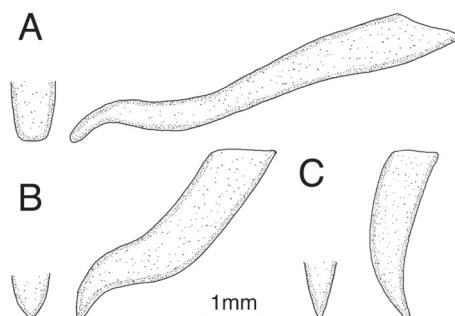


Fig. 15. Mochokid premaxillary teeth in lateral view, tips shown in anterior view; A) *Euchilichthys*, B) *Synodontis* and C) *Mochokus*.

Atopodontus; Atopochilus; Euchilichthys)

2: Tips of premaxillary teeth bicuspid. (*Tetracamphilius*)

Plesiomorphically, among catfishes, the tips of the premaxillary teeth are pointed or conical, with a single cusp (Fig. 15B–C). In *Acanthocleithron* and many chiloglanidins the premaxillary teeth are flattened at the tip, having a spatulate shape (Fig. 15A); in some species of *Chiloglanis* the premaxillary teeth are pointed. In *Tetracamphilius* the premaxillary teeth are distinctly bicuspid.

Suspensorium

39. Shape of autopalatine facet for lateral ethmoid. (CI = 0.200, RI = 0.636)

0: Autopalatine with flat or very slightly concave facet.

1: Autopalatine with distinctly concave facet. (*Parauchenoglanis*; *Malapteruridae*; *Amphilidae*; *Bagre*; all Mochokidae except *Mochokus brevis* [0])

Plesiomorphically, among catfishes, the autopalte rests on the lateral ethmoid without any well-formed facet. In most outgroup taxa the articulating surface is at most a raised area along the medial or dorsal side of the autopalte with a flat or slightly concave surface (Fig. 16A). In a number of outgroup taxa and in all mochokids except *Mochokus brevis* the autopalte has a well-developed articulating facet with a distinctly concave surface, characterized by a raised ridge anteriorly for cupping the antero-lateral corner of the lateral ethmoid (Fig. 16B). The assertion that a distinctly concave facet is present in *Mochokus* (Diogo, 2005) is not entirely accurate because he only examined *Mochokus niloticus* in that study.

40. Dimensions of autopalatine (ORDERED). (CI = 1.000, RI = 1.000)

0: Autopalatine cylindrical, several times longer than wide (more than 3X).

1: Autopalatine cylindrical, only slightly longer than wide (up to 3X).

(*Chiloglanis*)

2: Autopalatine block-like, length less than 2X width. (*Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the autopalte is an elongate bone, usually several times longer than wide (Fig. 16A–B). This is true even for the Diplomystidae, where the autopalte is generally bifurcated anteriorly (Arratia, 1987). Among the chiloglanidins the autopalte is shortened to various extents. In *Chiloglanis* the autopalte is relatively short, still cylindrical, but only up to three times as long as wide (Fig. 17A). The autopalte is further shortened in *Atopodontus*, *Atopochilus* and *Euchilichthys*, where the element is block-like and only slightly longer than wide (Fig. 17B). Because state 1 represents an

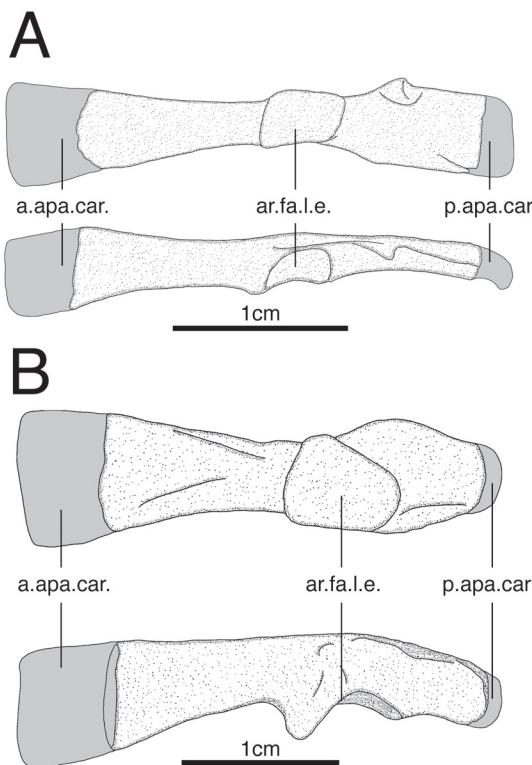


Fig. 16. Dorsomedial (top) and dorsolateral (bottom) views of autopalatine of A) *Ictalurus punctatus*; CU 79412 and B) *Synodontis longirostris*; SU 54222, right side.

intermediate state, the character is treated as ordered in the analysis.

41. Presence or absence of posterior cartilage of autopalatine. (CI = 0.333, RI = 0.909)

0: Posterior autopalatine cartilage present.

1: Posterior autopalatine cartilage absent. (*Amphililus*; *Tetraclamphilius*; *Zaireichthys*; *Phractura*; *Malapteruridae*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the posterior end of the autopalatine is capped by a small plug of cartilage (Fig. 16A–B). In all chiloglanidins, the Malapteruridae and all Amphiliidae except *Doumea* the posterior end of the autopalatine is without cartilage (Fig. 17A–B). In *Doumea* examined the posterior end of the autopalatine is capped by a very small amount of cartilage, contrary to the assertion of Diogo (2005).

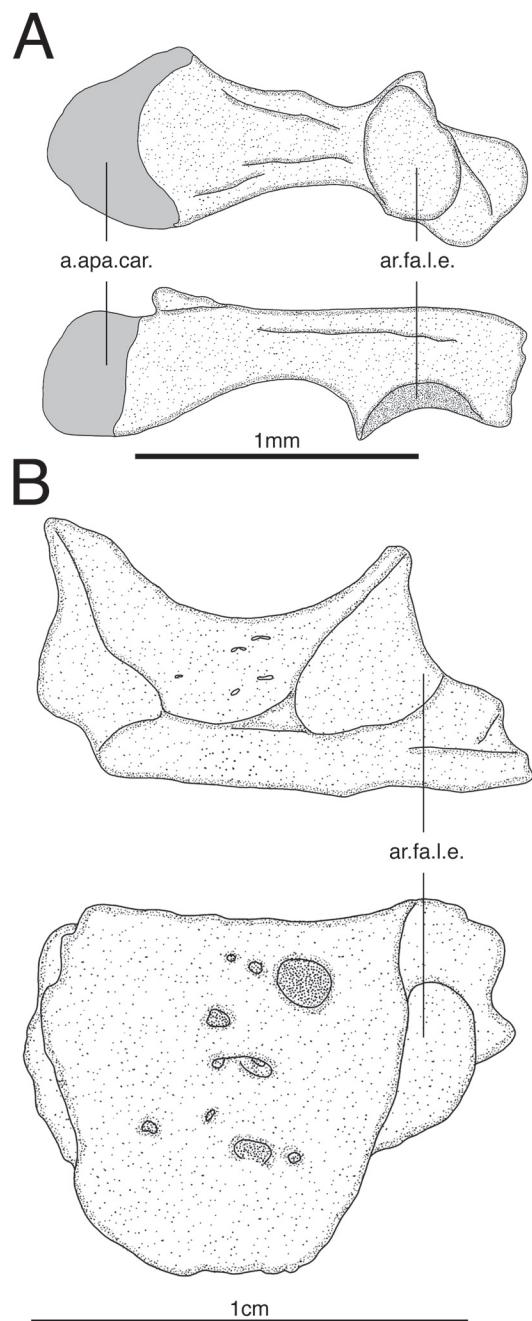


Fig. 17. Medial (top) and dorsal (bottom) views of autopalatine of A) *Chiloglanis batesii*; CU 91434 and B) *Euchilichthys royauxi*; CU 91764, right side.

42. Presence or absence of hyomandibular process. (CI = 0.500, RI = 0.952)

0: Hyomandibular process absent.

1: Hyomandibular process present. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*)

Plesiomorphically, among catfishes, the anteromedial edge of the hyomandibula is relatively smooth, or at least without any well-developed, elongate processes (Fig. 18A). In *Mochokiella*, *Acanthocleithron*, *Microsynodontis* and *Synodontis* there is a well-formed elongate process along the anteromedial edge of the hyomandibula (Fig. 18B). The hyomandibular process is notably absent in all chiloglanidins. In *Mochokus* the medial edge of the hyomandibular exhibits a sudden bend, creating a small vertical flange. The flange is broad and not at all pointed. This small flange is not considered homologous to the process seen in other mochokids.

43. Shape of dorsal articulating surface of hyomandibula (ORDERED). (CI = 0.333, RI = 0.905)

0: Dorsal articulating surface of hyomandibula elongate.

1: Dorsal articulating surface of hyomandibula roughly oval. (*Mochokiella*; *Microsynodontis*; all *Synodontis* except *S. acanthomias* [2], *S. pleurops* [2], *S. clarias* [2] and *S. sorex* [2])

2: Dorsal articulating surface of hyomandibula round. (*Synodontis acanthomias*; *S. pleurops*; *S. clarias*; *S. sorex*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

In all outgroup taxa examined the dorsal articulating surface of the hyomandibula (for articulation with the underside of the neurocranium) is elongate, many times longer than wide (Fig. 18A). Within the Mochokidae the dorsal articulating surface is shortened to various extents. *Mochokus* and *Acanthocleithron* show the plesiomorphic state, with an elongate articulating surface. In *Mochokiella*, *Microsynodontis* and some *Synodontis* the condyle is oval in dorsal view, around two times longer than wide (Fig. 18B). In the chiloglanidins and the remaining *Synodontis* the condyle is further shortened, generally rounded and often spherical (Fig. 18C). Despite the very small articulation in these taxa, the hyomandibula is still quite firmly attached. The ball-and-socket articulation may serve to strengthen the articulation in the absence of a lengthy articulation or a pterotic spine (character 11). Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

44. Development of anterior pterygoid element (tendon bone). (CI = 0.400, RI = 0.900)

0: Greatly reduced anterior pterygoid element (tendon bone) absent.

1: Greatly reduced anterior pterygoid element (tendon

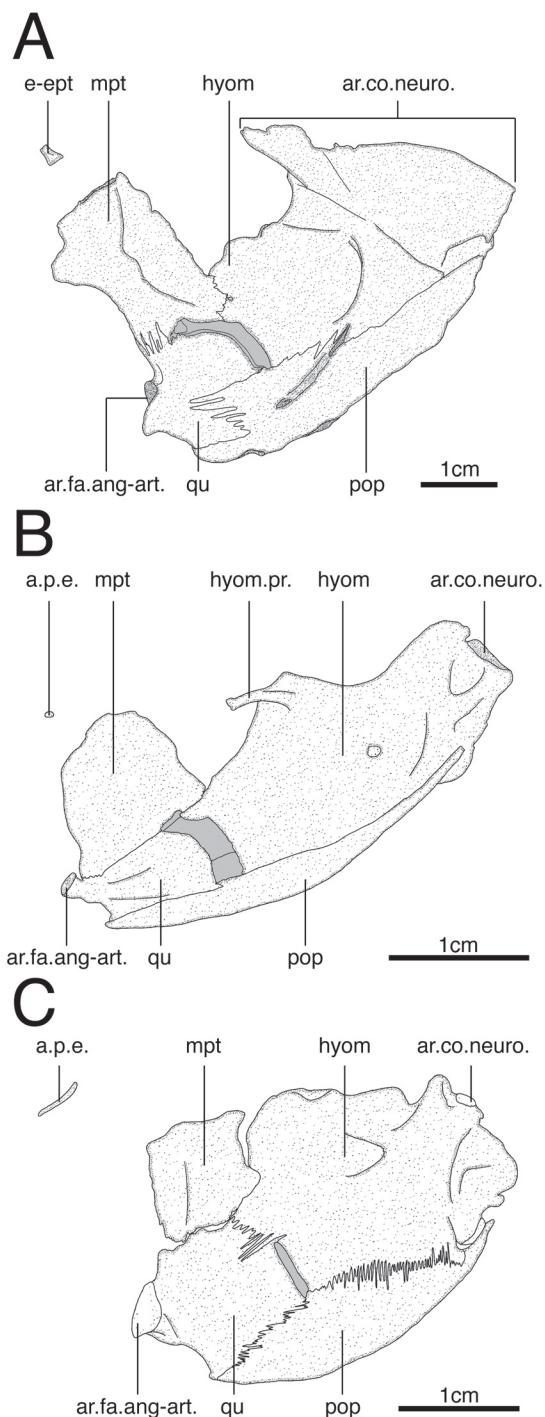


Fig. 18. Dorsolateral view of suspensorium of A) *Ictalurus punctatus*; CU 79412, B) *Synodontis acanthomias*; CU 91613 and C) *Euchilichthys royauxi*; CU 91614.

bone) present, spherical or ovoid. (*Microsynodontis*; *Synodontis*; all *Chiloglanis* except *Chiloglanis* sp. ‘igamba’ [2], *C. occidentalis* [2] and *C. congicus* [2])

2: Greatly reduced anterior pterygoid element (tendon bone) present, elongate and rod-like. (*Chiloglanis* sp. ‘igamba’; *C. occidentalis*; *C. congicus*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Among catfishes the number, shape and size of pterygoid elements is highly variable. In the Mochokidae the metapterygoid is the only unambiguous pterygoid element. In a large number of mochokids, however, there is also a tiny spherical or rod-shaped element anterior to the metapterygoid (Fig. 18B–C). This element may be the sesamoid entopterygoid of Arratia (1992), being somewhat medial to the palatoquadrate and formed as mineralizations within a ligament (also referred to as a ‘tendon bone’). The homology of this element to various plate-like pterygoid bones in other catfishes remains unclear. A greatly reduced ‘anterior pterygoid element’ is nonetheless a useful diagnostic character for the Mochokidae. Furthermore, the shape of this element is predictably variable within the family, making it phylogenetically informative. For these reasons, state 0 is the absence of the greatly reduced anterior pterygoid element (tendon bone), and may include the presence of (and possible replacement by) a more typical plate-like pterygoid element. Within the Mochokidae, a greatly reduced anterior pterygoid element is entirely absent in *Mochokus*, *Mochokiella* and *Acanthocleithron*. Alternatively, *Microsynodontis*, *Synodontis* and some species of *Chiloglanis* have a small spherical anterior pterygoid element within a ligament joining the metapterygoid and the articulation of the autopalatine with the lateral ethmoid. A similar but elongate element is found in other species of *Chiloglanis* as well as *Atopodontus*, *Atopochilus* and *Euchilichthys*.

Opercular Series

45. Presence or absence of opercular spines. (CI = 0.500, RI = AUT)

0: Posterior tip of operculum without a well-developed spine.

1: Posterior tip of operculum with a well-developed spine, larger in males than in females. (*Mochokiella*; *Synodontis acanthopercra*)

Plesiomorphically, among catfishes, and in most mochokids, the posterior vertex of the roughly triangular operculum is gently rounded and not formed as a sharp spine. In two species of mochokids, *Mochokiella paynei* and *Synodontis acanthopercra*, there is a well-developed spine at the posterior vertex of the operculum (Friel and Vigliotta, 2006; Figs. 1–3), which protrudes from the skin and is visible externally. In each case this feature is sex-

ually dimorphic, wherein males have a much larger spine than females. A sexually dimorphic opercular spine is also found in a related undescribed species of *Synodontis* (Vreven, personal communication). Because the opercular spine is easily missed, extra care was taken to examine males and females of all mochokid species when available. No other species showed this feature, though sexually dimorphic spines on other bony elements are fairly common within the Mochokidae. The presence of sexually dimorphic, spiny ornamentation in the Mochokidae is reviewed by Friel and Vigliotta (2006).

Hyoid and Branchial Arches

46. Development of parurohyal. (CI = 1.000, RI = 1.000)

0: Parurohyal not reduced.

1: Parurohyal greatly reduced. (Auchenipteridae; Doradidae; Mochokidae)

In most catfishes, as in most outgroup taxa examined, the parurohyal is composed of an articulating portion anteriorly, with a posteriorly directed process along the dorsal midline and a posterolaterally directed process on each side. The three processes are joined by well-formed lamina ventrally, giving the look of wings (Fig. 19A–B). In the Auchenipteridae, Doradidae and Mochokidae the postero-lateral processes and ventral lamina are absent, leaving only the oddly shaped anterior portion that articulates with the dorsohyal and venterohyal (Fig. 19C–D).

47. Fusion of dorsohyal and venterohyal. (CI = 0.200, RI = 0.692)

0: Dorsohyal and venterohyal separate.

1: Dorsohyal and venterohyal fused. (*Tetracamphilius*; *Zaireichthys*; *Phractura*; *Chiloglanis*; *Atopodontus*)

In most of the taxa examined here the dorsohyal and venterohyal are present as separate elements, joined to each other on each end by cartilage and separated from each other towards the middle by a gap (Fig. 20A). As a unit, the elements and the cartilage form a ring. In *Chiloglanis*, *Atopodontus* and some amphilids the dorsohyal and venterohyal are wholly fused to each other forming a solid bony ring, without cartilage joining their ends (Fig. 20B). Contrary to Mo’s (1991) assertion, the dorsohyal and venterohyal are not fused in all amphilids.

48. Shape of posterohyal. (CI = 0.500, RI = 0.947)

0: Posterohyal subtriangular, with distal point.

1: Posterohyal oddly shaped, not triangular. (*Doumea*; *Phractura*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the posterohyal is

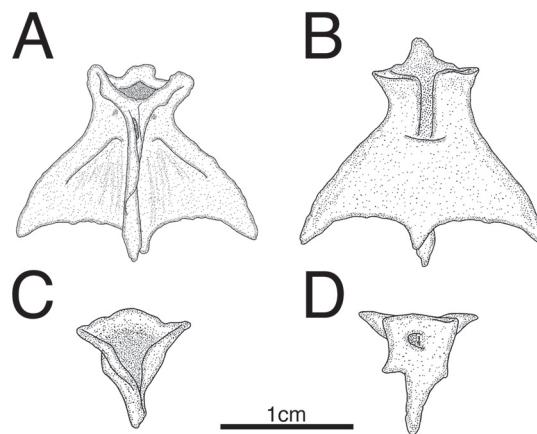


Fig. 19. Dorsal (A) and ventral (B) views of parurohyal of *Ictalurus punctatus*; CU 79412. Dorsal (C) and ventral (D) views of parurohyal of *Synodontis acanthomias*; CU 89763.

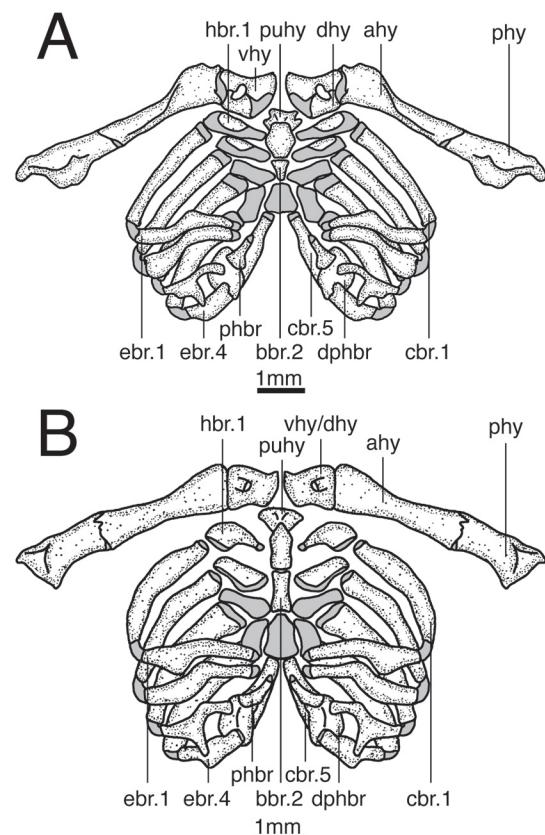


Fig. 20. Dorsal view of branchial arches of A) *Euchilichthys royauxi*; SAIAB 74306 and B) *Chiloglanis macropterus*; CU 91007.

roughly triangular, tapering distally to a point (Fig. 21A). In *Doumea*, *Phractura* and all chiloglanidins the postero-hyal is oddly shaped, the distal end being wider than the proximal end (Fig. 21B).

49. Presence or absence of interhyal. (CI = 0.333, RI = 0.867)

0: Interhyal present.

1: Interhyal absent. (*Tetracamphilius*; *Doumea*; *Phractura*; Mochokidae)

Plesiomorphically, among catfishes, and in the majority of the outgroup taxa a small interhyal is present near the distal end of the postero-hyal (Fig. 21A). In the Mochokidae and some amphiliids the interhyal is entirely absent (Figs. 20A–B, 21B). Mo (1991) did not list either of these families as missing the interhyal.

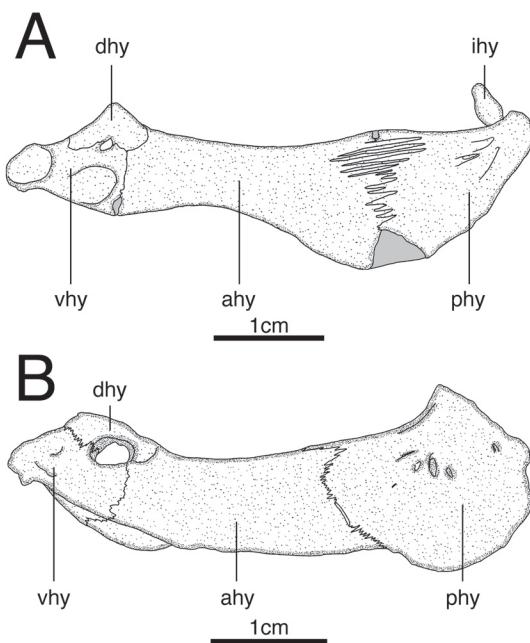


Fig. 21. Posteromedial view of hyoid bar of A) *Ictalurus punctatus*; CU 79412 and B) *Euchilichthys royauxi*; CU 91764, right side.

