

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

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ABSTRACT– A hypothesis of phylogenetic relationships, based on maximum parsimony analysis of 92 morphological characters, is presented for the Mochokidae for the first time. Forty-two ingroup taxa are considered in a heuristic search, and a subset of 17 taxa in a smaller exhaustive search. The results of the two analyses are largely in agreement and reveal the following: the Mochokidae are a monophyletic group, sister to a group composed of the South American Doradidae + Auchenipteridae; new synapomorphies for the family include features of the pectoral girdle, caudal fin and mandibular sensory canal; monotypic *Mochokiella*, *Acanthocleithron* and *Atopodontis* are valid as separate genera; *Mochokus* and *Microsynodontis* are monophyletic; *Synodontis* must include *Hemisynodontis membranaceous* and *Brachysynodontis batensoda* to be monophyletic; *Chiloglanis* is rendered paraphyletic by nested placement of *Atopochilus*, *Euchilichthys* and *Atopodontis*; and *Euchilichthys* is rendered paraphyletic by nested placement of *Atopochilus savognani*. Monophyly of *Atopochilus* was not tested because only one species was available. The recovered topology presents the following well-supported groups: *Atopochilus* and *Euchilichthys* form a monophyletic group, despite the paraphyly of *Euchilichthys*; *Atopodontis*, *Atopochilus* and *Euchilichthys* form a monophyletic

group; *Chiloglanis*, *Atopodontis*, *Atopochilus* and *Euchilichthys* form a monophyletic group, despite the paraphyly of *Chiloglanis*; that group delimits the redefined subfamily Chiloglanidinae; the Chiloglanidinae form a trichotomy with *Synodontis* and *Microsynodontis*. Remaining intrafamilial groups are based on the placement of *Mochokus*, *Mochokiella* and *Acanthocleithron* towards the base of the tree; support for these groups is poor. Synapomorphies are listed for each major clade recovered. Well-supported groups within the Mochokidae are largely defined by a combination of characters pertaining to the teeth, oral jaws, and suspensorium. Changes in the jaw and suspensorium are a key theme in mochokid evolution. The results of this analysis indicate the need for the revision of several mochokid groups. Higher-level systematics of the Mochokidae can be greatly improved with continued emphasis on broader, lower-level taxonomic work.

ADDITIONAL KEYWORDS: *Chiloglanis* – morphology – osteology – phylogeny – squeakers – *Synodontis* – systematics – upside-down catfish.

## INTRODUCTION

The Mochokidae are a family of African catfishes distributed throughout the freshwaters of Africa. Commonly known as squeakers or upside-down catfishes, they are most well known for their appearance in the pet trade; in truth, most species found in the pet trade belong to a single large genus, *Synodontis*. Not surprisingly, the common names for the family are largely attributed to species of *Synodontis*. Species in the genus are capable of making a squeaking noise by stridulation of the pectoral spine against the

pectoral girdle (Jubb, 1967); stridulation is also apparent in *Mochokiella paynei* and species in the genus *Atopochilus* (personal observation). Even more peculiar is the habit of some species of *Brachysynodontis* and *Synodontis* that are known to swim upside-down. This habit seems to be correlated with feeding while upside-down at the water's surface (Bishai & Abu Gideiri, 1965), but upside-down catfishes will rest and swim in the 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. While these common names may refer to members of the genus *Synodontis*, the family is actually much more interesting when taken as a whole.

Species in the family are quite variable in terms of morphology. Species of *Synodontis*, *Hemisyndontis*, *Brachysynodontis* and *Microsynodontis* are known for their ventrally directed mouths, S-shaped teeth, branched mandibular barbels, well developed nuchal shields and bold pigmentation patterns. Species of *Chiloglanis*, *Atopochilus*, *Euchilichthys* and *Atopodontis* are rather drab in comparison and exhibit a distinctive, ventrally-directed oral disc. Lesser known mochokids, like *Mochokus*, *Mochokiella* and *Acanthocleithron* exhibit unique morphologies of their own. Size is also quite variable within the family. Altogether, mochokids range in size from 40mm SL in some species of *Chiloglanis* and *Microsynodontis* up to 800mm SL in some species of *Synodontis*. In addition to morphological variability, mochokids are known to exhibit obvious sexual dimorphism. For example, several species in the genus *Chiloglanis* show dimorphism of the anal and caudal fins (Roberts, 1989; Seegers, 1996; Friel & Vigliotta, 2006); some *Chiloglanis* also display sexual dimorphism of the cleithral process, wherein males possess a greatly enlarged process shielding the flank. In the genus *Atopochilus*, sexual