50. Shape of basibranchials. (CI = 1.000, RI = 1.000)

0: Basibranchials cylindrical and elongate.

1: Basibranchials flattened and laterally expansive. (*Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, as in the Diplostomatidae (Arratia, 1987), there are two roughly cylindrical and elongate basibranchials (Fig. 20B). In *Atopochilus* and *Euchilichthys* the basibranchials are flattened dorso-ventrally and rounded or many-sided in ventral or dorsal

view (Fig. 20A). The first basibranchial is always greatly expanded in *Atopochilus* and *Euchilichthys*, while the second basibranchial may be somewhat reduced in size, but still not elongate as in other catfishes.

51. Length of gill rakers (branchiospines). (CI = 1.000, RI = 1.000)

0: Gill rakers short.

1: Gill rakers extremely elongated. (*Synodontis membranacea*; *Synodontis batensoda*)

In the great majority of the taxa presented here the gill rakers (branchiospines) are rather short, their lengths slightly to a few times greater than their widths at the base. In *Synodontis membranacea* and *Synodontis batensoda* the gill rakers are extremely elongated, being several times longer than the width of their bases (greater than 10X). Among the several other *Synodontis* species examined the gill rakers were always rather short in comparison.

52. Number of branchiostegal rays (ORDERED). (CI = 0.150, RI = 0.528)

0: Eight or more branchiostegal rays.

1: Seven branchiostegal rays.

2: Six branchiostegal rays.

3: Five branchiostegal rays.

The number of branchiostegal rays is highly variable among catfishes. Nonetheless, the number of rays is predictably variable between certain higher-level groups. Putatively basal catfishes, including the Diplomystidae, have a minimum of eight branchiostegal rays (Arratia, 1987). Members of the Mochokidae possess five to eight branchiostegal rays, with a notable reduction to five or six in nearly all species of *Chiloglanis* (never greater than seven). As a count of discrete elements, this character allowed for the hypothesis of a transformational series and is treated as ordered in the analyses. Refer to the matrix for a more exact distribution of states.

Pectoral Girdle and Fins

53. Size of postcleithral process. (CI = 0.400, RI = 0.900)

0: Postcleithral process short.

1: Postcleithral process long. (*Zaireichthys*; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*)

2: Postcleithral process altogether absent. (*Amphilus*; *Doumea*; *Phractura*; Malapteruridae)

Plesiomorphically, among catfishes, a posteriorly directed postcleithral (humeral) process is found just above the pectoral spine articulation. It is triangular, pointed and relatively short, reaching only slightly past the posterior

extremity of the dorsal processes of the cleithrum (Fig. 22A). Within the Mochokidae, all chiloglanidins possess a relatively short postcleithral process. In the Doradidae, Auchenipteridae, *Zaireichthys* and remaining mochokids the postcleithral process is generally pointed and triangular, but sometimes blunt-ended, and in all cases quite long, extending well beyond the posterior extremities of the dorsal processes of the cleithrum (Fig. 22B). In general, the most impressive postcleithral processes are found in those taxa that also have large and strongly serrated pectoral spines. In some amphiliids and all malapterurids the postcleithral process is absent altogether. The small dorsally located process on the cleithrum in some amphiliids is not considered homologous with the more ventrally placed postcleithral process in other catfishes.

54. Shape of postcleithral process. (CI = 0.667, RI = 0.750)

0: Postcleithral process pointed.

1: Postcleithral process rounded or truncate. (*Acanthocleithron*; *Synodontis pleurops*; *S. congica*)

2: Postcleithral process shape sexually dimorphic, pointed in females and enlarged and rounded in males. (*Chiloglanis occidentalis*; *C. batesii*; *C. polypogon*)

Inapplicable: In *Amphilus*, *Doumea* and *Phractura* and Malapteruridae, because the postcleithral process is absent.

In most of the taxa presented here, including most mochokids, the postcleithral process is acutely pointed in lateral view (Fig. 22A–B). Within the Mochokidae the depth (and therefore the angle of the posterior vertex) of the postcleithral process may vary, but in most taxa it is clearly pointed. Rarely, as in *Acanthocleithron* and some species of *Synodontis*, the postcleithral process is rounded or truncate, with a blunt posterior end. In *Synodontis*, the presence of a truncate postcleithral process seems to be restricted to certain species within the Congo River basin. In all instances the truncate shape is notably different than the shape seen in the remaining *Synodontis* species. Poll (1971; plates 8–12) illustrates a large number of postcleithral processes for the genus *Synodontis*. In *Chiloglanis* the shape of the postcleithral process can be sexually dimorphic (Roberts, 1989). In certain species, females display the plesiomorphic pointed postcleithral process and males possess an enlarged, rounded process that shields the flank (Fig. 22C).

55. Presence or absence of mesocoracoid arch. (CI = 0.500, RI = 0.800)

0: Mesocoracoid arch present.

1: Mesocoracoid arch absent.

(Ariidae; Auchenipteridae; Doradidae)

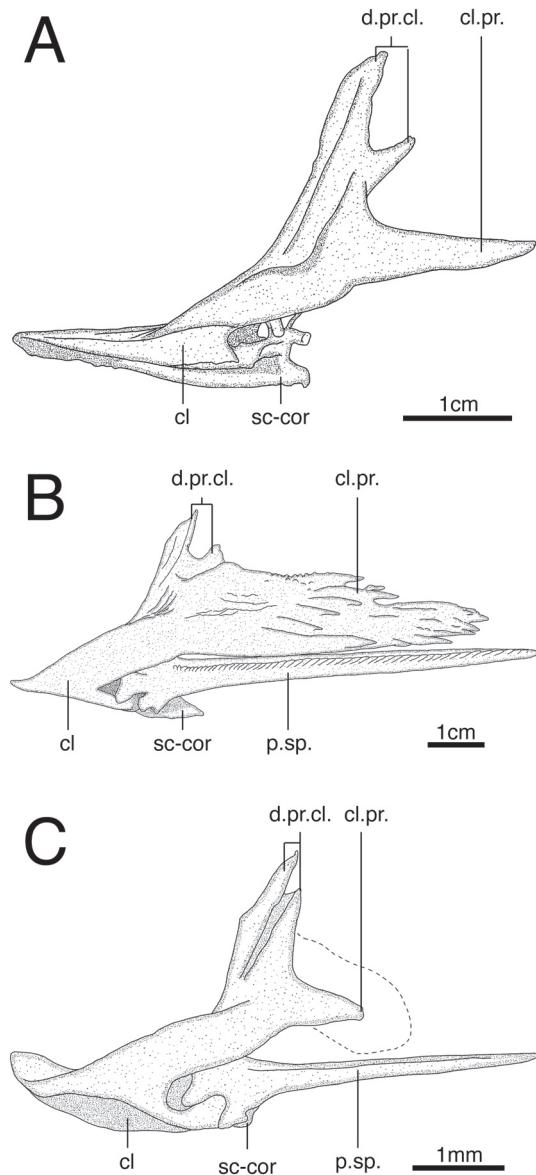
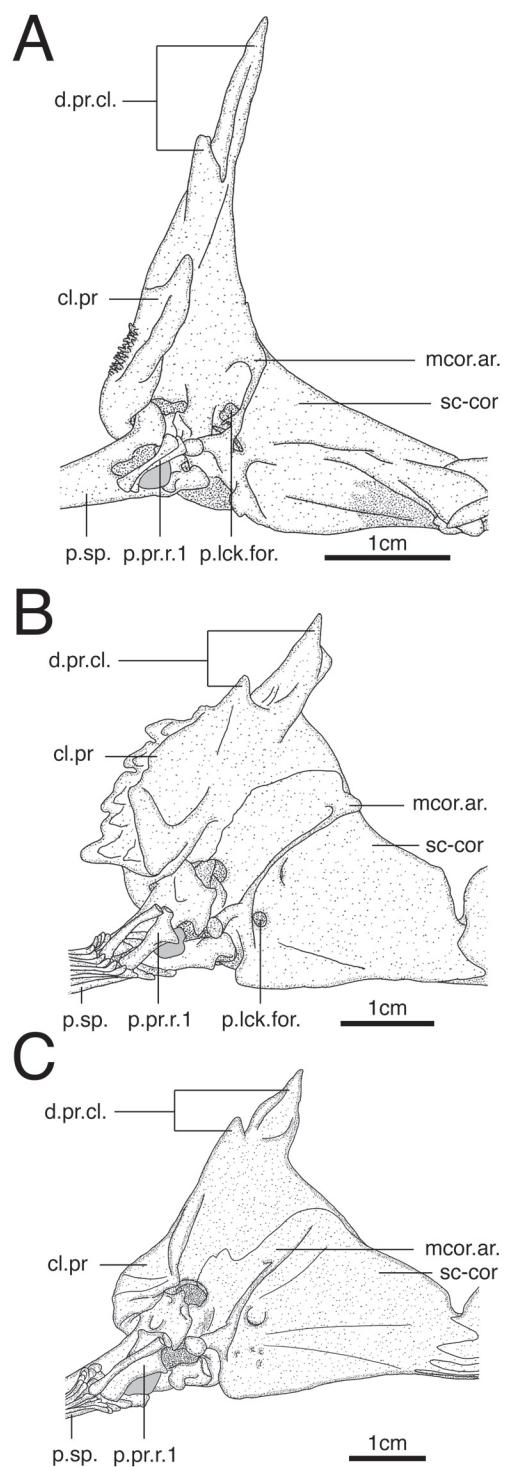


Fig. 22.(above) Lateral view of pectoral girdle of A) *Ictalurus punctatus*; CU 79403, B) *Synodontis acanthomias*; CU 91613 and C) *Chiloglanis batesii*; CU 91434. Dashed line indicates margin of enlarged postcleithral process found in males in *Chiloglanis batesii*. Pectoral spine removed in A.

Fig. 23.(right) Posterior view of pectoral girdle of A) *Ictalurus punctatus*; CU 79403, B) *Synodontis acanthomias*; CU 91613 and C) *Euchilichthys royauxi*; CU 91614.



Plesiomorphically, among catfishes, the mesocoracoid arch is a thin bridge of bone on the posterior side of the vertical scapulo-coracoid lamina that surrounds the adductor profundus muscle (Fig. 23A–C). Within the Mochokidae the mesocoracoid arch is variably shaped, but always present. Alternatively, in the Ariidae, Auchenipteridae and Doradidae the mesocoracoid arch is entirely absent (Mo, 1991; Diogo, 2005).

56. Shape of dorsal terminus of mesocoracoid arch. (CI = 0.333, RI = 0.917)

0: Mesocoracoid arch terminating at dorsal edge of scapulo-coracoid lamina with obvious bend in arch.

1: Mesocoracoid arch broadly joined to rear of scapulo-coracoid lamina without any obvious bend in arch. (Amphiliidae; *Mochokus*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Inapplicable: In the Ariidae, Doradidae and Auchenipteridae, because the mesocoracoid arch is absent.

Among taxa possessing a mesocoracoid arch its dorsal terminus attaches to the dorsal edge of the vertical lamina of the scapulo-coracoid at a sharp angle, producing a dorsally or posterodorsally directed prominence (Fig. 23A–B). In *Mochokus* and all chiloglanidins, as well as the Amphiliidae, the mesocoracoid arch does not terminate at the dorsal edge, but is broadly joined to the posterior side of the vertical lamina of the scapulo-coracoid, without any dorsally directed prominence (Fig. 23C).

57. Presence or absence of pectoral-locking foramen. (CI = 0.333, RI = 0.926)

0: Pectoral-locking foramen present.

1: Pectoral-locking foramen absent. (Amphiliidae; Ariidae; Auchenipteridae; Doradidae; all *Chiloglanis* except *C. macropterus* [0]; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

In many catfishes, there is a foramen in the scapulo-coracoid just medial to the glenoid cavity, which is obstructed or partially obstructed when the spine is fully extended (Fig. 23A–B). This is the pectoral-locking foramen of Brousseau (1976). Among the outgroup taxa, the Amphiliidae, Ariidae, Auchenipteridae and Doradidae lack a pectoral-locking foramen. The nature of this character within the Diplomystidae and Malapteruridae was unclear. Within the Mochokidae the pectoral-locking foramen is generally present, but absent in all chiloglanidins except *Chiloglanis macropterus*.

58. Development of proximal portion of first ossified pectoral-fin proximal radial. (CI = 0.250, RI = 0.829)

0: First ossified pectoral-fin proximal radial without processes proximally.

1: First ossified pectoral-fin proximal radial with a ventral process proximally. (*Chrysichthys*; *Parauchenoglanis*; Schilbidae; *Mochokiella*; *Microsynodontis*; all *Synodontis* except *S. contracta* [0])

2: First ossified pectoral-fin proximal radial with dorsal and ventral processes proximally. (Ariidae; *Chiloglanis disneyi*; *C. macropterus*; *C. conicus*; *C. carnosus*; *Chiloglanis* sp. ‘chambeshi’; *Chiloglanis* sp. ‘kalungwishi’; *Chiloglanis* sp. ‘burundi’; *Atopochilus*; *Euchilichthys*)

Among catfishes, including the Diplomystidae, there are three pectoral-fin proximal radials, the first cartilaginous and the next two ossified. Plesiomorphically, among catfishes, as in the Diplomystidae, the first ossified proximal radial of the pectoral fin is elongate and narrow along its entire length (Arratia, 1987), without any conspicuous ventral or dorsal processes at the proximal end (Fig. 23A). Within the Mochokidae, this plesiomorphic condition is notably present in *Mochokus*; a few species of *Chiloglanis* and *Synodontis* show this state as well. In a small number of outgroup taxa, as well as *Mochokiella*, *Microsynodontis* and most *Synodontis*, the proximal portion of the element has a ventrally directed process (Fig. 23C). In several chiloglanidins and the Ariidae the proximal portion of this element exhibits both ventral and dorsal processes (Fig. 23B). This multistate character is left unordered because there is no obvious transformational series. The presence of a ventral process is most likely not required before the addition of a dorsal process. A more logical intermediate state would be the presence of modest processes, both ventrally and dorsally at the proximal end of the element.

59. Presence or absence of anterior pectoral-spine serra. (CI = 0.250, RI = 0.889)

0: Anterior margin of pectoral spine without serra.

1: Anterior margin of pectoral spine with well-formed serra. (Pangasiidae; *Chrysichthys*; Schilbidae; Ariidae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; all *Synodontis* except *S. contracta* [0] and *S. pleurops* [0])

The presence or absence of serra along the anterior margin of the pectoral spine is phylogenetically informative for groups within the Siluriformes, including the Mochokidae. Among putatively basal catfishes, including the Diplomystidae, the anterior margin of the pectoral spine is keeled, but without well-formed serra (Arratia, 1987). In all mochokids, except the chiloglanidins and some *Synodontis*, the anterior margin of the pectoral spine has very well formed serra. Anterior pectoral-spine serra are also present in several outgroup taxa.

60. Presence or absence of posterior pectoral-spine serra. (CI = 0.286, RI = 0.773)

- 0:** Posterior margin of pectoral spine with serrae.
1: Posterior margin of pectoral spine with small denticulations. (Ictaluridae; *Synodontis contracta*; *Chiloglanis macropterus*; *Chiloglanis* sp. ‘burundi’; *Atopodontus*; *Euchilichthys*)
2: Posterior margin of pectoral spine without serrae. (Malapteruridae; *Amphilios*; *Tetracamphilius*; *Doumea*; *Phractura*; all *Chiloglanis* except *C. macropterus* [1] and *Chiloglanis* sp. ‘burundi’ [1])

The presence or absence of serrae along the posterior margin of the pectoral spine is phylogenetically informative for groups within the Siluriformes. In some putatively basal catfishes, including the Diplomystidae, the posterior margin of the pectoral spine has well-formed, pointed serrae (Arratia, 1987). Size of the serrae along the posterior margin of the pectoral spine is highly variable within the Mochokidae. Well developed serrae are present in many mochokids, but they are notably reduced in most chiloglanidins and sometimes altogether absent. Serrae are necessarily absent in the Malapteruridae and most amphiliids because the pectoral spine is flexible, not ossified as in a great majority of catfishes.

61. Number of pectoral-fin rays (ORDERED). (CI = 0.211, RI = 0.651)

- 0:** Nine or more pectoral-fin rays.
1: Eight pectoral-fin rays.
2: Seven pectoral-fin rays.
3: Six pectoral-fin rays.
4: Five pectoral-fin rays.

The number of pectoral-fin rays is highly variable among catfishes, but does characterize species and some higher-level groups. For example, within the Mochokidae, the number of pectoral-fin rays is reduced in *Microsynodontis* and *Mochokus*. Plesiomorphically, among catfishes, as in the Diplomystidae, there are nine or more soft pectoral-fin rays (Arratia, 1987). In the Mochokidae the number of pectoral-fin rays is between five and nine. Number of pectoral-fin rays can vary within a species and in each instance the count reported is modal. As a count of discrete elements, this character allowed for the hypothesis of a transformational series and is treated as ordered in the analyses. Refer to the matrix for a more exact distribution of states.

Dorsal Fin

62. Presence or absence of anterior dorsal-spine serrae. (CI = 0.250, RI = 0.500)

- 0:** Anterior margin of dorsal spine without well-formed serrae.
1: Anterior margin of dorsal spine with well-formed serrae

along entire face. (Auchenipteridae; Doradidae; *Mochokus niloticus*; *Synodontis clarias*; *S. batesii*)

Inapplicable: In the Malapteruridae, because these taxa do not have a dorsal spine.

Plesiomorphically, among catfishes, as in the Diplomystidae, the anterior margin of the dorsal spine is without any conspicuous serrae (Arratia, 1987). In the Auchenipteridae, the Doradidae, *Mochokus niloticus* and a small number of *Synodontis* the dorsal spine has well-formed, pointed serrae along the entire anterior margin (Friel and Sullivan, 2008). Some *Synodontis* exhibit serrae along the proximal or distal ends of the dorsal spine, with the number and size of these few serrations being highly variable within a species (sometimes absent). These taxa are coded as showing state 0.

63. Presence or absence of posterior dorsal-spine serrae. (CI = 0.143, RI = 0.778)

- 0:** Posterior margin of dorsal spine without well-formed serrae.
1: Posterior margin of dorsal spine with well-formed serrae.

(Ariidae; *Centrodoras*; *Platydoras*; *Mochokiella*; all *Microsynodontis* except *M. vigilis*; *Synodontis*; *Chiloglanis macropterus*; *C. occidentalis*; *C. polypogon*; *Chiloglanis* sp. ‘burundi’)

Inapplicable: In the Malapteruridae, because these taxa do not have a dorsal spine.

Plesiomorphically, among catfishes, as in the Diplomystidae, the posterior margin of the dorsal spine is without any conspicuous serrae (Arratia, 1987). Small, blunt denticulations are sometimes found in a longitudinal groove along the posterior margin, but truly well-formed and acutely pointed serrae are absent. In some of the Ariidae, Doradidae and Mochokidae the posterior margin of the dorsal spine has well-formed and pointed serrae.

64. Number of dorsal-fin rays (ORDERED, user-defined). (CI = 0.250, RI = 0.679)

- 0:** Seven or more dorsal-fin rays.
1: Six dorsal-fin rays.
2: Five dorsal-fin rays.
3: No dorsal-fin rays.

Among catfishes, the number of dorsal-fin rays is quite variable, but phylogenetically informative for certain groups, including the Mochokidae. In some putatively basal taxa there are seven or more soft rays in the dorsal fin. In states 1 and 2 the number of rays is reduced to six and five, respectively. Within the Mochokidae, the number of dorsal-fin rays is notably reduced in most chiloglanidins (usually five or six rays). In the Malapteruridae (state 3) there are no dorsal-fin rays or other typical dorsal-fin elements. To

maintain independence of characters, in all other characters where dorsal-fin elements are taken into account, the state in the Malapteruridae is considered inapplicable. The nature of this character, being a count of discrete elements allowed for the hypothesis of a transformational series and is treated as ordered. In this instance, state 3 required the use of a user-defined step matrix. The matrix expresses the idea that it is possible to move from any state to the state 3 in a single step and vice versa; movements between states 0 through 2 are of a typical ordered nature. Refer to the matrix for a more exact distribution of states.

Pelvic Fin and Basipterygia

65. Number of pelvic-fin rays. (ORDERED) (CI = 0.400, RI = 0.812)

0: Six pelvic-fin rays.

1: Seven pelvic-fin rays. (*Centrodoras*; *Platydoras*; all Mochokidae except *Chiloglanis* sp. ‘ntumbachushi’ [2])

2: Eight pelvic-fin rays. (Ictaluridae; Pangasiidae; *Chiloglanis* sp. ‘ntumbachushi’)

Among catfishes, the number of pelvic-fin rays is modestly variable, but quite conserved within certain families and therefore phylogenetically informative. There are six pelvic-fin rays (plus a bony splint) in the Diplomystidae, as well as several outgroup taxa. In states 1 and 2 the number of pelvic-fin rays is seven and eight respectively. All mochokids, except a single undescribed species of *Chiloglanis* (eight rays), have seven pelvic-fin rays. A small number of outgroup taxa also show an elevated number of pelvic-fin rays. As a count of discrete elements, this character allowed for the hypothesis of a transformational series and is treated as ordered in the analyses.

66. Presence or absence of pelvic splint. (CI = 0.125, RI = 0.682)

0: Pelvic splint present.

1: Pelvic splint absent.

Among various ingroup and outgroup taxa, including the Diplomystidae (Arratia, 1987), a small splint-like element is present just lateral to the base of the outermost pelvic-fin ray (Fig. 24A, C). Within the Mochokidae, a pelvic splint is found in several *Synodontis* and several chiloglanidins. A pelvic splint is entirely absent in several of the outgroup taxa and remaining mochokids, most notably *Mochokus*, *Mochokiella*, *Acanthocleithron*, *Microsynodontis* and *Atopodontus* (Fig. 24B). Refer to the matrix for a more exact distribution of states.

67. Development of anterior processes of basipterygia. (CI = 0.750, RI = 0.952)

0: Anterolateral process extending further anteriorly.

1: Anteromedial process extending further anteriorly. (Malapteruridae)

2: Anterolateral and anteromedial processes terminating at roughly same level. (*Amphilus*; *Tetracamphilius*; *Zaireichthys*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

3: Anterolateral and anteromedial processes of basipterygia indistinguishable. (*Doumea*; *Phractura*)

Plesiomorphically, among catfishes, as in the Diplomystidae (Arratia, 1987), the anterolateral process of the basipterygia extends further anteriorly than the anteromedial process (Fig. 24B); within the Mochokidae, this state is found in *Mochokus*, *Mochokiella*, *Acanthocleithron*, *Microsynodontis* and *Synodontis*. In the Malapteruridae the opposite is true, wherein the anteromedial process of the basipterygia extends further anteriorly. In *Amphilus*, *Tetracamphilius*, *Zaireichthys* and all chiloglanidins the anterior processes terminate at about the same level (Fig. 24C). In *Doumea* and *Phractura* the individual processes are indistinguishable, completely joined by laminar bone.

68. Development of cartilage of anterior processes of basipterygia. (CI = 0.500, RI = 0.950)

0: Cartilage of anterior processes not continuous.

1: Cartilage of anterior processes continuous. (*Amphilus*; *Tetracamphilius*; *Zaireichthys*; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Inapplicable: In the *Doumea* and *Phractura*, because the anterior processes are indistinguishable.

Plesiomorphically, among catfishes, the anterior processes of the basipterygia are capped by small lengths of cartilage that terminate without joining the cartilage of the neighboring process (Fig. 24A–B). In *Amphilus*, *Tetracamphilius*, *Zaireichthys* and all chiloglanidins the anterior cartilages of the anterolateral process and the anteromedial process are joined to each other on each half of the pelvic girdle (Fig. 24C). In addition, the arcs of cartilage from each half of the pelvic girdle are joined to each other at the midline.

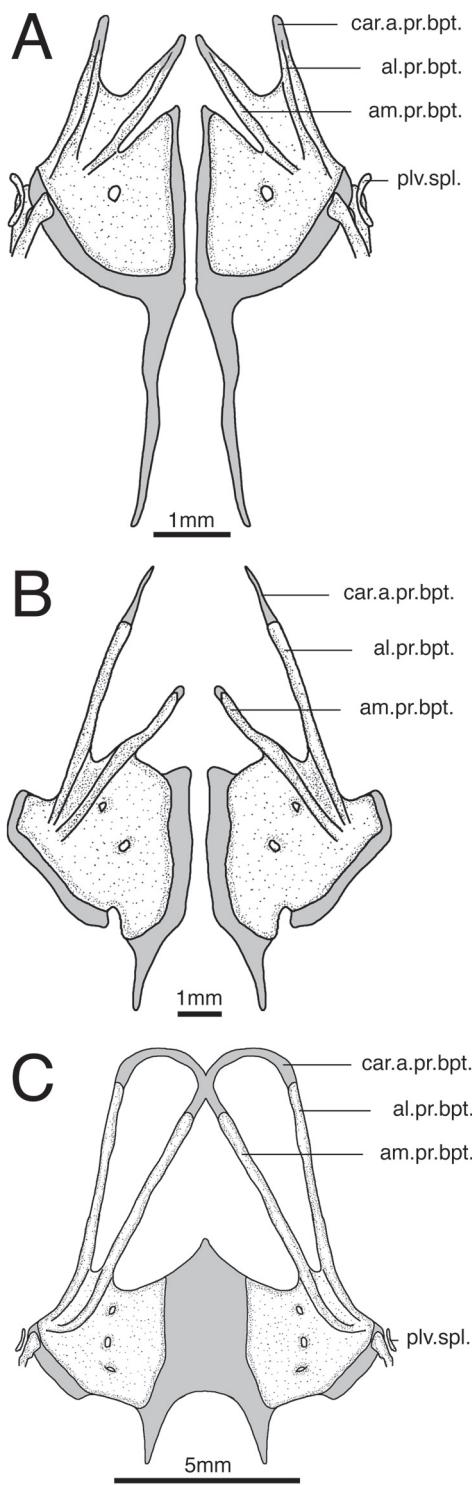
Anal, Adipose and Caudal Fins

69. Development of first anal-fin pterygiophore. (CI = 0.500, RI = 0.938)

0: First anal-fin pterygiophore developed as slender, elongate element.

1: First anal-fin pterygiophore developed as flat, rounded, plate-like element. (all *Chiloglanis* except *C. batesii* [0]; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

In all of the outgroup taxa, as well most mochokids, the first anal-fin pterygiophore is a slender, elongate element like all of the succeeding pterygiophores. In all



chiloglanidins except *Chiloglanis batesii* the first anal-fin pterygiophore is flattened and rounded when viewed ventrally, a disc-like element just below the surface of the skin.

70. Adipose fin. (CI = 1.000, RI = 1.000)

0: Adipose fin without rays.

1: Adipose fin with rays. (*Mochokus*)

Plesiomorphically among catfishes, as in the vast majority of the taxa here, the adipose fin is a fleshy fin, without any rays for support. In *Mochokus* the adipose fin has ossified rays similar to those found in all other fins. There are no radial elements associated with the rays. The adipose fin does not have rays in *Acanthocleithron chapini*, as reported in the original description (Nichols and Griscom, 1917).

71. Fusion of lower caudal-fin elements (ORDERED). (CI = 0.286, RI = 0.750)

0: Parhypural, hypural one and hypural two autonomous.

1: Parhypural autonomous, hypurals one and two fused. (*Amphilophus*; *Ariidae*; *Centrodoras*; *Agamyxis*; *Euchilichthys guentheri*; *E. royauxi*)

2: Parhypural, hypural one and hypural two fused. (*Tetraacanthophilus*; *Zaireichthys*; *Doumea*; *Phractura*; *Malaapteruridae*; *Auchenipteridae*; *Platydoras*; all Mochokidae except *Euchilichthys guentheri* and *E. royauxi* [1])

Among catfishes, the hypural elements of the caudal fin show various degrees of fusion. The lower hypurals (parhypural, hypural one and hypural two) are largely separated from the upper hypurals (hypural three and beyond) by a gap in most catfishes and therefore treated separately in this work. In some outgroups, including the Diplomystidae (Arratia, 1987), the parhypural, hypural one and hypural two are completely autonomous (Fig. 25A). In a small number of taxa, including *Euchilichthys*, there is an intermediate level of fusion in these elements, where hypurals one and two are fused, but the parhypural is autonomous (Fig. 25B). In the remainder of the Mochokidae, and several outgroups, there is greater fusion of these elements, where hypurals one and two and the parhypural are wholly fused (Fig. 25C). Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

72. Fusion of upper caudal-fin elements (ORDERED). (CI = 0.250, RI = 0.793)

0: All upper hypurals autonomous.

Fig. 24.(left) Ventral view of basipterygia of A) *Ictalurus punctatus*; CU 81105, B) *Synodontis acanthomias*; AMNH 235705 and C) *Euchilichthys royauxi*; SAIAB 40150.

1: Hypurals fusion pattern intermediate. (*Doumea*; Malapteruridae; Ariidae; Auchenipteridae; Doradidae; *Chiloglanis* sp. ‘igamba’; *Chiloglanis* sp. ‘ntumbachushi’; *Atopochilus*; *Euchilichthys*)

2: Upper hypurals completely fused. (*Tetracamphilius*; *Zaireichthys*; *Phractura*; all Mochokidae except *Chiloglanis* sp. ‘igamba’ [1], *Chiloglanis* sp. ‘ntumbachushi’ [1], *Atopochilus* [1] and *Euchilichthys* [1])

As with the lower hypurals, the upper hypurals show various degrees of fusion in catfishes. In some outgroups, including the Diplomystidae (Arratia, 1987), the upper hypurals (three through five OR three through six) are totally autonomous (Fig. 25A). In *Euchilichthys* and some *Chiloglanis*, as well as a number of outgroup taxa, some of the upper hypurals are fused, but at least one is autonomous (Fig. 25B). In the remainder of the Mochokidae and some Amphiliidae the upper hypurals are wholly fused (Fig. 25C). Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

73. Proximity of upper and lower hypurals. (CI = 0.333, RI = 0.500)

0: Hypurals two and three divided by obvious space.

1: Hypurals two and three joined or closely set. (*Doumea*; *Phractura*; Malapteruridae; *Mochokus*)

As noted above, the upper and lower hypurals are separated by an obvious space in many catfishes; this is true for the majority of the taxa considered here (Figs. 25A–C). Alternatively, in *Doumea*, *Phractura*, the Malapteruridae and *Mochokus* hypural fusion is taken to the extreme and the upper and lower hypurals are joined to each other, not separated by a space (Fig. 25D).

74. Number of principal caudal-fin rays (ORDERED). (CI = 0.235, RI = 0.350)

0: 9 + 9 principal caudal-fin rays.

1: 8 + 9 principal caudal-fin rays.

2: 7 + 8 principal caudal-fin rays.

3: 7 + 7 principal caudal-fin rays.

4: 6 + 7 principal caudal-fin rays.

5: 6 + 6 principal caudal-fin rays.

Among catfishes the number of principal caudal-fin rays is highly variable, but phylogenetically informative for certain taxa. In the Diplomystidae the principal caudal-fin ray count is 9 + 9 (Arratia, 1987). For a great number of catfishes, including many mochokids, the count is reduced by one in the upper lobe, 8 + 9 (state 1); this represents the highest caudal-fin ray count for any mochokid. In states 2 through 5 the principal caudal-fin count is further reduced. Within the Mochokidae, the number of principal caudal-fin rays is notably reduced in *Mochokus* (6 + 7 or 7 + 8), *Mochokiella* (7 + 8) and *Microsynodontis* (6 + 6 to 7 + 7).

As a count of discrete elements, this character allowed for the hypothesis of a transformational series and is treated as ordered in the analyses. Refer to the matrix for a more exact distribution of states.

75. Shape of caudal fin. (CI = 0.100, RI = 0.250)

0: Caudal fin forked.

1: Caudal fin truncate or rounded. (*Ameiurus*; *Parauchenoglanis*; *Zaireichthys*; Malapteruridae; Auchenipteridae; *Microsynodontis*; *Chiloglanis* sp. ‘igamba’; *C. disneyi*; *C. macrostomus*; *C. carnosus*; *Chiloglanis* sp. ‘kalungwishi’)

Among catfishes, the shape of the caudal fin is highly variable, but phylogenetically informative for some groups, including some mochokids. In the majority of the taxa considered here the caudal fin is forked. In state 1 the caudal fin is best described as truncate or rounded. Within the Mochokidae, *Microsynodontis* and some species of *Chiloglanis* display a truncate or rounded caudal fin.

Vertebrae, Weberian Apparatus and associated structures

76. Autonomy of anterior parapophyses of compound centrum. (CI = 0.333, RI = 0.920)

0: Anterior parapophyses of compound centrum not free.

1: Anterior parapophyses of compound centrum free. (Ariidae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Atopochilus*; *Euchilichthys*)

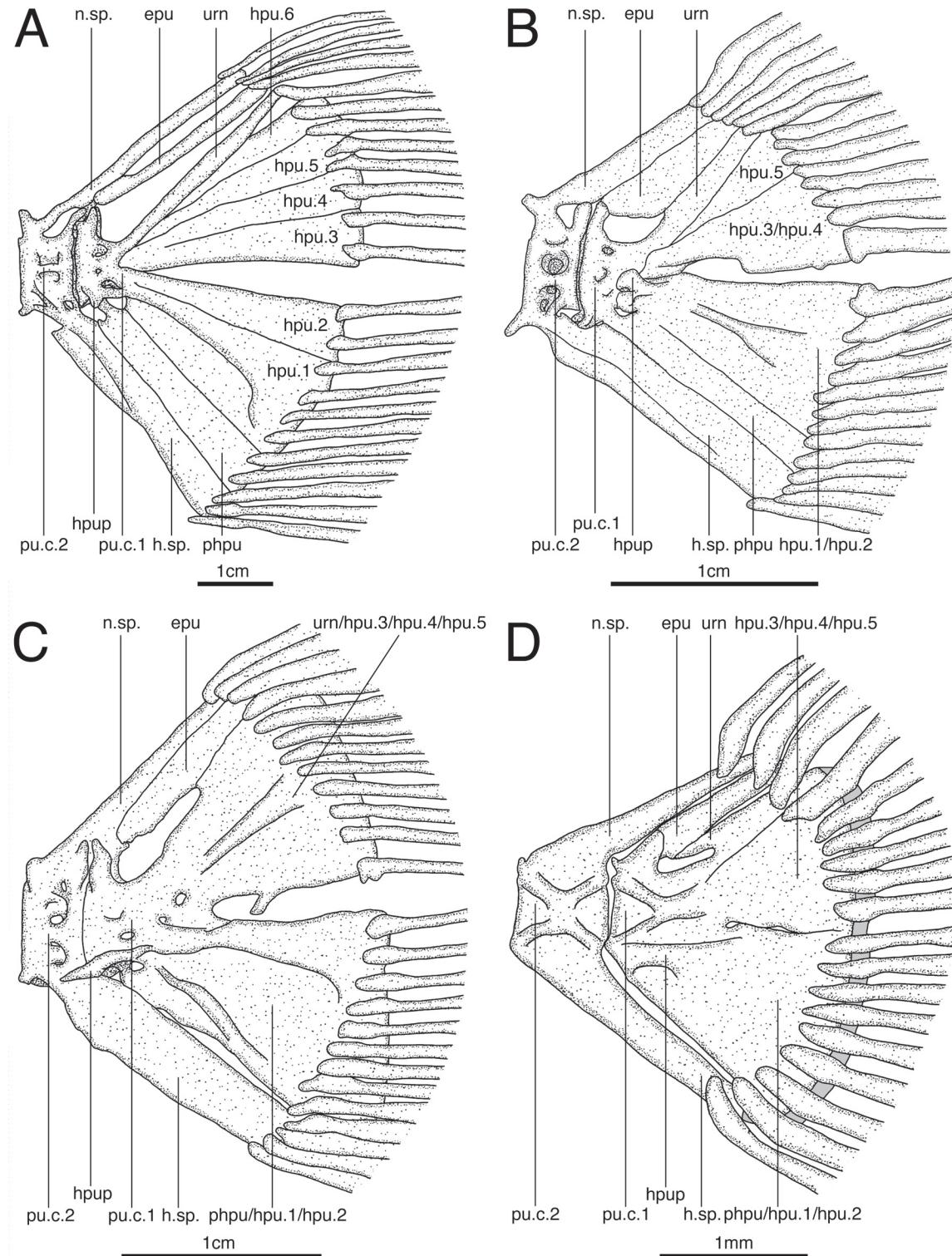
Plesiomorphically, among catfishes, as in the Diplomystidae, the anterior parapophyses of the compound centrum are tightly joined to the ventral processes of the ossified transcapular ligament (Fig. 3A). In the Ariidae, Auchenipteridae, Doradidae and several mochokids the anterior parapophyses are free of this articulation (Fig. 3B–C); a free parapophysis, such as this, has been referred to as the elastic spring apparatus (Bridge and Haddon, 1889, 1892; Alexander, 1965). Despite a similar shape, the anterior parapophyses of the compound centrum are not free of the ossified transcapular ligament in the Malapteruridae; these elements are closely joined by a very short, rigid ligament, apparently ossified in many instances.

77. Elaboration of anterior parapophyses of compound centrum. (CI = 0.333, RI = 0.840)

0: Anterior parapophyses not elaborated distally.

1: Anterior parapophyses plate-like distally. (Malapter-

Fig. 25.(page 105) Lateral view of caudal skeleton of A) *Ictalurus punctatus*; CU 79403, B) *Euchilichthys royauxi*; CU 91614, C) *Synodontis acanthomias*; CU 91613, D) *Mochokus niloticus*; CU 91386.



uridae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Atopochilus*; *Euchilichthys*)

2: Anterior parapophyses flap-like distally. (all *Chiloglanis* except *C. macropterus* [0], *Chiloglanis* sp. ‘kalungwishi’ [0] and *Chiloglanis* sp. ‘burundi’ [0]; *Atopodontus*)

In most outgroup taxa considered, the anterior parapophyses of the compound centrum are unspecialized, angular and without enlarged plates or expansions distally (Fig. 3A); the Ariidae show this state, despite the presence of a free elastic spring apparatus. In the Malapteruridae, Auchenipteridae, Doradidae and many mochokids the anterior parapophyses of the compound centrum are elaborated as enlarged plates distally (Fig. 3B–C). Among mochokids, in *Atopodontus* and most species of *Chiloglanis* the anterior parapophyses of the compound centrum are elaborated as enlarged flap-like structures distally. The flap-like structures surround a portion of the gas bladder anteroventrally (Fig. 5).

78. Development of anterior portion of anterior parapophyses of compound centrum. (CI = 0.250, RI = 0.760)

0: Anterior parapophysis of compound centrum unornamented anteriorly.

1: Anterior parapophysis of compound centrum with an obvious bend anteriorly. (Malapteruridae; *Mochokus*; *Acanthocleithron*; *Microsynodontis emarginatus*; *Microsynodontis vigilis*; *Synodontis contracta*; *Synodontis batesii*; *Atopochilus*; *Euchilichthys*)

2: Anterior parapophysis of compound centrum with well-formed anteriorly directed process anteriorly. (all *Synodontis* except *S. nigriventris* [0], *S. contracta* [1] and *S. batesii* [1])

Plesiomorphically, among catfishes, the anterior margin of the anterior parapophyses of the compound centrum are relatively smooth without anteriorly directed ornamentation. In the Malapteruridae and some mochokids the anterior parapophyses have an obvious bend along their length, creating a sharp anteriorly or anterodorsally directed angle. There are no well-formed anteriorly directed projections or processes at this bend (Fig. 3C). Alternatively, in most *Synodontis* the anterior margin of the anterior parapophysis is ornamented by a well-developed anteriorly directed process (Figs. 3B, 26).

79. Development of posterior parapophyses of compound centrum. (CI = 0.500, RI = 0.923)

0: Posterior parapophyses broadly joined to anterior.

1: Posterior parapophyses deeply divided from anterior. (Malapteruridae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Chiloglanis*

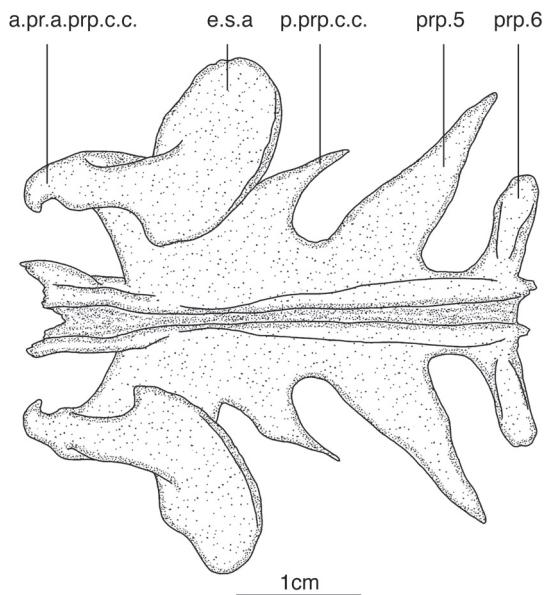


Fig. 26. Ventral view of compound centrum and elastic spring apparatus of *Synodontis geledensis*; UMMZ 241265.

macropterus; *Chiloglanis* sp. ‘burundi’; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

2: Posterior parapophyses entirely absent. (Auchenipteridae; Doradidae)

Plesiomorphically, among catfishes, as in the Diplostomatidae (Arratia, 1987), the posterior parapophyses of the compound centrum are broadly joined to the anterior parapophyses, creating a modestly formed dorsal shield over the gas bladder (Figs. 3A, 5). In the Malapteruridae and most mochokids the parapophyses of the compound centrum are deeply divided to their bases, or nearly so (Fig. 3B–C). In the Auchenipteridae and Doradidae the posterior parapophyses are very poorly developed or entirely absent.

80. Development of parapophyses of 5th centrum. (CI = 0.286, RI = 0.667)

0: Parapophyses of 5th centrum deeply divided from those of compound centrum.

1: Parapophyses of 5th centrum broadly joined to those of compound centrum. (*Amphilophus*; *Phractura*; Ariidae; *Acanthocleithron*; *Chiloglanis disneyi*; *Chiloglanis* sp. ‘chambeshi’; *C. batesii*; *C. occidentalis*; *C. polypogon*; *Chiloglanis* sp. ‘ntumbachushi’; *Chiloglanis* sp. ‘igamba’)

2: Parapophyses of the 5th centrum entirely absent. (*Tetracamphilius*; *Zaireichthys*; Doradidae)

Plesiomorphically, among catfishes, as in a large maj-

ority of the taxa considered here, the parapophyses of the 5th centrum are formed as elongate lateral projections which are deeply divided and separate from the parapophyses of the compound centrum (Fig. 3A–C). In the Ariidae, *Amphilinius*, *Phractura*, *Acanthocleithron* and some *Chiloglanis* the parapophyses of the 5th centrum are broadly joined to the posterior parapophyses of the compound centrum, helping to form a dorsal shield over the gas bladder (Fig. 5). In *Tetraacanthophilius*, *Zaireichthys* and the Doradidae the parapophyses of the 5th centrum are entirely absent.

81. Development of parapophyses of 6th centrum. (CI = 1.000, RI = 1.000)

0: Parapophyses of 6th centrum simple.

1: Parapophyses of 6th centrum as enlarged struts. (*Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, the parapophyses of the 6th centrum are formed as moderately elongate, laterally directed processes supporting the first pleural rib (Fig. 3A–B). In all chiloglanidins the parapophyses of the 6th centrum are incorporated into an elongate venterolaterally directed strut that does not support a pleural rib (Figs. 3C, 5). The rib supported by the 6th parapophysis in other catfishes may be lost or incorporated into the bony strut in these taxa.

82. Fusion of anterior centra (ORDERED). (CI = 0.333, RI = 0.739)

0: Fusion of centra two through four. (Diplomystidae)

1: Fusion of centra one through five. (Ictaluridae; Pangasiidae; *Chrysichthys*; *Parauchenoglanis*; Schilbidae; Amphilidae; Malapteruridae; *Agamyxis*)

2: Fusion of centra one through six. (Ariidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; all *Synodontis* except *S. contracta* [3]; all *Chiloglanis* except *C. congicus* [3] and *Chiloglanis* sp. ‘burundi’ [3]; *Atopodontus*)

3: Fusion of centra one through seven. (Auchenipteridae; *Centroadoras*; *Platyadoras*; *Synodontis contracta*; *Chiloglanis congicus*; *Chiloglanis* sp. ‘burundi’; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, fewer centra are fused to the compound centrum. In the Diplomystidae, for example, the second through fourth centra are deeply sutured and fused (Arratia, 1987). Alternatively, in some putatively basal siluroids the second through fifth centra are fused as such (state 1); in addition, the first centrum is wafer-like and presumably fused to the compound centrum in these taxa (Fig. 3A). In state 2 the sixth centrum is tightly fused to this complex (Figs. 3B, 5); all mochokids show fusion through the sixth centrum, at least. In state 3 the seventh centrum is tightly fused to the complex (Fig.

3C). The nature of this character as a successive fusion of elements allowed for the hypothesis of transformational series and is treated as ordered in the analyses.

83. Development of os suspensoria. (CI = 0.667, RI = 0.800)

0: Ventral extremity of os suspensorium angular.

1: Ventral extremity of os suspensorium flattened and hammer shaped. (*Chiloglanis disneyi*; *C. carnosus*; *Chiloglanis* sp. ‘kalungwishi’; *Chiloglanis* sp. ‘ntumbachushi’)

2: Ventral extremity of os suspensorium flattened, paddle-shaped and greatly enlarged. (*Chiloglanis occidentalis*; *C. batesii*; *C. polypogon*)

In all of the outgroup taxa and most ingroup taxa the ventral extremity of the os suspensorium is formed as a rounded or angular nodule that lies tightly against the compound centrum (Fig. 3A). In derived states the ventral extremity of the os suspensorium is flattened and relatively free of the compound centra. In some species of *Chiloglanis* the ventral extremity of the os suspensorium is hammer-shaped. Alternatively, in some species of *Chiloglanis* the ventral extremity is an enlarged, paddle-shaped structure (Fig. 5).

84. Position of pleural rib articulations. (CI = 1.000, RI = 1.000)

0: Ribs articulating with ventral or posteroventral face.

1: Ribs articulating with dorsal face. (Doradidae)

2: Ribs articulating with posterior face. (Auchenipteridae)

3: Ribs articulating largely on dorsal face, but wrapping around posterior face to touch ventral surface as well. (Amphilidae)

Among catfishes, the position of the pleural rib articulation is highly variable, but phylogenetically informative for certain families. In several outgroup taxa, including the Diplomystidae, and in the Mochokidae the pleural ribs articulate on the ventral surface or the posteroventral surface of the parapophyses. Alternatively, in the Doradidae the ribs articulate on the dorsal surfaces of the parapophyses, while in the Auchenipteridae the ribs articulate with the posterior face. Finally, in the Amphilidae the ribs have a complex articulation, in which the rib sits on the dorsal side of the parapophysis and wraps posteriorly to the ventral surface.

85. Size of anterior pleural ribs. (CI = 0.250, RI = 0.812)

0: Anterior pleural ribs not particularly enlarged.

1: Anterior pleural ribs greatly enlarged. (*Parauchenoglanis*; Auchenipteridae; Doradidae; *Microsynodontis*; *Synodontis*)

Inapplicable: In the *Chiloglanis*, *Atopodontus*, *Atopo-*

chilus and *Euchilichthys*, as the first rib might be absent or fully incorporated into a strut-like process as described in character 81.

Plesiomorphically, among catfishes, the pleural ribs vary by length but are generally of similar thickness from anterior to posterior (Fig. 3A). Among mochokids, this plesiomorphic state is present in *Mochokus* and *Acanthocleithron*. In *Parauchenoglanis*, the Auchenipteridae, the Doradidae and remaining mochokids the pleural ribs are greatly enlarged anteriorly; the first rib is particularly enlarged (Fig. 3B). The ribs are modestly enlarged beyond the first and decrease in size moving posteriorly.

Lateralis System

86. Number of sensory-canal pores at each site. (CI = 0.333, RI = 0.714)

- 0:** One pore at each site along cephalic sensory canals.
- 1:** Multiple pores at each site along cephalic sensory canals. (*Chrysichthys*; *Parauchenoglanis*; Schilbidae; Ariidae; *Euchilichthys geuntheri*; *E. royauxi*)

The cephalic sensory canals open at the surface by a number of pores along each branch. In most of the taxa considered, including the Diplomystidae (Arratia and Huaquin, 1995) there is one pore (occasionally two or three) at each site along the cephalic sensory canals. However, in some species of *Euchilichthys*, as well as several outgroup taxa, the short tubules running to the skin surface from the cephalic sensory canals are ramified, resulting in numerous pores (sometimes as many as 10 or 12) at each site.

87. Number of pores in mandibular sensory canal. (CI = 0.625, RI = 0.912)

- 0:** Mandibular sensory canal with at least five pores.
- 1:** Mandibular sensory canal with four pores. (*Centrodoras*; *Platydoras*)
- 2:** Mandibular sensory canal with three pores. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; all *Synodontis* except *S. congica* [3])
- 3:** Mandibular sensory canal with two pores. (*Tetra-camphilius*; *Zaireichthys*; *Mochokus*; *Synodontis congica*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)
- 4:** Mandibular sensory canal with one pore. (*Doumea*; *Phractura*)
- 5:** No mandibular sensory canal. (*Chiloglanis*)

Plesiomorphically, among catfishes, there is a sensory canal running through each half of the mandible with a number of pores emanating from the canal. Herein, only those pores emanating from a hole in the lower jaw are counted. Pores emanating from the canal at the interface of the mandible and quadrate are excluded. In most of the outgroup taxa the mandibular sensory canal has more than

five pores; the number of pores emanating from the mandibular sensory canal was not known for the Diplomystidae. Mochokids show various reductions in the number of pores in the mandibular sensory canal. In derived states 1 through 4 the number of canal pores on each half of the mandible is reduced to as few as one. In state 5 the mandibular sensory canal is entirely absent and thus, no pores are present. This multistate character is left unordered because pores do not exist in an orderly fashion along the mandibular sensory canal. Determining which pores are homologous in the several different states described is difficult and orderly transitions between states are not apparent.

Barbels, Lips and Mouth

88. Development of lateral mandibular barbels. (CI = 0.571, RI = 0.919)

- 0:** Lateral mandibular barbels absent. (Diplomystidae)
- 1:** Lateral mandibular barbels present, without branches. (Ictaluridae; *Chrysichthys*; *Parauchenoglanis*; Schilbidae; Amphiliidae; Malapteruridae; *Sciades*; Auchenipteridae; Doradidae; *Mochokus brevis*)
- 2:** Lateral mandibular barbels present, with single branches. (*Mochokus niloticus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; all *Synodontis* except *S. contracta* [3], *S. nigrita* [3], *S. longirostris* [3], *S. sorex* [3], *S. clarias* [3], *S. pleurops* [3] and *S. congica* [3])
- 3:** Lateral mandibular barbels present, with two branches. (*Synodontis contracta*; *S. nigrita*; *S. longirostris*; *S. sorex*; *S. clarias*; *S. pleurops*; and *S. congica*)
- 4:** Lateral mandibular barbels present, incorporated into oral disc. (*Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

The development of the mandibular barbels is highly variable among catfishes, but phylogenetically informative for the Mochokidae, among other families. Within the Mochokidae, the respective development of the lateral and medial mandibular barbels can vary within a species; generally, the medial mandibular barbels are more complex. As such, lateral and medial mandibular barbels are treated separately. Furthermore, development and complexity of the mandibular barbels is independent of size.

Plesiomorphically, among catfishes, as in the Diplomystidae (Arratia, 1987), the lateral mandibular barbels are absent. Among basal siluroid catfishes, as in the Ictaluridae, the lateral mandibular barbels are straight, slender and unbranched (state 1); among mochokids, an unbranched lateral mandibular barbel is only found in *Mochokus brevis*. In *Mochokus niloticus*, *Mochokiella*, *Acanthocleithron*, *Microsynodontis* and most *Synodontis* the lateral mandibular barbels have single branches at each point along their lengths (Fig. 27A). In remaining *Synodontis* the lateral

mandibular barbels have two branches at various points along their lengths, directly opposing each other basally and closely alternating distally. Barbels with two branches at each point often show secondary branching (Fig. 27B). In all chiloglanidins the lateral mandibular barbels are largely incorporated into the lower lip of an oral disc (Fig. 27C), only extending a small distance beyond the rim of the oral disc and unbranched along that portion.

89. Development of medial mandibular barbels. (CI = 1.000, RI = 1.000)

- 0:** Medial mandibular barbels absent. (Diplomystidae)
- 1:** Medial mandibular barbels present, without branches. (Ictaluridae; *Chrysichthys*; *Parauchenoglanis*; Schilbidae; Amphiliidae; Malapteruridae; *Sciades*; Achenipteridae; Doradidae)
- 2:** Medial mandibular barbels present, with single branches. (*Mochokus*; *Mochokiella*)
- 3:** Medial mandibular barbels present, with two branches. (*Acanthocleithron*; *Microsynodontis*; *Synodontis*)
- 4:** Medial mandibular barbels present, incorporated into oral disc. (*Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

Plesiomorphically, among catfishes, as in the Diplomystidae (Arratia, 1987), the medial mandibular barbels are absent. Among basal siluroid catfishes, as in the Ictaluridae, the medial mandibular barbels are straight, slender and unbranched (state 1); unbranched medial mandibular barbels are not found in the Mochokidae. In *Mochokus* and *Mochokiella* the medial mandibular barbels have single branches at each point along their lengths (Fig. 27A). In *Acanthocleithron*, *Microsynodontis* and *Synodontis* the medial mandibular barbels have two branches at various points along their lengths, directly opposing each other basally and closely alternating distally. Barbels with two branches at each point often show secondary branching (Fig. 27B). In all chiloglanidins the medial mandibular barbels are largely incorporated into the lower lip of an oral disc (Fig. 27C), only extending a small distance beyond the rim of the oral disc and unbranched along that portion.

90. Presence or absence of basal membrane of maxillary barbels. (CI = 0.500, RI = 0.875)

- 0:** Maxillary barbels without basal membrane.
- 1:** Maxillary barbels with prominent basal membrane. (*Synodontis longirostris*; *S. schall*; *S. pleurops*; *S. nigrita*; *S. congica*; *S. clarrias*; *S. sorex*; *S. membranacea*; *S. batensoda*)
- Inapplicable:** In the *Chiloglanis*, *Atopodontus*, *Atopochilus* and *Euchilichthys*, because the state is obscured by the fact that the maxillary barbel is largely incorporated into

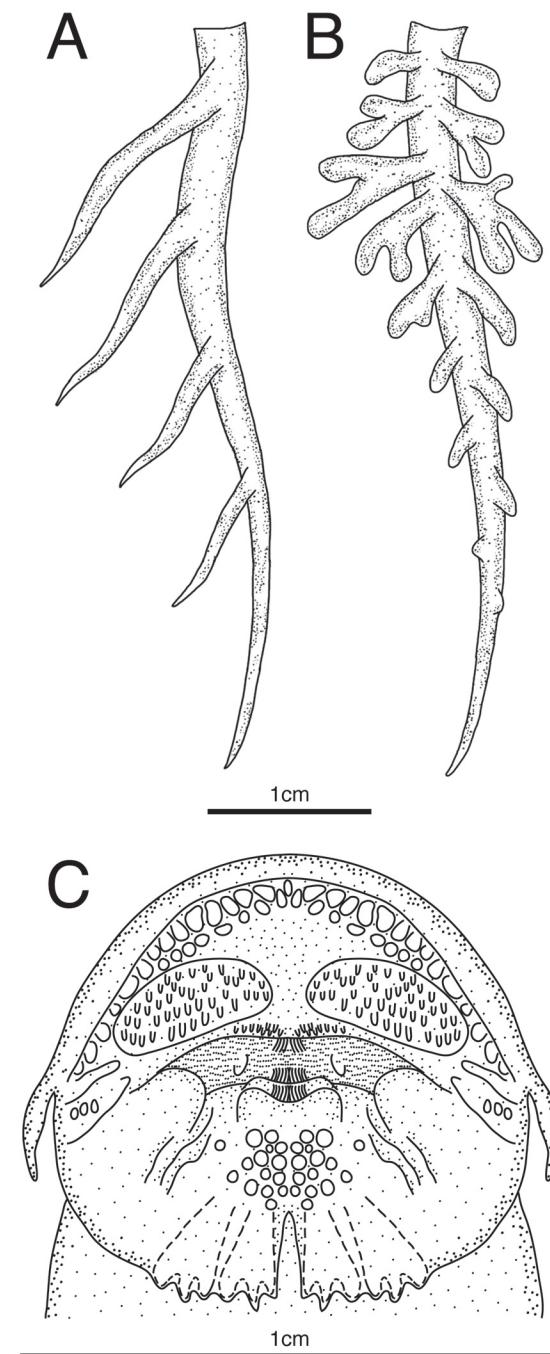


Fig. 27. Singly branched mandibular barbels (A), doubly branched mandibular barbels (B) and barbels incorporated into an oral disc (C) in the Mochokidae. Dashed lines represent elastin bases of mandibular barbels.

the enlarged oral disc.

In all of the outgroup taxa and many of the ingroup taxa the base of the maxillary barbels is rounded in cross section and without an obvious flap-like membrane along the posterior/medial margin. In some species of *Synodontis* the base of the barbel has a membranous flap along the medial/posterior margin.

Miscellaneous

91. Presence or absence of free orbital margin. (CI = 0.167, RI = 0.808)

0: Free orbital margin present.

1: Free orbital margin absent. (Amphiliidae; Malapteruridae; Auchenipteridae; *Agamyxis*; *Platydoras*; *Mochokus*; *Mochokiella*; *Microsynodontis*; *Chiloglanis*)

Plesiomorphically, among catfishes, as in the Diplo-mystidae (Arratia, 1987), there is a groove around the perimeter of the eye, generally referred to as a free orbital margin. Alternatively, the skin covering the eye may be confluent with the skin surrounding the eye, as in several outgroups and some mochokids. Among mochokids, a free orbital margin is absent in *Mochokus*, *Mochokiella*, *Microsynodontis* and *Chiloglanis*.

92. Size of opercular openings. (CI = 0.250, RI = 0.800)

0: Opercular openings open to isthmus ventrally.

1: Opercular openings largely restricted to sides of head. (Malapteruridae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Microsynodontis*; all *Synodontis* except *S. membranacea* [0]; *Chiloglanis*; *Atopodontus*; *Atopochilus*; *Euchilichthys*)

In several of the outgroup taxa, including the Diplo-mystidae (Arratia, 1987), the opercular openings run from the isthmus ventrally to the level of the eye dorsally. Alternatively, in the Malapteruridae, Auchenipteridae, Doradidae and the great majority of mochokids the opercular openings are largely restricted to the sides of the head, from near the base of the pectoral spine to the level of the eye. Among mochokids, only *Synodontis membranacea* and *Acanthocleithron* have opercular openings extending to the isthmus. In *Synodontis batensoda* the opercular openings are open to below the pectoral spine. Nevertheless, the openings are largely restricted to the sides of the head in this species (state 1).

93. Development of gas bladder (ORDERED). (CI = 0.333, RI = 0.879)

0: Gas bladder not reduced, with large anterior and posterior chambers.

1: Gas bladder somewhat reduced, with large anterior chamber and small posterior chambers. (*Chiloglanis* sp.)

'kalungwishi'; *Chiloglanis* sp. 'burundi'; *Atopochilus*; *Euchilichthys*)

2: Gas bladder greatly reduced, with small anterior chamber only. (Amphiliidae; all *Chiloglanis* except *C. macropterus* [0], *Chiloglanis* sp. 'kalungwishi' [1] and *Chiloglanis* sp. 'burundi' [1]; *Atopodontus*)

Plesiomorphically, among catfishes, the gas bladder is formed as a large, roughly heart-shaped structure, longer than wide and occupying a position just ventral to the fused vertebrae of the compound centrum (Fig. 3B). A T-shaped septum divides the gas bladder into three chambers, one anterior chamber and two posterior chambers. In the plesiomorphic condition the posterior chambers are large, extending well beyond the fused vertebrae. The plesiomorphic condition is present in all mochokids except the majority of chiloglanidins; among chiloglanidins, an unreduced gas bladder is seen in *Chiloglanis macropterus* only. In *Atopochilus*, *Euchilichthys* and a small number of *Chiloglanis* species the gas bladder is somewhat reduced in size and shorter than wide. The anterior chamber is of typical size, but the posterior chambers are much reduced, only reaching to the end or slightly past the compound centra (Fig. 3C). In *Atopodontus* and the remaining *Chiloglanis* species, as well as the Amphiliidae, the posterior chambers of the gas bladder are absent. The gas bladder is formed by the anterior chamber only, with bulbs on each side of the compound centrum joined to each other by a narrow tube traversing the ventral surface of the compound centrum; bulbs of the gas bladder are surrounded by the enlarged parapophyses of the compound centrum dorsally. In some instances the parapophyses and other processes of the compound centra almost completely surround the bulbs of the gas bladder (Fig. 5). Because state 1 represents an intermediate state, the character is treated as ordered in the analysis.

PHYLOGENETIC RECONSTRUCTION AND LISTS OF SYNAPOMORPHIES

The tree bisection-reconnection heuristic search algorithm resulted in two equally parsimonious trees of 405 steps, CI = .3654 and RI = .8539. The recovered trees differ in the placement of the genus *Microsynodontis* only. The strict consensus of the trees (406 steps, CI = .3645, RI = .8533) is shown with labeled clades for use in the discussion, Bremer decay indices and branch lengths recovered under ACCTRAN optimization (Fig. 28). Bootstrap values could not be calculated due to the extensive search time required. A simplified tree (Fig. 29) illustrates important results for the Mochokidae, with the same labeled clades and simple line drawings illustrating various mochokid taxa.

Labeled clades in both trees (A, B, C, etc.) are out-

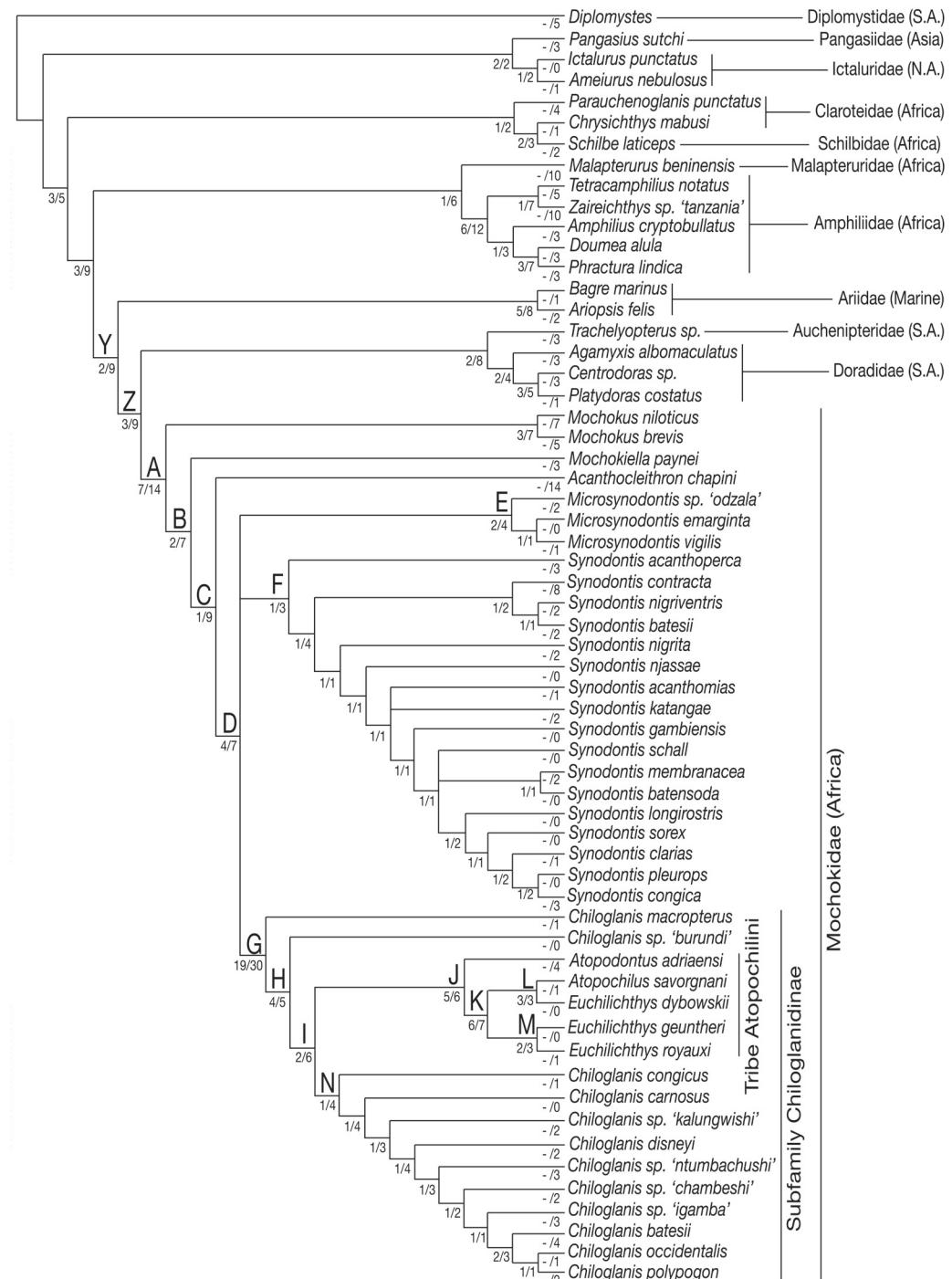


Fig. 28. Results of Analysis: 61 taxa, 93 characters. Strict consensus (406 steps, CI = .3645, RI = .8533) of 2 equally parsimonious trees. Clades are labeled with letters above the branches for use in discussion. Numbers below the branches are decay indices and branch lengths under ACCTRAN optimization, separated by a slash.

lined below, with a list of synapomorphies for each clade following bold-faced character state transformations (e.g. – (27; **0>1**) signifies a change from state 0 to 1 for character 27). Convergences and reversals are given for each of the synapomorphies. All listed synapomorphies were recovered unambiguously (i.e. – under both ACCTRAN and DELTRAN optimizations).

Several pieces of information suggest that it is prudent to leave most of the newly recovered groups within the Mochokidae unnamed. For example, within the genus *Chiloglanis* several (15+) new species are already known to exist and await formal description; extensive research on the genus has also revealed some definite substructure. In addition, new and distinctive mochokid taxa are still being discovered, such as the new genus *Atopodontus* (Friel and Vigliotta, 2008). Finally, a molecular phylogeny of African catfishes is being undertaken, including a large number of mochokids (pers. comm., John Sullivan), to which the results here may be compared. At this point, flooding mochokid taxonomy with new names seems ill advised. However, the available subfamily name Chiloglanidinae is redefined herein to include all suckermouthed species and is more thoroughly diagnosed. A particularly well supported tribe within the subfamily Chiloglanidinae is also named for the first time. Other suprageneric clades within the family are not particularly well supported and left unnamed.

The ‘arioids’ – (Clade Y)

(decay index: 2; branch length: 9)

The ‘arioid’ group includes the Mochokidae, Doradidae, Auchenipteridae and Ariidae (Fig. 28). Synapomorphies hypothesized to characterize the group include:

(12; 0>1): Absence of basioccipital pit. Independently acquired in *Zaireichthys* and *Tetracampphilus*.

(13; 0>1): Venterolateral expansions of basioccipital that join ossified transcapular ligament (Lundberg, 1993). Independently acquired in *Zaireichthys*.

(17; 0>1): Modestly developed nuchal shield. Independently acquired in *Pangasius* and *Chrysichthys*. Even more well-developed in the ‘doradoids’ (17; 1>2), with subsequent reversal to modest development in several species of *Chiloglanis* sensu stricto (sensu stricto: clade N, excluding *Chiloglanis macropterus* and *Chiloglanis* sp. ‘burundi’).

(23; 1>2): Reduction to four infraorbitals. Independently acquired in *Zaireichthys*, *Tetracampphilus* and *Paruchenoglanis*. Further reduced number of infraorbitals in some Doradidae, three in *Centrodoras* (23; 2>3). Reversal to five infraorbitals in all chiloglanidins.

(59; 0>1): Presence of moderate or strong serrae along anterior margin of pectoral spine. Independently acquir-

ed in *Chrysichthys*, *Schilbe* and *Pangasius*. Reversal to absence of serrae in all chiloglanidins.

(76; 0>1): Free and movable anterior parapophyses of compound centrum, known as an elastic spring apparatus (Mo, 1991; Lundberg, 1993; de Pinna, 1993). Reversal to parapophysis not free in chiloglanidins and subsequently reacquired in clade K (*Atopochilus* and *Euchilichthys* sensu lato).

(82; 1>2): Sixth centrum fused or deeply sutured to compound centrum. Further fusion to the seventh centrum, but independently acquired, in *Synodontis contracta*, *Chiloglanis* sp. ‘burundi’, *Chiloglanis congicus*, clade K and the Doradidae plus Auchenipteridae (82; 2>3), with subsequent reversal to fusion through the fifth only in *Agamyxis* (82; 3>1).

The ‘doradoids’ – (Clade Z)

(decay index: 3; branch length: 9)

The ‘doradoid’ group includes the Mochokidae, Doradidae and Auchenipteridae (Fig. 28). Synapomorphies hypothesized to characterize the group include:

(14; 0>1): Absence of distinct extrascapular (Mo, 1991). Independently acquired in the Amphiliidae.

(17; 1>2): Well-formed and wide nuchal shield (Mo, 1991). Reversal to modest development in several species of *Chiloglanis* sensu stricto.

(46; 0>1): Reduced and oddly shaped parurohyal (Mo, 1991).

(53; 0>1): Greatly enlarged postcleithral process (Mo, 1991; Diogo, 2005). Independently acquired in *Zaireichthys*. Reversal to small postcleithral process in all chiloglanidins.

(77; 0>1): Anterior parapophyses of the compound centrum with plate-like elaborations distally (Mo, 1991; Lundberg, 1993; de Pinna, 1993). Independently acquired in the Malapteruridae. Reversal in chiloglanidins and subsequently regained in clade K.

(92; 0>1): Restricted gill openings (Mo, 1991). Independently acquired in the Malapteruridae. Reversal to large gill openings in *Acanthocleithron* and *Synodontis membranacea*.

Family Mochokidae Jordan, 1923 - (Clade A)

(decay index: 7; branch length: 14)

The family Mochokidae, as currently delimited, is recovered as a monophyletic group. Synapomorphies hypothesized to characterize the family include:

(24; 0>1): Absence of an ascending Meckel’s cartilage (Mo, 1991; de Pinna, 1993; Diogo, 2005). Independently lost in the Malapteruridae and some Amphiliidae.

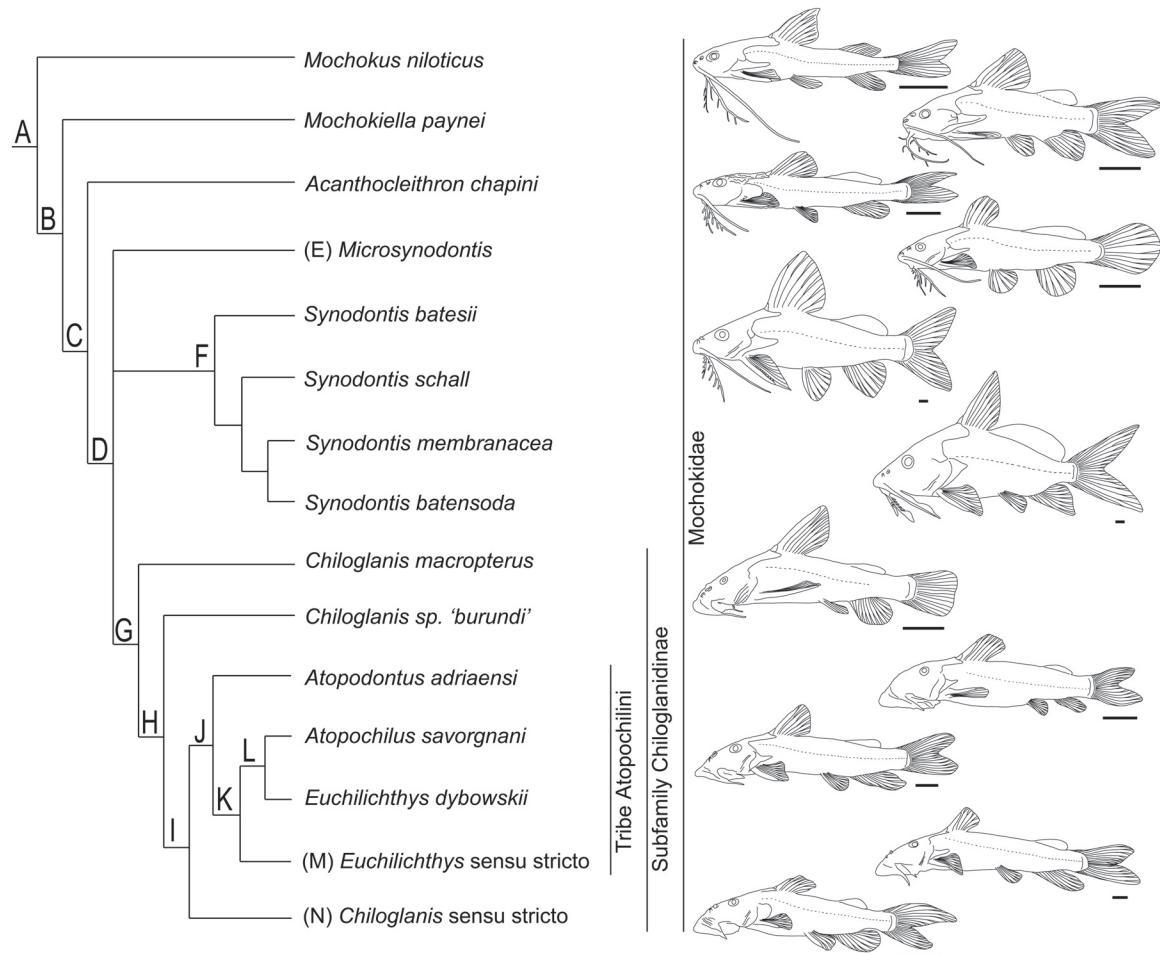


Fig. 29. Condensed representation of the cladogram in Fig. 28 illustrating important results for the Mochokidae. Clades are labeled with letters above branches for use in the discussion. Fish icons from top to bottom: *Mochokus niloticus*, *Mochokiella paynei*, *Acanthocleithron chapini*, *Microsynodontis* sp., *Synodontis* sp., *Synodontis membranacea*, *Chiloglanis macropterus*, *Atopodontus adriaensi*, *Atopochilus savorgnani*, *Euchilichthys dybowskii*, *Euchilichthys* sensu stricto, (M) *Euchilichthys* sensu stricto, and (N) *Chiloglanis* sensu stricto. Scale bars equal 1cm.

(25; 0>1): Shortened horizontal Meckel's cartilage (Mo, 1991; de Pinna, 1993; Diogo, 2005). Independently acquired in the Amphiliidae.

(26; 0>1): Absence or extreme reduction of the coronomeckalian (Mo, 1991; de Pinna, 1993; Diogo, 2005). Independently lost in the Malapteruridae.

(27; 0>1): Absence or extreme reduction of the coronoid process (de Pinna, 1993; Diogo, 2005).

(49; 0>1): The absence of the interhyal (Mo, 1991). Independently lost in some Amphiliidae.

(57; 1>0): Presence of a pectoral-locking foramen. Reversal to absence in all chiloglanidins except *Chiloglanis macropterus*.

(65; 0>1): Seven pelvic-fin rays (Mo, 1991). Independently acquired in some Doradidae. Increased to eight pelvic-fin rays in undescribed *Chiloglanis* sp. 'ntumbachusi'.

(72; 1>2): Complete fusion of the upper caudal-fin elements. Independently acquired in some Amphiliidae. Reversal in clade K and some *Chiloglanis* sensu stricto.

(89; 1>2): Ramified medial mandibular barbels. Further ramified for clade C (89; 2>3) and again for all chiloglanidins, where barbels are wholly incorporated into oral disc (89; 3>4). As with lateral mandibular barbels, some Doradidae have independently acquired branched medial mandibular barbels (Higuchi, 1992), but are not included in this analysis.

Genus *Mochokus* Joannis, 1835

(decay index: 3; branch length: 7)

The genus *Mochokus*, with just two species, is recovered as a monophyletic group. Synapomorphies hypothesized to characterize the genus include:

(56; 0>1): Straight mesocoracoid arch joining posterior face of vertical scapulo-coracoid lamina without any dorsal prominence. Independently acquired in all chiloglanidins.

(61; 2>3): Six or fewer pectoral-fin rays. Independently reduced in *Microsynodontis*.

(70; 0>1): Rayed adipose fin.

(73; 0>1): Absence of a space between the upper and lower hypurals.

(87; 2>3): Two mandibular sensory-canal pores on each side of the mandible. Independently acquired in both *Synodontis congica* and clade J.

Unnamed Clade B

(decay index: 2; branch length: 7)

Clade B includes all Mochokidae except *Mochokus*. Synapomorphies hypothesized to characterize the clade include:

(11; 0>1): Spinous projection on ventral side of pterotic. Reversal in all chiloglanidins except *Chiloglanis macropterus* and *Chiloglanis* sp. ‘burundi’.

(29; 0>1): Cup-shaped facet on angulo-articular for quadrate.

(42; 0>1): Spinous projection along the medial edge of the hyomandibula. Reversal (lost) in all chiloglanidins.

(58; 0>1): Ventral processes at proximal end of first ossified pectoral-fin proximal-middle radial. Reversal in *Synodontis contracta*. Further ornamented by dorsal process in most chiloglanidins (58; 1>2) and subsequent reversal to state 0 in *Atopodontus* and some species of *Chiloglanis* sensu stricto (58; 2>0).

Genus *Mochokiella* Howes, 1980

(branch length: 3)

Mochokiella is a monotypic genus. The following are recovered as autapomorphies for the species:

(22; 0>1): Third dorsal-fin proximal-middle radial joined by dorsolateral expansion to posterior nuchal plates (second dorsal-fin proximal-middle radial). Independently acquired in all species of *Synodontis*, except *S. acanthopercra*.

(45; 0>1): Well-formed sexually dimorphic opercular spine. Independently acquired in *Synodontis acanthopercra*.

(52; 1>2): Six branchiostegal rays. Independently derived in some species of *Chiloglanis* sensu stricto and some *Synodontis*.

Unnamed Clade C

(decay index: 1; branch length: 9)

Clade C includes all Mochokidae except *Mochokus* and *Mochokiella*. Synapomorphies hypothesized to characterize the clade include:

(2; 0>1): Modestly formed anterolateral cornua of mesethmoid. Further reduced (absent) in all chiloglanidins (2; 1>2).

(7; 1>0): Presence of foraminal remnant of posterior fontanelle at center of parieto-supraoccipital. Independently acquired in *Mochokus niloticus*. Reversal in all *Synodontis* except *S. acanthopercra* and clade H and subsequently regained in *Chiloglanis congicus*, *C. occidentalis* and *C. polypogon*.

(30; 0>1): Presence of tooth cup.

(74; 2>1): Count of 8 + 9 principal caudal-fin rays. Count reduced in *Microsynodontis* and occasionally reduced in *Synodontis* and *Chiloglanis* sensu stricto.

(89; 2>3): Two branches at each branching point along the length of the medial mandibular barbel. Barbels incorporated into enlarged lower lip in all chiloglanidins (89; 3>4).

Genus *Acanthocleithron* Nichols and Griscom, 1917

(branch length: 14)

Acanthocleithron is a monotypic genus. The following are recovered as autapomorphies for the species:

(6; 2>1): Posterior cranial fontanelle modestly developed, bounded by frontals anteriorly and just reaching parieto-supraoccipital posteriorly. Independently acquired in *Mochokus niloticus* and *Synodontis acanthopercra*.

(31; 1>2): Primary dentary teeth altogether absent. Independently acquired in all chiloglanidins and some *Synodontis*.

(32; 1>4): Gently recurved and robust auxiliary dentary teeth present, tips spatulate.

(38; 0>1): Spatulate premaxillary teeth. Independently acquired in clade I, but subsequently lost in several species of *Chiloglanis* sensu stricto.

(54; 0>1): Blunt or rounded postcleithral processes. Independently acquired in some species of *Synodontis*. Males of some sexually dimorphic *Chiloglanis* have rounded postcleithral processes; pointed in females.

(61; 2>1): Eight pectoral-fin rays. Independently derived in some *Synodontis* and some chiloglanidins.

(78; 0>1): Anterior parapophysis of compound centrum with an obvious bend anteriorly. Independently acquired in *Mochokus*, some *Microsynodontis*, some *Synodontis* and clade K.

(80; 0>1): Parapophyses of the 5th centrum broadly joined to those of compound centrum. Independently acquired in

several species of *Chiloglanis* sensu stricto.

(91; 1>0): Free orbit. Independently acquired in all *Synodontis* and clade J.

(92; 1>0): Gill openings extending to isthmus. Independently acquired in *Synodontis membranacea*.

Unnamed Clade D (decay index: 4; branch length: 7)

Clade D includes all Mochokidae except *Mochokus*, *Mochokiella* and *Acanthocleithron*. Synapomorphies hypothesized to characterize the clade include:

(4; 0>1): Anteroposteriorly elongated lateral ethmoid, without any great lateral prominence and a relatively straight lateral edge.

(28; 0>1): Large intermandibular angle, no less than 135 degrees. Reversal to smaller angle in *Synodontis membranacea*.

(35; 0>1): Premaxillae block-like and solid, with posterior and ventral tooth-bearing faces. Uniquely derived premaxillae shape in all chiloglanidins (35; 1>2) and again in several species of *Chiloglanis* sensu stricto (35; 2>3), but always with posterior and ventral tooth-bearing faces.

(36; 0>1): Differentiation of premaxillary teeth by size and shape from front to back.

(37; 0>1): S-shaped and cylindrical premaxillary teeth.

(44; 0>1): Greatly reduced anterior pterygoid element. Elongate anterior pterygoid element in clade J and some *Chiloglanis* sensu stricto (43; 1>2).

Genus *Microsynodontis* Boulenger, 1903 - (Clade E)

(decay index: 2; branch length: 4)

The genus *Microsynodontis*, represented in the analysis by three species, is recovered as a monophyletic group. Synapomorphies hypothesized to characterize the genus include:

(61; 2>3): Six pectoral-fin rays. Low count independently acquired in *Mochokus*, where the count may be even lower.

(74; 1>3): 7 + 7 caudal-fin rays. Polymorphic in one species, some individuals with count of 6 + 6.

(75; 0>1): Rounded or truncate caudal fin. Independently acquired in some species of *Chiloglanis* sensu lato.

Genus *Synodontis* Cuvier, 1816 - (Clade F)

(decay index: 1; branch length: 3)

The genus *Synodontis*, represented in the analysis by 17 species, is recovered as a monophyletic group. Synapomorphies hypothesized to characterize the genus include:

(78; 0>2): Anteriorly directed process on the elastic spring

apparatus. Uniquely derived in a small number of *Synodontis* (78; 2>1).

(91; 0>1): Free orbit. Independently acquired in all *Acanthocleithron* and clade J.

Subfamily Chiloglanidinae Riehl and Baensch, 1990

- (Clade G)

(decay index: 19; branch length: 30)

Type genus: *Chiloglanis* Peters, 1868.

Diagnosis: The subfamily name Chiloglanidinae is herein applied to the clade composed of all mochokids with an oral disc, including *Chiloglanis* sensu lato, *Atopodontus*, *Atopochilus* and *Euchilichthys* sensu lato. Synapomorphies diagnosing the subfamily include:

(2; 1>2): Total absence of anterolateral cornua of the mesethmoid.

(3; 0>1): Mesethmoid much wider ventrally. Independently derived in *Mochokus* and *Mochokiella*.

(8; 0>1): Posterolateral corner of neurocranium formed largely by prootic, exoccipital, pterotic and sphenotic.

(19; 0>1): Presence of only two nuchal plates because anterior and middle nuchal plates are fused or one is lost. Independently derived in some species of *Synodontis*. Reversal to three nuchal plates in *Atopochilus savorgnani*.

(23; 2>1): Presence of five infraorbitals.

(31; 1>2): Total absence of teeth on dorsal surface of tooth cup. Independently derived in *Acanthocleithron* and some *Synodontis*.

(33; 0>1): Very large maxilla.

(35; 1>2): Premaxillae block-like, with posterior and ventral tooth-bearing faces joined by swath of porous bone. Uniquely derived premaxillae shape in several species of *Chiloglanis* sensu stricto (35; 2>3), but with posterior and ventral tooth-bearing faces.

(40; 0>1): Shortened autopalatine. Further shortened in clade J (39; 1>2).

(41; 0>1): Absence of cartilage at posterior end of autopalatine.

(42; 1>0): Absence of process along medial edge of hyomandibula. Independently derived in *Mochokus*.

(43; 1>2): Round/spherical condyle along dorsal edge of hyomandibula. Independently acquired in some species of *Synodontis*.

(47; 0>1): Fusion of dorsohyal and venterhyal. Reversal in clade K.

(48; 0>1): Posterohyal with distal end wider than proximal end.

(53; 1>0): Relatively small postcleithral process.

(56; 0>1): Straight mesocoracoid arch joining posterior face of vertical scapulo-coracoid lamina without any dorsal

prominence. Independently acquired in *Mochokus*.

(58; 1>2): Ventral and dorsal processes at proximal end of first ossified pectoral-fin proximal-middle radial. Reversal to state 0 in *Atopodontus* and some species of *Chiloglanis* sensu stricto (58; 2>0).

(59; 1>0): Absence of serrae along anterior margin of pectoral spine. Independently derived in some *Synodontis*.

(60; 0>1): Marked reduction of serrae along posterior margin of pectoral spine. Independently derived in *Synodontis contracta*. Reversal to strong serrae in *Atopochilus savorgnani* and *Euchilichthys dybowskii*. Further reduced (absent) in *Chiloglanis* sensu stricto (59; 1>2).

(64; 0>1): Six dorsal-fin rays. Independently acquired in *Microsynodontis* sp. ‘odzala’ and *Mochokus brevis*. Reversal to seven or more rays in clade L. Further reduced to five rays in some *Chiloglanis* sensu stricto.

(66; 1>0): Presence of pelvic splint. Independently acquired in some *Synodontis*. Reversal in *Atopodontus* and several species of *Chiloglanis* sensu stricto.

(67; 0>2): Anterior processes of basipterygia terminating at approximately same point.

(68; 0>1): Anterolateral and anteromedial processes of the basipterygia joined to each other by cartilage.

(69; 0>1): Plate-like first anal-fin pterygiophore. Reversal in *Chiloglanis batesii* only.

(76; 1>0): Anterior parapophyses of the compound centrum tightly joined to the ossified transcapular ligament. Reversal to free parapophyses (elastic spring apparatus) in clade K.

(81; 0>1): Enlarged strut-like parapophysis of 6th centrum without a free-floating rib.

(87; 2>5): Mandibular sensory canal absent, no pores. Reversal to canal present with two pores on each side in clade J (86; 5>4).

(88; 2>4): Lateral mandibular barbels incorporated into oral disc.

(89; 3>4): Medial mandibular barbels incorporated into oral disc.

Unnamed Clade H

(decay index: 4; branch length: 5)

Clade H includes all Chiloglanidinae except *Chiloglanis macropterus*. Synapomorphies hypothesized to characterize the clade include:

(7; 0>1): Absence of foraminal remnant of posterior fontanelle at center of parieto-supraoccipital. Independently lost in all *Synodontis* except *Synodontis acanthoperca*. Reversal in *Chiloglanis congicus*, *C. occidentalis* and *C. polypogon*.

(57; 0>1): Absence of pectoral-locking foramen.

(61; 2>1): Eight pectoral-fin rays. Independently derived

in some *Synodontis* and some chiloglanidins. Increased to nine pectoral-fin rays in *Euchilichthys* sensu stricto (clade M) and some *Chiloglanis* sensu stricto (61; 1>0).

(93; 0>1): Gas bladder modestly reduced. Further reduced in *Atopodontus* and most *Chiloglanis* sensu stricto (93; 1>2).

Unnamed Clade I

(decay index: 2; branch length: 6)

Clade I includes all Chiloglanidinae except *Chiloglanis macropterus* and *Chiloglanis* sp. ‘burundi’. Synapomorphies hypothesized to characterize the clade include:

(11; 1>0): Absence of spinous projection on ventral side of pterotic. Independently derived in *Mochokus*.

(38; 0>1): Spatulate premaxillary teeth. Independently acquired in *Acanthocleithron*. Reversal in several species of *Chiloglanis* sensu stricto.

(63; 1>0): Absence of posterior dorsal-spine serrae. Independently acquired in *Mochokus*, *Acanthocleithron* and *Microsynodontis vigilis*. Reversal in *Chiloglanis occidentalis* and *Chiloglanis polypogon*.

(77; 0>2): Flap-like elaborations of anterior parapophyses of compound centrum. Reversal to unornamented, angular parapophyses in *Chiloglanis* sp. ‘kalungwishi’. Derived, plate-like elaborations of parapophyses in clade K (77; 2>1).

Tribe Atopochilini, New Tribe – (Clade J)

(decay index: 5; branch length: 6)

Type genus: *Atopochilus* Sauvage, 1879.

Diagnosis: The name Atopochilini is proposed herein for a monophyletic group composed of *Atopodontus*, *Atopochilus* and *Euchilichthys* sensu lato, within the subfamily Chiloglanidinae. Synapomorphies diagnosing the tribe include:

(1; 0>1): Distinct ventral mesethmoid process for articulation with premaxillae.

(5; 0>1): Hanging, laminar curtain along anterolateral edge of lateral ethmoid.

(32; 1>3): S-shaped auxiliary dentary teeth with trowel-shaped tips. Uniquely derived (spatulate tips) in *Atopochilus savorgnani* and *Euchilichthys dybowskii* (32; 3>2).

(40; 1>2): Block-like autopalatine.

(87; 5>3): Two pores emanating from mandibular sensory canal on each side. Independently derived in *Mochokus* and *Synodontis congica*.

(91; 1>0): Free orbit. Independently acquired in *Acanthocleithron* and *Synodontis*.

Genus *Atopodontus* Friel and Vigliotta, 2008
(branch length: 4)

Atopodontus is a monotypic genus. Friel and Vigliotta (2008) provided a complete diagnosis of the genus and discussion of its placement within the family. The following are recovered as autapomorphies for the species:

(52; 1>0): Eight branchiostegal rays. Independently derived in *Euchilichthys royauxi*.

(58; 2>0): First ossified pectoral-fin proximal radial without dorsal or ventral processes proximally. Independently derived in *Mochokus*, *Synodontis contracta* and several *Chiloglanis* sensu stricto.

Unnamed Clade K
(decay index: 6; branch length: 7)

Clade K includes *Atopochilus* and *Euchilichthys* sensu lato. Synapomorphies hypothesized to characterize the clade include:

(47; 1>0): Separate dorsohyal and venterohyal. Plesiomorphic condition for Mochokidae, but fused in all other Chiloglanidinae.

(50; 0>1): Flattened, many-sided and laterally expansive basibranchials.

(72; 2>1): Marginal, upper hypurals autonomous and not totally fused. Independently derived in some *Chiloglanis* sensu stricto.

(76; 0>1): Free and movable anterior parapophysis of compound centrum (elastic spring apparatus). Plesiomorphic condition for Mochokidae, but joined to ossified transcapular ligament in all other Chiloglanidinae.

(77; 2>1): Plate-like elaborations at distal end of anterior parapophyses of compound centrum. Plesiomorphic condition for Mochokidae, but not elaborated as such in all other Chiloglanidinae.

Unnamed Clade L
(decay index: 3; branch length: 3)

Clade L includes *Atopochilus savorgnani* and *Euchilichthys dybowskii*. Synapomorphies hypothesized to characterize the clade include:

(32; 3>2): S-shaped auxiliary dentary teeth with spatulate tips.

(60; 1>0): Posterior edge of pectoral spine with well-developed serrae. Plesiomorphic condition for Mochokidae, but greatly reduced in all other Chiloglanidinae.

(64; 1>0): Seven dorsal-fin rays. Apparently plesiomorphic condition for Mochokidae, reduced in all other Chiloglanidinae.

***Euchilichthys* sensu stricto – (Clade M)**
(decay index: 2; branch length: 3)

Clade M includes *Euchilichthys geuntheri* and *Euchilichthys royauxi*. Synapomorphies hypothesized to characterize the clade include:

(71; 2>1): Parhypural autonomous, hypurals one and two fused.

(86; 0>1): Multiple pores at each site along cephalic sensory canals.

***Chiloglanis* sensu stricto – (Clade N)**
(decay index: 1; branch length: 4)

Clade N includes all *Chiloglanis* except *Chiloglanis macropterus* and *Chiloglanis* sp. ‘burundi’. Synapomorphies hypothesized to characterize the clade include:

(52; 1>2): Six branchiostegal rays. Independently derived in *Mochokiella* and some *Synodontis*. Further reduced to five branchiostegal rays in *Chiloglanis disneyi*, *Chiloglanis* sp. ‘chambeshi’, *C. batesii*, *C. occidentalis* and *C. polypogon*.

(60; 1>2): Total lack of serrae along posterior edge of the pectoral spine.

(79; 1>0): Posterior parapophysis of compound centrum broadly joined to anterior parapophysis, forming dorsal shield over gas bladder.

DISCUSSION

Phylogenetic position of the Mochokidae

As with several previous morphological phylogenetic works, this analysis recovered the South American Doradidae plus Auchenipteridae as sister to the Mochokidae. In addition, the Ariidae are recovered as the sister group to the Mochokidae plus (Doradidae plus Auchenipteridae). These results agree with Lundberg’s (1993) hypothesis of an ‘aroid’ clade and a nested ‘doradoid’ clade, which are largely characterized by synapomorphies of the nuchal shield, the compound centrum and other elements at the junction between the neurocranium and the dorsal fin. In light of mounting molecular evidence these relationships are being seriously questioned for the first time (Hardman, 2005; Sullivan et al., 2006). Herein, considerable effort was made to utilize novel characters that would help elucidate relationships within the Mochokidae, but also help place the Mochokidae within the Siluriformes. Unfortunately, and perhaps not surprisingly, characters that have been used to support a relationship between the Mochokidae, Auchenipteridae and Doradidae are also useful for diagnosing clades within the Mochokidae. As a consequence,

characters are utilized whose derived states may be independently derived in the Auchenipteridae plus Doradidae (with respect to the Mochokidae). Indeed, the low support values for recovered clades outside of the Mochokidae (i.e. – clades Y and Z) and the relatively low consistency indices for the synapomorphies characterizing them (seldom greater than .500) are indicative of a high degree of homoplasy.

If we accept the results of the higher-level phylogenetic work in Sullivan et al. (2006), the morphological similarities between the Mochokidae and other ‘doradoids’ represent a remarkable example of extensive homoplasy. As noted, most of the synapomorphies for the ‘arioid’ and ‘doradoid’ groups are related to a limited number of systems including the nuchal shield, the compound centrum and other elements at the junction between the neurocranium and the dorsal fin. Because this work and prior works have repeatedly allied the Mochokidae with South American ‘doradoids’, such features are taken to be characteristic of a larger clade and not the Mochokidae alone. Closer observation reveals that, while the function and general morphology may be the same, the specific nature of the morphology of these complex regions is actually quite distinct in the Mochokidae (e.g. – character 18: dorsal suture between posttemporo-supracleithrum and nuchal plates). Furthermore, it has been suggested that modifications of the nuchal shield and the complex vertebra are directly correlated to each other in these groups (Alexander, 1965). Alexander notes that broad nuchal plates serve to strengthen the connection between the neurocranium and dorsal-fin elements. This is, he suggests, compensation for the presence of an elastic spring apparatus, which by nature weakens that same connection. Given the functional correlation, this suite of characters is more easily explained as convergence on a similar solution to the same problem. As such, it is important to consider that many of these features might actually be synapomorphies for the Mochokidae and independently derived with respect to other catfishes.

The inclusion of newly hypothesized sister groups of the Mochokidae, the Amphiliidae and the Malapteruridae (Sullivan et al., 2006), may also account for weak support of the ‘arioids’ and ‘doradoids’ herein. Several of the mochokid synapomorphies are independently derived for amphiliid and malapterurid taxa in the recovered topology. They could, in fact, represent synapomorphies for clades composed of the Amphiliidae, Mochokidae and Malapteruridae. Possible synapomorphies for the Mochokidae, Amphiliidae and Malapteruridae include: autopatine with a distinctly concave facet for the lateral ethmoid, characterized by a raised ridge anteriorly; and absence of the ascending Meckel’s cartilage (present in the Leptoglanidinae). In addition, the Mochokidae and Amphiliidae share a short-

ened horizontal Meckel’s cartilage, while the Mochokidae and Malapteruridae have both lost the coronomeckalian. Furthermore, the following are synapomorphies for the Amphiliidae plus Malapteruridae in the recovered topology: dorsal portion of the mesethmoid (where it fuses with the frontals posteriorly) narrower than ventral portion (where it joins to the lateral ethmoids synchondrally); and posterior autopatine cartilage absent. Within the Mochokidae, both of these are synapomorphies for the subfamily Chiloglanidinae (clade G).

Phylogenetic relationships within the Mochokidae

Morphological evolution in the Mochokidae is dominated by changes in the oral jaws and mouth. Synapomorphies for the family include the absence of ascending Meckel’s cartilage, the shortening of horizontal Meckel’s cartilage, the absence/reduction of the coronomeckalian, the reduction of the coronoid process, and the ramification of the medial mandibular barbels. In addition, a reduced number of mandibular sensory-canal pores (character 87) is ambiguously optimized for the family (ACCTRAN only). The number of mandibular sensory-canal pores is variable within the family, but always three or fewer. The adaptive nature, if any, behind these changes is unclear, but is perhaps related to a shift in feeding ecology. This study suggests that features of the pectoral girdle and caudal fin are also synapomorphies for the family. Finally, synapomorphies for the ‘arioid’ and ‘doradoid’ clades may be synapomorphies for the Mochokidae if the higher-level relationships are not correctly resolved.

Changes in the oral jaws and mouth also characterize a number of suprageneric clades within the family. The most inclusive of these is clade D, which includes all mochokids except *Mochokus*, *Mochokiella* and *Acanthocleithron*. The relationships of *Mochokus*, *Mochokiella* and *Acanthocleithron* to each other are not satisfactorily resolved, but small sets of derived features support the monophyly of each genus. In addition, these three genera present unique sets of seemingly plesiomorphic features, which account for their basal positions within the family. Synapomorphies for clade D include differentiated premaxillary teeth, premaxillae with multiple faces for support of teeth, S-shaped auxiliary dentary teeth and a large intermandibular angle. Each of these features is notably absent in *Mochokus*, *Mochokiella* and *Acanthocleithron*. In addition, all members of clade D, as well as *Acanthocleithron*, have a dentary tooth cup. The dentary is more or less flat and without a distinctive tooth cup in *Mochokus* and *Mochokiella*. Again, derived features in clade D are most likely correlated with feeding ecology. Members of clade D display a ventrally directed mouth, ideal for feeding either along the bottom or at the waters

surface (as in the upside-down catfishes).

Three subclades of clade D, *Microsynodontis* (clade E), *Synodontis* (clade F) and subfamily Chiloglanidinae (clade G) form an unresolved polytomy. *Microsynodontis* was the only clade within the Mochokidae varying in its placement within the set of most parsimonious trees. Grouping with *Synodontis* and the Chiloglanidinae in equal measure, the consensus required that the three be shown in a polytomy. Still, the monophyly of *Microsynodontis* is at least modestly supported by the analyses. More precise placement of *Microsynodontis* and resolution of the polytomy would be aided by a comprehensive taxonomic revision of the genus, because, like many small African fishes, the diversity of *Microsynodontis* is poorly known. At least one undescribed species is known and the recent description of eight new species (Ng, 2004) suggests that additional species await discovery.

While a relatively small number of known *Synodontis* species are included in this analysis, the genus is recovered as a monophyletic group. Establishing substructure within *Synodontis* was not an objective of this research and further investigation of the genus (over 120 species) is necessary to determine if it is truly monophyletic. However, the attempt here has led to one important conclusion. The genus *Synodontis* cannot be monophyletic without the inclusion of *S. batensoda* and *S. membranacea*. The generic assignment of these two species has wavered for decades, but there is no evidence to suggest they represent anything more than uniquely derived species of *Synodontis*. To maintain the monophyly of *Synodontis*, these two species should be considered members of the genus.

The most well supported suprageneric clade within the Mochokidae is the subfamily Chiloglanidinae (clade G), comprising all suckermouthed species. The monophyly of the Chiloglanidinae is almost certain with regard to the taxa examined here. The subfamily receives the strongest character support of any clade on the tree, with 29 unambiguously resolved synapomorphies. As with other well supported clades, a large number of the synapomorphies for the subfamily are related to the oral jaws and mouth. However, these are accompanied by changes throughout the body, which may be attributed to an increased benthic existence in fast-flowing water. For example, an enlarged strut-like parapophysis of the 6th centrum is found in all members of the Chiloglanidinae; enlarged strut-like processes or ribs are found in other benthic, rheophilic catfishes, including loricariids (Armbruster, 2004). Similarly, sucker-like oral discs are found in many benthic stream fishes (e.g. – loricarioid catfishes and some sisorid catfishes). Yet, the adaptive nature of the numerous changes for this clade is probably not related to feeding ecology. A shift in diet would be expected during evolution of the oral

disc, but it was probably not the driving force; maintaining position within fast-flowing water probably played a more prominent role.

The largest genus in the subfamily, *Chiloglanis*, is paraphyletic in the recovered topology. Of the *Chiloglanis* examined, *Chiloglanis macropterus* and *Chiloglanis* sp. 'burundi' appear unusual at first glance, with large spines and body shapes more typical of mochokids without an oral disc. Thus, it is not surprising that osteology and gross morphology do not support their relationship to other *Chiloglanis*. Further research on the Chiloglanidinae may require new genera for these species. Alternatively, the basal position recovered for these two species may be the results of homoplasious reversals. In either case, the genus *Chiloglanis* sensu lato requires much revision. Several undescribed species that would be most appropriately placed in this genus are already known. For this reason, the paraphyletic nature of *Chiloglanis* may not be accurately depicted here and should be considered tentative at best. In fact, members of the genus *Chiloglanis* sensu lato do share a small number of derived features, including the absence of a mandibular sensory canal, the absence of a free orbit, and the presence of a modestly shortened autopalatine (up to 3X as long as wide).

New tribe Atopochilini (clade J), comprised of *Atopochilus*, *Atopodontus* and *Euchilichthys*, is another well supported clade characterized by features of the oral jaws and mouth, including the following: two mandibular sensory canal pores on each side; a distinct ventral mesethmoid process for articulation with the premaxillae; and a hanging, laminar curtain along the anterolateral edge of the lateral ethmoid. The tribe is also characterized by the presence of a free orbital margin and a block-like autopalatine. Apart from features included in the analysis, diet and gut length are possibly diagnostic for this clade. Gut contents in members of the tribe include silt, detritus and occasionally invertebrates, whereas most mochokids (including *Chiloglanis*) feed selectively on invertebrates. Gut length is notably longer in members of the tribe as well (up to 7 times TL vs. 1-2 times TL in other mochokids). Gut contents and gut length, and their relationships to each other have not been extensively studied in the Mochokidae, but may be phylogenetically informative.

The next more exclusive clade (K), containing *Atopochilus* and *Euchilichthys* sensu lato, is well supported and presents some important results. First, the sister group relationship between clade K and *Atopodontus* is important because it supports the notion that *Atopodontus* is a valid genus (apart from possible paraphyly of *Chiloglanis*). A complete description and diagnosis of *Atopodontus* (as well as illustrations) are provided in Friel and Vigliotta (2008). Next, subclades L and M illustrate the taxonomic dilemma

of *Atopochilus* and *Euchilichthys*. The distinction between these genera has been unclear historically (Pellegrin, 1938; Poll, 1959; 1967) and to date they have not been satisfactorily diagnosed. Unfortunately, only a single species currently placed in the genus *Atopochilus* (*A. savorgnani*, type species) was available at the time of this work. However, it is clear that *Euchilichthys dybowskii* is more closely related to *Atopochilus savorgnani* than to other *Euchilichthys*, implying that *Euchilichthys* is paraphyletic as per current taxonomy. The author's preferred solution is reassignment of *Euchilichthys dybowskii* to the genus *Atopochilus*, making both genera monophyletic herein, but more members of each genus need to be examined before formal reassessment. Alternatively, all species of *Euchilichthys* sensu lato could be reassigned to *Atopochilus*, apparently the taxonomic preference of Pellegrin (1938). Synapomorphies for clades L and M form the basis of diagnoses for *Atopochilus* and *Euchilichthys* respectively, but the diagnoses will be more robust if a larger number of known species are considered. Taxonomic changes, including the generic reassessment of *Euchilichthys dybowskii*, should be made in that context.

CONCLUSIONS

It is evident that the systematics of the Mochokidae is a work in progress. The following results illustrate the need for alpha-level systematic work before continuing with mochokid phylogeny: *Chiloglanis* may be a paraphyletic group, which may require the description of new genera; substructure within the large genus *Synodontis* is still largely unknown; *Euchilichthys* is paraphyletic as per current taxonomic standards and needs to be properly diagnosed along with *Atopochilus*; the relationship of *Microsynodontis* to other mochokids is unresolved; and finally, the relationships of *Mochokus*, *Mochokiella* and *Acantholeichthron* at the base of the Mochokidae are best described as unresolved. In addition, several new species are already awaiting description and many more are likely to be discovered. Targeted phylogenetic treatments of particularly large genera like *Synodontis* and *Chiloglanis* are needed. In order to accurately represent the evolutionary history of the family, proper taxon sampling is essential. Stable, complete and hierarchical taxonomy should be the first step to that end. Finally, the relationship of the Mochokidae to other catfishes deserves further examination. A large part of this work involved accurately and thoroughly characterizing the morphology of the Mochokidae. Previous works considered little more than the 'stand-in' mochokid, *Synodontis*. Higher-level catfish phylogeny can hopefully benefit from the more thorough characterization of the Mochokidae provided in this work.

KEY TO THE GENERA OF THE MOCHOKIDAE

The following key is largely based on easily observable external characters derived from the phylogenetic work above. However, some characters in the key were added after the main body of work was completed and therefore not utilized above.

- 1a.** Lips and barbels modified into oral disc (Fig. 27C); postcleithral process short (Fig. 22C); 5 infraorbitals (Figs. 2C, 4B); pelvic-fin origin at vertical at end of dorsal-fin base.....**2**
- 1b.** Lips and barbels not modified into oral disc; postcleithral process quite long (Fig. 22B); 4 infraorbitals (Figs. 2B, 4A); pelvic-fin origin beyond end of dorsal-fin base.....**5**
- 2a.** Mandibular teeth bunched (in bouquet) at midline (Fig. 3D in Friel and Vigliotta, 2008) in or spread across mouth opening in one or two discrete rows (Fig. 3E–F in Friel and Vigliotta, 2008); eyes without free orbital margin; mandibular sensory-canals absent; 4 to 6 dorsal-fin rays (typically 5); 5 to 7 branchiostegal rays (typically 5 or 6).....***Chiloglanis* sensu lato**
- 2b.** Mandibular teeth spread across mouth opening in more than two discrete rows (Fig. 3A–C in Friel and Vigliotta, 2008); eyes with free orbital margin; mandibular sensory-canals present, with 2 pores on each side; 6 to 7 dorsal-fin rays; 7 to 8 branchiostegal rays.....**3**
- 3a.** Small anteriorly directed pocket underneath lower lip produced by folds of skin (Fig. 4A in Friel and Vigliotta, 2008); width of mandibular tooth rows less than 66% width of paired premaxillae (Fig. 3A in Friel and Vigliotta, 2008); caudal fin emarginate; gas bladder extremely reduced to two small bulbs (Fig. 5).....***Atopodonotus***
- 3b.** Small anteriorly directed pocket underneath lower lip absent (Fig. 4B in Friel and Vigliotta, 2008); width of mandibular tooth rows more than 66% width of paired premaxillae (Fig. 3B–C in Friel and Vigliotta, 2008); caudal fin forked; gas bladder only modestly reduced (Fig. 3C).....**4**
- 4a.** Mandibular teeth spatulate and unicuspид (Fig. 10C); large posterior pectoral-spine serrae; one or only a few pores at sites along the cephalic sensory canals; fewer than 40 vertebrae.....***Atopochilus***
- 4b.** Mandibular teeth with lengthwise keel creating trowel

shape and sometimes bicuspid from wear (Fig. 10A); small posterior pectoral-spine serrae; several pores at various sites along the cephalic sensory canals; more than 40 vertebrae.....*Euchilichthys sensu stricto*

5a. S-shaped auxiliary dentary teeth present (Fig. 10A, C–F); premaxillary teeth differentiated by shape and size front to back; lips plicate (with folds at corners of mouth).....**6**

5b. S-shaped auxiliary dentary teeth absent (Fig. 10B); premaxillary teeth showing little, if any, differentiation from front to back; lips papillose, but not plicate (without folds).....**7**

6a. Eyes with free orbital margin; 17 principal caudal-fin rays (only 13 in *Synodontis contracta*); tail forked; 6 to 10 pectoral-fin rays (usually 8 or 9); lateral mandibular barbels with single, gracile branches at each point along length or doubly branched (Fig. 27A–B).....*Synodontis*

6b. Eyes without free orbital margin; 12 to 14 principal caudal-fin rays; tail truncate or rounded; 6 or 7 pectoral-fin rays (typically 6); lateral mandibular barbels with single, gracile branches at each point along length (Fig. 27A).....*Microsynodontis*

7a. Dorsal surface of the head and nuchal shield covered by large ridges and spinous projections; cleithrum bearing spine in males; rounded, blunt postcleithral process; anus and urogenital opening distant; free orbital margin present; gill openings open to isthmus; tips of mandibular teeth spatulate; medial mandibular barbels with multiple, thick branches at each point along length (Fig. 27B); 8 to 9 pectoral-fin rays; 17 caudal-fin rays; more than 40 vertebrae.....*Acanthocleithron*

7b. Dorsal surface of the head and nuchal shield without ridges and spinous projections; cleithrum without spine in males; pointed postcleithral process; anus and urogenital opening very close; free orbital margin absent; gill openings restricted to sides of the head; tips of mandibular teeth pointed; medial mandibular barbels with single, gracile branches at each point along length (Fig. 27A); 5 to 7 pectoral-fin rays; 13 or 15 caudal-fin rays; fewer than 36 vertebrae.....**8**

8a. Adipose fin with rays; tips of pelvic fins not reaching origin of anal fin; opercle without obvious spine in males; 5 to 6 pectoral-fin rays; 2 mandibular sensory-canal pores on each side.....*Mochokus*

8b. Adipose fin without rays; tips of pelvic fins just reaching

origin of anal fin; opercle bearing obvious spine in males; 7 pectoral-fin rays; 3 mandibular sensory-canal pores on each side.....*Mochokiella*

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APPENDIX 1: COMPARATIVE MATERIAL EXAMINED

Amphiliidae

***Amphilius cryptobullatus*:** CU 91076, 1 DS, 6 ALC, Zambia, Itabu River; CU 91067, 2 C&S, 77 ALC, Zambia, Lufubu River; CU 91075, 44 ALC, Zambia, Kalunguishi River. ***Andersonia leptura*:** CU 91440, 1 C&S, 8 ALC, Central African Republic, Gribingui River. ***Belonoglanis tenuis*:** CU 91536, 2 C&S, 54 ALC, Central African Republic, Tomi River; CU 91534, 8 ALC, Central African Republic, Oubangui River. ***Doumea alula*:** CU 91611, 1 DS, Central African Republic, Mbourou River; CU 91472, 2 ALC, Central African Republic, Kotto River; CU 91046, 2 C&S, 69 ALC, Zambia, Mutoloshi River. ***Phractura lindica*:** CU 91606, 4 C&S, 181 ALC, Central African Republic, Kotto River; CU 91607, 16 ALC, Central African Republic, Liwa River; CU 88356, 2 C&S, 17 ALC, Republic of Congo, Mambili River. ***Tetraacanthophilius notatus*:** CU 91422, 1 C&S, 5 ALC, Central African Republic, Tomi River. ***Zaireichthys sp. 'tanzania'*:** CU 90475, 3 C&S, 42 ALC, Tanzania, Moyowosi River.

Ariidae

***Bagre marinus*:** CU 81214, 1 C&S, unspecified, unspecified; CU 4075, 1 ALC, USA, 10 mi. W of Daytona; CU 79369, 1 DS, USA, Off Florida State Marine Lab. ***Sciades felis*:** CU 83737, 5 ALC, Trinidad and Tobago, Beach at N Chatham Road, SW shore; CU 81211, 2 C&S, unspecified, unspecified; CU 79400, 1 DS, USA, Off Florida State Marine Lab.

Auchenipteridae

***Asterophysus batrachus*:** CU 79418, 1 DS, Venezuela, unspecified. ***Auchenipterichthys thoracatus*:** CU 81193, 2 C&S, unspecified, unspecified; CU 88997, 6 ALC, unspecified, unspecified. ***Entomocorus benjamini*:** FMNH 97085, 1 C&S, Venezuela, Rio Orinoco. ***Entomocorus gameroi*:** CU 76232, 10 ALC, Venezuela, Prestamo #23, 25.7 km W of Bruzual-Elorza Hwy. on road paralleling Rio Caicara. ***Trachelyopterus galeatus*:** CU 88996, 1 DS,

6 ALC, unspecified, unspecified. *Trachelyopterus* sp.: CU 81182, 1 C&S, Brazil, unspecified; CU 79417, 1 DS, Venezuela, Rio Cunaviche.

Claroteidae

Auchenoglanis occidentalis: CU 90832, 1 DS, Republic of Congo, Lékoli River. *Chrysichthys mabusi*: CU 91695, 2 C&S, 30 ALC, Zambia, Luapula River. *Parauchenoglanis punctatus*: CU 91865, 1 DS, Central African Republic, Mbourou River; CU 80568, 2 C&S, 18 ALC, Gabon, Motoboi Village; Kiené Creek; CU 90232, 1 DS, Republic of Congo, Lékoli River.

Doradidae

Agamyxis albomaculatus: CU 91905, 1 DS, unspecified, unspecified; CU 80966, 2 C&S, 13 ALC, Venezuela, Rio Orinoco. *Centrodoras brachiatus*: CU 79413, 1 DS, Brazil, Unspecified; CU 81225, 1 DS, Brazil, Rio Solimões; CU 81235, 4 ALC, Brazil, Amazonas above Para. *Centrodoras* sp.: CU 81181, 1 C&S, Brazil, Rio Negro. *Hemidoras* sp.: CU 90916, 1 DS, Brazil, Rio Negro below Branco. *Leptodoras* sp.: CU 90915, 1 DS, Brazil, Rio Branco above Rio Negro. *Oxydoras niger*: CU 73180, 1 ALC, Brazil, unspecified; CU 81237, 1 DS, Brazil, Solimões R.; CU 79380, 1 DS, unspecified, unspecified; CU 81207, 1 C&S, unspecified, unspecified. *Platydoras costatus*: CU 81198, 1 C&S, unspecified, unspecified. *Pterodoras rivasi*: CU 79376, 1 DS, unspecified, unspecified; CU 79407, 1 DS, Venezuela, unspecified. *Rhinodoras* sp.: CU 81184, 3 C&S, Brazil, unspecified. *Trachydoras* sp.: CU 2746, 1 ALC, Brazil, unspecified; CU 81206, 1 C&S, unspecified, unspecified.

Ictaluridae

Ameiurus nebulosus: CU 81202, 1 C&S, USA, unspecified; CU 87382, 16 ALC, USA, New York, Oneida Lake. *Ameiurus* sp.: CU 9866, 1 DS, unspecified, unspecified. *Ictalurus punctatus*: CU 79378, 1 DS, unspecified, unspecified; CU 79403, 1 DS, unspecified, unspecified; CU 79412, 1 DS, unspecified, unspecified; CU 83206, 16 ALC, USA, Ohio R. *Ictalurus* sp.: CU 81185, 2 C&S, unspecified, unspecified.

Loricariidae

Panaque nigrolineatus: CU 91906, 1 DS, unspecified, unspecified. *Pterygoplichthys* sp.: CU 81222, 1 DS, Brazil, Margin of Japma.

Malapteruridae

Malapterurus beninensis: CU 90009, 3 C&S, Cameroon, Ndingui creek; CU 80551, 1 DS, Gabon, Diengué Creek; CU 81646, 1 ALC, Gabon, Ogouee R. *Malapterurus microstoma*: CU 91879, 1 DS, Central African Republic, Baïdou River. *Malapterurus monsemeensis*: CU 90839, 1 DS, Republic of Congo, Lékoli River; CU 90961, 1 DS, Republic of Congo, Lékoli River. *Malapterurus* sp.: AMNH 90265, 1 DS, unspecified, unspecified.

Mochokidae

Acanthocleithron chapini: AMNH 6548, 1 ALC, Congo, Ituri River; AMNH 6575, 1 ALC, Congo, Ituri River; MRAC 138179, 1 ALC, Congo Belge, riv. Liturumbu. *Atopochilus savorgnani*: CU 86329, 1 C&S, 1 DS, 5 ALC, Gabon, Okano River; CU 80738, 4 ALC, Gabon, Ntem River; MRAC 95-030-P-1411-1427, 2 C&S, 15 ALC, Cameroon, riv. Ntem. *Atopodontus adriaensi*: CU 92320, 1 C&S, 6 ALC, Gabon, Rapids at Loa-Loa; MRAC 049-P-0334, 1 ALC, Gabon, Loa Loa, Ivindo riv. *Chiloglanis batesii*: CAS 60803, 2 C&S, 33 ALC, Congo, Trib. to Riviere Luala; USNM 303409 10 ALC, 2 C&S, Cameroon, Upper Ndian System; CU 91434, 3 C&S, 81 ALC, Central African Republic, Gribingui River. *Chiloglanis carnosus*: MCZ 50541, 3 C&S, Zaire, Zaire River near Inga hydroelectric dam; MCZ 50241, 21 ALC, Zaire, Zaire River near Bulu. *Chiloglanis conicus*: MCZ 50149, 2 ALC, Zaire, Zaire River at Gombe; MCZ 50540, 3 C&S, 10 ALC, Zaire, Zaire River near Inga hydroelectric dam. *Chiloglanis disneyi*: USNM 303505, 2 C&S, 8 ALC, Cameroon, Akpa-Yafe System. *Chiloglanis macropterus*: CU 91007, 2 C&S, 111 ALC, Zambia, Luongo River. *Chiloglanis occidentalis*: SU 62926, 2 C&S, 44 ALC, Ghana, 46 miles from Dunkwa on the road to Bibiani; UMMZ 182016, 1 ALC, 1 C&S, Senegal, Trib. Of Senegal, 150km from Bamako. *Chiloglanis polypogon*: AMNH 222889, 10 ALC, Cameroon, Southern Munaya River; USNM 304263, 1 C&S, Cameroon, Cross System. *Chiloglanis* sp. 'burundi': CU 90387, 1 C&S, 10 ALC, Burundi, River Rugoma. *Chiloglanis* sp. 'chambeshi': UMMZ 199975, 1 C&S, Zambia, Trib to Lwombe River. *Chiloglanis* sp. 'igamba': CU 94005, 2 C&S, 49 ALC, Tanzania, Malagarasi River. *Chiloglanis* sp. 'kalungwishi': CU 91005, 1 C&S, 10 ALC, Zambia, Kalungwishi River. *Chiloglanis* sp. 'ntumbachushi': CU 91017, 1 C&S, 24 ALC, Zambia, Ng'ona River. *Euchilichthys dybowskii*: CU 91376, 1 C&S, 2 ALC, Central African Republic, Baïdou River. *Euchilichthys geuntneri*: MCZ 50538, 1 C&S, 26 ALC, Zaire, Zaire River near Inga hydroelectric dam; SU 54221, 1 DS, Democratic Republic

of the Congo, Kisangani (Stanleyville). *Euchilichthys royauxi*: CU 91612, 1 DS, Central African Republic, markets in Bangui; CU 91614, 1 DS, Central African Republic, markets in Bangui; CU 91764, 1 DS, Central African Republic, fishermen in Mobaye; CU 91828, 1 DS, Central African Republic, fishermen in Mobaye; CU 91380, 2 C&S, 50 ALC, Central African Republic, Oubangui River; CU 91379, 4 ALC, Central African Republic, Kotto River; SAIAB 40150, 2 C&S, 16 ALC, Zambia, Rapids near Chinsala pontoon. *Euchilichthys sp.*: AMNH 6472, 1 DS, Congo, Stanleyville, Junction Lualaba River with Congo River; SAIAB 74306, 2 C&S, 13 ALC, Congo, Lower Congo Rapids at Brazzaville. *Microsynodontis emarginata*: CU 80567, 1 C&S, 28 ALC, Gabon, Kiené Creek. *Microsynodontis vigilis*: CU 80133, 1 C&S, 16 ALC, Gabon, Nzorbang creek. *Microsynodontis sp. 'odzala'*: CU 88266, 2 C&S, 42 ALC, Republic of Congo, Lékénie River. *Mochokiella paynei*: AMNH 215709, 1 ALC, Sierra Leone, River Kasini (Kasenay Stream); BMNH 1979.8.22.1, 1 ALC, Sierra Leone, Kassewe Forest Reserve; CU 91904, 1 ALC, Sierra Leone, unspecified; BMNH 1979.8.22.2–3, 2 ALC, Sierra Leone, Kassewe Forest Reserve; CU 91903, 2 C&S, 4 ALC, Sierra Leone, unspecified; AMNH 58398, 2 C&S, unspecified, unspecified. *Mochokus brevis*: BMNH 1981.2.17.1941–1947, 5 of 7 ALC, Niger, northwest shore of Lake Chad; BMNH 1907.12.2.2529–2542, 1 C&S, 14 ALC, Sudan, White Nile. *Mochokus niloticus*: AMNH 228532, 1 ALC, Central African Republic, Bamingui River; AMNH 228721, 1 ALC, Central African Republic, N'goumbiri River; AMNH 230647, 1 ALC, Central African Republic, Vakaga River; CU 91384, 1 ALC, Central African Republic, Gribingui River; CU 91385, 4 ALC, Central African Republic, Gribingui River; CU 91386, 2 C&S, 5 ALC, Central African Republic, Gribingui River; AMNH 55403, 2 ALC, Egypt, Luxor; AMNH 55113, 2 ALC, Guinea, Milo River; MRAC P.119455–119456, 2 C&S, Guinea, riv. Milo. *Synodontis acanthomias*: CU 91613, 1 DS, Central African Republic, from fishermen in Mobaye; CU 91388, 4 ALC, Central African Republic, Oubangui River; AMNH 235705, 1 C&S, Republic of Congo, Downstream from Brazzaville; CU 89763, 1 DS, Republic of Congo, Mambili River; CU 90963, 1 DS, Republic of Congo, Mambili River; AMNH 235705, 7 ALC, Republic of Congo, Downstream from Brazzaville; MCZ 50152, 4 C&S, Zaire, Zaire River at Gombe. *Synodontis acanthoperca*: CU 80105, 1 C&S, 7 ALC, Gabon, Louétsi River; CU 89005, 1 ALC, Gabon, Ogooué R.; CU 89006, 2 ALC, Gabon, Ogooué R.; CU 91830, 10 ALC, Gabon, Ogooué R. *Synodontis alberti*: CU 91393, 2 C&S, 31 ALC, Central African Republic, Oubangui River; AMNH 235718, 1 C&S, 4 ALC, Republic of Congo, west bank of

Congo River, ca. 1 kilometer upstream of Foulakari River. *Synodontis angelica*: AMNH 90250, 1 DS, unspecified, unspecified; AMNH 94488, 1 DS, unspecified, unspecified. *Synodontis batensoda*: USNM 230106, 1 C&S, 6 ALC, Nigeria, Nigeria: Sokoto R.; MRAC P.168272–168276, 1 C&S, 5 ALC, Senegal, lac de Guiers. *Synodontis batesii*: CU 80361, 1 DS, Gabon, Ntem River; CU 80417, 2 ALC, Gabon, Ntem River; CU 86373, 2 C&S, 39 ALC, Gabon, Lower Balé Creek. *Synodontis clarias*: AMNH 19678, 1 C&S, Central African Republic, Birao; USNM 229746, 1 C&S, 8 ALC, Nigeria, Rima R. *Synodontis congica*: CU 91397, 1 C&S, 18 ALC, Central African Republic, Oubangui River; CU 88252, 1 ALC, Republic of Congo, Lékoli River. *Synodontis contracta*: CU 88584, 2 C&S, 39 ALC, Republic of Congo, Lékoli River. *Synodontis decora*: CU 91398, 1 C&S, 10 ALC, Central African Republic, Oubangui River; AMNH 55626, 1 DS, unspecified, unspecified. *Synodontis euptera*: CU 89004, 1 ALC, unspecified, unspecified; CU 91990, 1 DS, unspecified, unspecified; CU 91991, 1 DS, unspecified, unspecified; CU 91992, 1 DS, unspecified, unspecified. *Synodontis gambiensis*: USNM 317205, 1 C&S, 9 ALC, Togo, Togo - Zio R. *Synodontis geledensis*: UMMZ 241265, 2 DS, Ethiopia, Omo River. *Synodontis granulosa*: AMNH 90242, 1 DS, unspecified, unspecified. *Synodontis haugi*: CU 80694, 1 DS, Gabon, Ogooué River; CU 86528, 1 ALC, Gabon, Ogooué River; CU 86400, 4 ALC, Gabon, Ogooué River. *Synodontis katangae*: CU 91003, 1 C&S, 10 ALC, Zambia, Chambeshi River. *Synodontis longirostris*: CU 91861, 1 DS, Central African Republic, fish markets in Bangui; SU 54222, 1 DS, Democratic Rep. of the Congo, Kisangani (Stanleyville); MCZ 50245, 1 C&S, 12 ALC, Zaire, Zaire River near Bulu; SAIAB 74303, 2 ALC, Congo, Lower Congo Rapids at Brazzaville. *Synodontis macrostigma*: UMMZ 200089, 2 DS, Zambia, Kafue River; UMMZ 200075, 8 ALC, Zambia, Kafue River. *Synodontis membranacea*: CU 51996, 1 ALC, Ghana, Volta R.; SU 63500, 2 ALC, Ghana, Bosua-Atimpoku-Senchi Ferry; CU 89007, 1 ALC, 1 DS, unspecified, unspecified; USNM 313584, 1 C&S, Ghana, Lanto; USNM 086639, 1 ALC, Niger, Guran River. *Synodontis nigrita*: USNM 230125, 1 C&S, 23 ALC, Nigeria, Sokoto R.; CU 91993, 1 DS, unspecified, unspecified; CU 91994, 1 DS, unspecified, unspecified; CU 91995, 1 DS, unspecified, unspecified. *Synodontis nigriventris*: CU 89165, 3 C&S, 28 ALC, Republic of Congo, Lékoli River; AMNH 55166, 1 C&S, unspecified, Congo Basin. *Synodontis njassae*: USNM 266765, 1 C&S, Malawi, Lake Malawi; USNM 261879, 1 C&S, 9 ALC, Malawi, Lake Malawi. *Synodontis notata*: CU 91418, 1 ALC, Central African Republic, Oubangui River; CU 91875, 1 DS, Central African Republic, fish markets in Bangui. *Synodontis*

ocellifer: USNM 230099, 1 C&S, Niger, Middle/Upper Niger. *Synodontis pleurops*: CU 91415, 1 C&S, 6 ALC, Central African Republic, Oubangui River; CU 91876, 1 DS, Central African Republic, Mbourou River; CU 87571, 1 ALC, Republic of Congo, Mambili River; CU 90919, 1 DS, unspecified, unspecified. *Synodontis rebeli*: CU 90827, 1 DS, Cameroon, Chutes of Nachtigal; CU 89984, 6 ALC, Cameroon, Chutes of Nachtigal. *Synodontis schall*: USNM 229774, 1 C&S, 13 ALC, Nigeria, confluence of Sokoto and Niger; USNM 229806, 1 C&S, Nigeria, Rima R.; ANSP 78057, 1 DS, Sudan, Khartoum. *Synodontis schoutedeni*: MRAC P.44789, 1 C&S, Congo Belge, Kunungu. *Synodontis sorex*: ANSP 78053, 1 DS, Sudan, Khartoum; SU 62494, 1 C&S, 2 ALC, Ghana, Daboya; USNM 229795, 3 ALC, Nigeria, Sokoto R. *Synodontis sp.*: AMNH 236078, 3 C&S, Sierra Leone, River Moa; AMNH 22643, 1 DS, unspecified, unspecified; CU 79375, 1 DS, unspecified, unspecified; CU 81204, 1 C&S, unspecified, unspecified. *Synodontis unicolor*: CU 91011, 1 C&S, 10 ALC, Zambia, Lake Mwueru. *Synodontis victoriae*: CAS 211279, 4 ALC, Kenya, Lake Victoria and creeks in Nandi Hills; UMMZ 187335, 1 DS, 6 ALC, Uganda, Lake

Victoria. *Synodontis zambezensis*: CU 81680, 1 DS, Namibia, Zambezi River; CU 81681, 1 DS, Namibia, Zambezi River; CU 81682, 1 DS, Namibia, Zambezi River; CU 81683, 1 DS, Namibia, Zambezi River; CU 81684, 1 DS, Namibia, Zambezi River; CU 81685, 1 DS, Namibia, Zambezi River; CU 81686, 1 DS, Namibia, Zambezi River; CU 81687, 1 DS, Namibia, Zambezi River; CU 81688, 1 DS, Namibia, Zambezi River; CU 81689, 1 DS, Namibia, Zambezi River; CU 81690, 1 DS, Namibia, Zambezi River; CU 81273, 10 ALC, South Africa, Phongolo R.

Pangasiidae

Pangasius sutchi: CU 81170, 2 C&S, unspecified, unspecified.

Schilbidae

Schilbe grenfelli: CU 87558, 1 DS, Republic of Congo, Mambili River. *Schilbe intermedius*: CU 88310, 1 DS, Republic of Congo, Mambili River. *Schilbe laticeps*: CU 86377, 1 C&S, 16 ALC, Gabon, Balé Creek.

APPENDIX 2: CHARACTER STATE MATRIX

Character or matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 1-31

APPENDIX 2: CHARACTER STATE MATRIX CONT.

Character matrix of 93 characters for the examined species of the Mochokidae and outliers; characters 1–31.

Taxon	Character																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Auchenipteridae																															
<i>Trachelyopterus</i> sp.	0	0	0	0	2	1	0	0	1	0	1	1	1	0	2	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	
Doradidae																															
<i>Agamyxis albomaculatus</i>	0	1	0	0	0	2	1	0	0	1	0	1	1	1	0	2	1	0	1	0	0	2	0	0	0	0	0	0	0	0	
<i>Centrodoras</i> sp.	0	1	0	1	0	2	1	0	0	1	0	1	1	1	0	2	1	0	1	0	3	0	0	0	0	0	0	0	0	0	
<i>Platydoras costatus</i>	0	1	0	0	0	2	1	0	0	1	0	1	1	1	0	2	1	0	1	0	2	0	0	0	0	0	0	0	0	0	
Mochokidae																															
<i>Acanthocleithron chapini</i>	0	1	0	0	0	1	0	0	?	1	1	1	1	1	0	2	0	0	1	0	2	?	1	?	1	0	1	1	2	1	
<i>Atopochilus savorgnani</i>	1	2	1	1	1	2	1	1	-	0	0	1	1	1	0	2	0	0	0	0	0	0	1	1	1	1	1	1	1	1	
<i>Atopodonthus adriensis</i>	1	2	1	1	1	2	1	1	-	0	0	1	1	1	1	0	2	0	1	-	0	0	1	1	1	1	1	1	1	2	
<i>Chiloglanis batesii</i>	0	2	1	1	0	0	-	1	-	0	0	1	1	1	0	1	0	1	0	-	0	0	1	1	1	1	1	1	1	2	
<i>Chiloglanis carnosus</i>	0	2	1	1	0	2	1	1	-	0	0	1	1	1	0	2	0	1	-	0	0	1	1	1	1	1	1	1	1	2	
<i>Chiloglanis congicus</i>	0	2	1	1	0	2	0	1	-	0	0	1	1	1	0	2	0	1	0	1	-	0	0	1	1	1	1	1	1	2	
<i>Chiloglanis disneyi</i>	0	2	1	1	0	2	1	1	-	0	0	1	1	1	0	2	0	1	0	1	-	0	0	1	1	1	1	1	1	2	
<i>Chiloglanis macropterus</i>	0	2	1	1	0	2	0	1	-	0	1	1	1	1	0	2	0	1	0	2	0	1	-	0	0	1	1	1	1	2	
<i>Chiloglanis occidentalis</i>	0	2	1	1	0	2	0	1	-	0	0	1	1	1	0	1	0	1	0	1	0	-	0	0	1	1	1	1	1	2	
<i>Chiloglanis polypogon</i>	0	2	1	1	0	2	0	1	-	0	0	1	1	1	0	1	0	1	0	1	0	-	0	0	1	1	1	1	1	2	
<i>Chiloglanis</i> sp. 'burundi'	0	2	1	1	0	2	1	1	-	0	1	1	1	1	0	2	0	1	0	2	0	1	-	0	0	1	1	1	1	2	
<i>Chiloglanis</i> sp. 'chambeshi'	0	2	1	1	0	2	1	1	-	0	0	1	1	1	0	1	0	1	0	1	0	-	0	0	1	1	1	1	1	2	
<i>Chiloglanis</i> sp. 'igamba'	0	2	1	1	0	2	1	1	-	0	0	1	1	1	0	1	0	1	0	1	0	-	0	0	1	1	1	1	1	2	
<i>Chiloglanis</i> sp. 'kalengwishi'	0	2	1	1	0	2	1	1	-	0	0	1	1	1	0	2	0	1	0	2	0	1	-	0	0	1	1	1	1	2	
<i>Chiloglanis</i> sp. 'ntumbachushi'	0	2	1	1	0	2	1	1	-	0	0	1	1	1	0	2	0	1	0	2	0	1	-	0	0	1	1	1	1	2	
<i>Euchilichthys dybowskii</i>	1	2	1	1	2	1	1	-	0	0	1	1	1	0	2	0	1	0	2	0	1	-	0	0	1	1	1	1	1	1	
<i>Euchilichthys geomtheri</i>	1	2	1	1	2	1	1	-	0	0	1	1	1	0	2	0	1	1	1	1	0	-	0	0	1	1	1	1	1	1	
<i>Euchilichthys roauxi</i>	1	2	1	1	2	1	1	-	0	0	1	1	1	0	2	0	1	1	1	1	0	-	0	0	1	1	1	1	1	1	

APPENDIX 2: CHARACTER STATE MATRIX CONT.

Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 1–31.

APPENDIX 2: CHARACTER STATE MATRIX CONT.

Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 32-62.

Taxon	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62		
	Character																																
Diplomystidae	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Ictaluridae																																	
<i>Anisotremus nebulosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0			
<i>Ictalurus punctatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0			
Pangasiidae																																	
<i>Pangasius sutchi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0			
Clariotinae																																	
<i>Chrysichthys maculsi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0		
Auchenoglanidinae																																	
<i>Parauchenoglanis punctatus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
Schilbidae																																	
<i>Sciliibe laticeps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0		
Malapteruridae																																	
<i>Malapterurus beninensis</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	0	0	?	0	0	2	1		
Amphiliidae																																	
<i>Amphilophus cryptobullatus</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	-	0	1	1	0	0	2	0		
<i>Doumea alula</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	2	-	0	1	1	0	0	2	0	0	0		
<i>Phractura limica</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1&2	2	-	0	1	1	0	0	2	0	0	0	0	0		
<i>Tetracamphilius notatus</i>	0	0	0	0	0	0	2	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	2	1	0	0	0		
<i>Zaireichthys</i> sp. ‘tanzania’	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	2	0	0	0	0		
ArIIDae																																	
<i>Sciades felis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	-	1	2	1	0	0	0		
<i>Bagre marinus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	-	1	2	1	0	0	0	0		

APPENDIX 2: CHARACTER STATE MATRIX CONT.

Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 32-62.

Taxon	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
	Character																														
Auchenipteridae																															
<i>Trachelyopterus</i> sp.																															
Doradidae																															
<i>Agamyxis albomaculatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	1	0	3	1		
<i>Centrodoras</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	-	1	0	1	0	1&2	1		
<i>Platydoras costatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	-	1	0	1	0	2	1	
Mochokidae																															
<i>Acanthocheilichthys chapini</i>	4	0	0	0	0	0	1	1	0	?	1	0	0	1	0	0	1	0	0	1	1	1	?	?	?	1	0	1	0		
<i>Atopochilus savorgnani</i>	2	1	0	2	1	1	1	2	1	0	2	2	0	1	0	1	1	1	0	0&1	0	0	0	1	1	2	0	0	1	0	
<i>Atopodontus adriensis</i>	3	1	0	2	1	1	1	2	1	0	2	2	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	
<i>Chiloglanis batexii</i>	1	1	1	3	1	1	1	1	1	0	2	1	0	1	1	1	0	0	3	0	2	0	1	1	0	0	2	1	0		
<i>Chiloglanis carnosus</i>	1	1	0	2	1	1	1	1	0	2	1	0	1	1	1	0	0	2	0	0	0	1	1	2	0	2	0	0	0		
<i>Chiloglanis conicus</i>	1	1	0	2	1	1	1	1	0	2	2	0	1	1	1	0	0	2	0	0	0	1	1	2	0	2	0	0	0		
<i>Chiloglanis disneyi</i>	1	1	1	2	1	1	1	1	0	2	1	0	1	0	1	0	1&0	1	1	0	0	3	0	0	0	1	1	2	0		
<i>Chiloglanis macropterus</i>	1	1	0	2	1	1	0	1	1	0	2	1	0	1	1	1	0	0	1	0	0	0	1	0	0	2	0	1	2	0	
<i>Chiloglanis occidentalis</i>	1	1	1	3	1	1	0	1	1	0	2	2	0	1	1	1	0	0	?	0	2	0	1	1	0	0	2	1	0		
<i>Chiloglanis polyodon</i>	1	1	1	3	1	1	0	1	1	0	2	1	0	1	0	1&0	1	1	0	0	3	0	2	0	1	1	0	0	2	1	
<i>Chiloglanis sp. 'burundi'</i>	1	1	0	2	1	1	0	1	1	0	2	1	0	1	1	1	0	0	1	0	0	0	1	1	2	0	1	1	0		
<i>Chiloglanis</i> sp. 'chambeshi'	1	1	1	3	1	1	0	1	1	0	2	1	0	1	1	1	0	0	3	0	0	0	1	1	2	0	2	1	0		
<i>Chiloglanis</i> sp. 'iganga'	1	1	1	3	1	1	0	1	1	0	2	2	0	1	1	1	0	0	2&3	0	0	0	1	1	0	0	2	1	0		
<i>Chiloglanis</i> sp. 'kalungwishi'	1	1	1	0	2	1	1	0	1	1	0	2	1	0	1	1	1	0	0	1	0	0	1	2	0	1	1	0			
<i>Chiloglanis</i> sp. 'numbachushi'	1	1	1	3	1	1	0	1	1	0	2	1	0	1	1	1	0	0	2	0	0	0	1	1	2	0	2	1	0		
<i>Euchiloglanis dybowskii</i>	2	1	0	2	1	1	1	1	2	1	0	2	2	0	1	0	1	1	0	0	0	1	1	2	0	0	1	0			
<i>Euchiloglanis geuntheri</i>	3	1	0	2	1	1	1	2	1	0	2	2	0	1	0	1	1	0	0	0	1	1	2	0	1	0	1	&1	0		
<i>Euchiloglanis royauxi</i>	3	1	0	2	1	1	2	1	0	2	2	0	1	0	1	1	0	0	0	0	0	1	1	2	0	1	0	0	0		

APPENDIX 2: CHARACTER STATE MATRIX CONT.
Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 32-62.

Taxon	Character																														
	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Mochokidae (cont.)																															
<i>Microsynodontis emarginata</i>	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	1	1	0	3	0	
<i>Microsynodontis vigilis</i>	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	0	3	0		
<i>Microsynodontis</i> sp. 'odzala'	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	1	1	0	1	1	0	3	0			
<i>Mochokiella paynei</i>	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	0	2	1	0	0	0	1	1	0	2	0		
<i>Mochokus brevis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	4	0		
<i>Mochokus niloticus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	3	1	0	0	1	0	1	0	3	1		
<i>Synodontis acanthomias</i>	1	0	0	1	1	0	1	0	0	1	2	1	0	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	0		
<i>Synodontis acanthopercra</i>	1	0	0	1	1	0	1	0	0	1	1	1	0	0	1	0	0	2	1	0	0	0	0	0	1	1	0	2	0		
<i>Synodontis batensoda</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0			
<i>Synodontis batesii</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	2	1	0	0	0	0	1	1	0	2	1	
<i>Synodontis claritas</i>	1	0	0	1	1	0	1	0	0	1	2	1	0	1	0	0	1	0	0	2	1	0	0	0	1	1	0	1	1		
<i>Synodontis congica</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0		
<i>Synodontis contracta</i>	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	2	1		
<i>Synodontis gambiensis</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	2	1	0	0	0	1	1	0	1	1		
<i>Synodontis katangae</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	2	1	0	0	0	1	1	0	0	0		
<i>Synodontis longirostris</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0		
<i>Synodontis membranacea</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0		
<i>Synodontis nigrita</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	2	0			
<i>Synodontis nigriventris</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	2	1	0	0	0	1	1	0	1	0	1	0			
<i>Synodontis nyassae</i>	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	1	0			
<i>Synodontis pleurops</i>	1	0	0	1	1	0	1	0	0	1	2	1	0	1	0	0	2	1	1	0	0	0	1	0	0	1	0	0			
<i>Synodontis schall</i>	1	0	0	1	1	0	1	0	0	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0			
<i>Synodontis sorex</i>	1	0	0	1	1	0	1	0	0	1	2	1	0	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0			

APPENDIX 2: CHARACTER STATE MATRIX CONT.

Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 63-93.

Taxon	Character																														
	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
Diplomystidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0			
Ictaluridae																															
<i>Ameiurus nebulosus</i>	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0			
<i>Ictalurus punctatus</i>	0	0&1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0			
Pangasidae																															
<i>Pangasius sutchii</i>	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0				
Clariinae																															
<i>Chrysichthys mebusi</i>	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0			
Auchenoglanidinae																															
<i>Parauchenoglanis punctatus</i>	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0			
Schilbidae																															
<i>Schilbe laticeps</i>	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0			
Malapteruridae																															
<i>Malapterurus beninensis</i>	-	3	0	1	1	0	0	0	2	1	1	2	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0			
Amphiliidae																															
<i>Amphilophus cryptobullatus</i>	0	0	0	1	2	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	3	0	0	0	1	1	0	1	2		
<i>Doumea alula</i>	0	0	0	1	3	-	0	0	2	1	1	0	0	0	0	0	0	1	?	3	0	0	4	1	1	0	1	2			
<i>Phractura lindica</i>	0	0	0	1	3	-	0	0	2	2	1	2	0	0	0	0	1	0	1	?	3	0	0	4	1	1	0	2			
<i>Tetraacanthilus notatus</i>	0	0	0	1	2	1	0	0	2	2	0	4	0	0	0	0	2	0	1	?	3	0	0	3	1	1	0	2			
<i>Zaireichthys sp. 'tanzania'</i>	0	1	0	1	2	1	0	0	2	2	0	1	1	0	0	0	2	0	1	?	3	0	0	3	1	1	0	2			
Ariidae																															
<i>Sciaudes felis</i>	1	0	0	1	0	0	0	1	1	0	2	0	1	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0			
<i>Bagre marinus</i>	1	0	0	1	0	0	0	1	1	0	2	0	1	0	0	1	0	0	2	0	0	1	0	?	0	0	0				

APPENDIX 2: CHARACTER STATE MATRIX CONT.
Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 63-93.

Taxon	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
	Character																														
Auchenipteridae																															
<i>Trachelyopterus</i> sp.																															
Doradidae																															
<i>Agamyxis albomaculatus</i>	0	1	0	1	0	0	0	0	1	1	0	2	0	1	1	0	2	2	0	1	0	1	1	0	1	1	0	1	1	0	
<i>Centrodoras</i> sp.	1	1	1	0	0	0	0	1	1	0	1	0	1	1	0	2	2	0	3	0	1	1	0	1	1	0	0	1	0	0	
<i>Platydoras costatus</i>	1	1	1	0	0	0	0	2	1	0	1	0	1	1	0	2	2	0	3	0	1	1	0	1	1	0	1	1	0	1	
Mochokidae																															
<i>Acanthocheilichthys chapini</i>	0	0	1	1	0	?	0	0	2	2	0	1	0	1	1	1	1	0	2	0	0	0	2	2	3	0	0	0	0	0	
<i>Atopochilus savorgnani</i>	0	0	1	0	2	1	1	0	1&2	1	0	1	0	1	1	1	0	1	3	0	0	-	0	3	4	4	-	0	1	1	
<i>Atopodontus adriensis</i>	0	1	1	2	1	1	0	2	2	0	1	0	0	2	0	1	0	1	2	0	0	-	0	3	4	4	-	0	1	2	
<i>Chiloglanis batexii</i>	0	1	1	2	1	0	0	2	2	0	1	0	0	2	0	0	1	1	2	2	0	-	0	5	4	4	-	1	1	2	
<i>Chiloglanis carnosus</i>	0	1	0	2	1	1	0	2	2	0	1	0	2	0	0	0	1	2	1	0	-	0	5	4	4	-	1	1	2		
<i>Chiloglanis conicus</i>	0	1	1	0	2	1	1	0	2	2	0	1	0	0	2	0	0	1	3	0	0	-	0	5	4	4	-	1	1	2	
<i>Chiloglanis disneyi</i>	0	2	1	1	2	1	1	0	2	2	0	1	1	0	2	0	0	1	1	2	1	0	-	0	5	4	4	-	1	1	2
<i>Chiloglanis macropterus</i>	1	1&2	1	0	2	1	1	0	2	2	0	1	1	0	0	0	1	0	1	2	0	0	-	0	5	4	4	-	1	1	0
<i>Chiloglanis occidentalis</i>	1	1	1	1	2	1	1	0	2	2	0	1	0	0	2	0	0	1	1	2	2	0	-	0	5	4	4	-	1	1	2
<i>Chiloglanis polyodon</i>	1	2	1	1	2	1	1	0	2	2	0	2	0	0	2	0	0	1	1	2	2	0	-	0	5	4	4	-	1	1	2
<i>Chiloglanis sp. 'burundi'</i>	1	1	1	0	2	1	1	0	2	2	0	1	0	0	0	1	0	1	3	0	0	-	0	5	4	4	-	1	1	1	
<i>Chiloglanis</i> sp. 'chambeshi'	0	2	1	0	2	1	1	0	2	2	0	1	0	0	2	0	0	1	1	2	0	0	-	0	5	4	4	-	1	1	2
<i>Chiloglanis</i> sp. 'iganga'	0	1	1	2	1	1	0	2	1	0	1	1	0	2	0	0	1	1	2	0	0	-	0	5	4	4	-	1	1	2	
<i>Chiloglanis</i> sp. 'kalungwishi'	0	2	1	0	2	1	1	0	2	2	0	1	1	0	0	0	0	1	2	1	0	-	0	5	4	4	-	1	1	1	
<i>Chiloglanis</i> sp. 'numbachushi'	0	2	2	1	2	1	1	0	2	1	0	1	0	0	2	0	0	1	1	2	1	0	-	0	5	4	4	-	1	1	2
<i>Euchiloglanis dybowskii</i>	0	0	1	0	2	1	1	0	2	1	0	1	1	0	1	1	1	0	1	3	0	0	-	0	3	4	4	-	0	1	1
<i>Euchiloglanis geuntheri</i>	0	1	1	0	2	1	1	0	1	1	0	1	1	0	1	1	1	0	1	3	0	0	-	1	3	4	4	-	0	1	1
<i>Euchiloglanis royauxi</i>	0	0&1	1	0	2	1	1	0	1	1	0	1	1	0	1	1	1	0	1	3	0	0	-	1	3	4	4	-	0	1	1

APPENDIX 2: CHARACTER STATE MATRIX CONT.

Character matrix of 93 characters for the examined species of the Mochokidae and outgroups; characters 63-93.

Taxon	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
	Character																														
Mochokidae (cont.)																															
<i>Microsynodontis emarginata</i>	1	0	1	1	0	0	0	2	2	0	3	1	1	1	1	1	0	0	2	0	0	1	0	2	2	3	0	1	1	0	
<i>Microsynodontis vigilis</i>	0	0	1	1	0	0	0	0	2	2	0	3	1	1	1	1	0	0	2	0	0	1	0	2	2	3	0	1	1	0	
<i>Microsynodontis</i> sp. 'odzala'	1	1	1	1	0	0	0	0	2	2	0	3&5	1	1	1	0	1	0	2	0	0	1	0	2	2	3	0	1	1	0	
<i>Mochokiella paynei</i>	1	0	1	1	0	0	0	0	2	2	0	2	0	1	1	0	1	0	2	0	0	1	0	2	2	0	1	1	0	0	
<i>Mochokus brevis</i>	0	1	1	0	0	0	1	2	2	1	2	0	1	1	1	0	0	0	2	0	0	0	0	3	1	2	0	1	1	0	
<i>Mochokus niloticus</i>	0	0	1	1	0	0	0	1	2	2	1	4	0	1	1	1	0	0	2	0	0	0	0	3	2	2	0	1	1	0	
<i>Synodontis acanthomias</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	1	2	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0
<i>Synodontis acanthopercula</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	1	2	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0
<i>Synodontis batensoda</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	1	2	1	0	0	2	0	0	1	0	2	2	3	1	0	1	0
<i>Synodontis batesii</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	1	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0	0
<i>Synodontis claritas</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	2	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0	0
<i>Synodontis congica</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	1	0	1	0
<i>Synodontis contracta</i>	1	0	1	1	0	0	0	2	2	0	4	0	1	1	1	1	0	0	3	0	0	1	0	2	2	3	0	0	1	0	0
<i>Synodontis gambiensis</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0
<i>Synodontis katangae</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0
<i>Synodontis longirostris</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	1	0	1	0
<i>Synodontis membranacea</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	1	0	0	0
<i>Synodontis nigrita</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0
<i>Synodontis nigriventris</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	0	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0	0
<i>Synodontis nyassae</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	0	0	1	0
<i>Synodontis pleurops</i>	1	0	1	1	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	3	3	1	0	1	0
<i>Synodontis schall</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	2	3	1	0	1	0
<i>Synodontis sorex</i>	1	0	1	0	0	0	0	2	2	0	1	0	1	1	2	1	1	0	0	2	0	0	1	0	2	3	3	1	0	1	0