dimorphism of the anal fin is sometimes evident (personal observation). Some mochokids also exhibit spiny ornamentation of the skull roof bones, opercular series and pectoral girdle (Friel & Vigliotta, 2006). In the case of *Synodontis acanthoperca*, a spine found at the rear of the opercle is, itself, sexually dimorphic. The spines of males are much larger than those of females. This is also true for *Mochokiella paynei*, which was previously unknown to possess opercular spines or exhibit sexual dimorphism.

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 Africa, southern Africa, and eastern Africa, including the Nile River, Lake Victoria, Lake Tanganyika and Lake Nyasa. Like a handful of other catfishes, some mochokids are known to swim in mid-water; other members of the family are primarily benthic. Likewise, some mochokids shoal while others are rather solitary. As a rule they are most active during the night, but they can be found hiding amongst plants, logs and other submerged structure during the day. Fossil mochokids, of the genus *Synodontis*, have been found in deposits from eastern and northern Africa dating to the early Miocene (at least 20 mya) (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 a large number of those names are now considered junior synonyms. The number of valid, described species is approaching 200 and several undescribed species are known to exist. This makes the Mochokidae one of the largest families of catfishes and the largest family of African catfishes by far. Ferraris (2007) provides the most recent list of mochokid

species and synonymies (188 listed as valid). *Synodontis acanthoperca* 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 also resurrect two species of *Synodontis* from synonymy. Two new mochokid species are also described in separate papers within this special volume (Friel and Vigliotta, 2008; Friel and Sullivan, 2008). In all, nearly one third of African catfishes belong to the family Mochokidae.

As with most African freshwater fishes, phylogenetic treatments of African catfishes are considerably rare. Taxonomic revisions of the African Schilbeidae (De Vos, 1995) and Malapteruridae (Norris, 2002) have been undertaken, but the only African group treated in a phylogenetic framework is the Amphiliidae (He et al., 1999; Diogo, 2003). For the several other families of catfishes inhabiting the African continent there has been very little phylogenetic work done. Beyond some recent work on the *Synodontis* from Lake Tanganyika (Koblmuller et al., 2006; Day and Wilkinson, 2006), phylogenetic treatment of the Mochokidae is practically non-existent.

The objectives of the this research were threefold and prioritized as such: (1) to assess the monophyly of known mochokid genera and to determine the phylogenetic relationships between these genera, (2) to assess the monophyly of the Mochokidae and (3) to support/establish a clade of catfishes as the sister group to the Mochokidae. I have approached these objectives by performing a broad survey of the gross morphology of several mochokid species in addition to several species serving as outgroups. A data matrix based on this survey was analyzed using parsimony methods in order to reconstruct a phylogeny for these taxa.

## TAXONOMIC AND SYSTEMATIC HISTORY OF THE MOCHOKIDAE

The family Mochokidae was established long after the description of many of its component taxa; the history of the family is, as a result, fairly complicated. What follows is a mostly chronological account of the taxonomic history of the family and its genera.

The first mochokid species (*Synodontis clarias* today) was described by Linnaeus (1758) and placed in the genus *Silurus*. Cuvier (1816) described the first mochokid genus, *Synodontis*. He recognized it as distinct from other catfishes by placing it in his group “Des Schals” and characterized the group by the form of the teeth, among other features. The presence of S-shaped teeth remains an important characteristic of many mochokids today. Presently, there are approximately 120 species in the genus *Synodontis*. To date, no substructure has been proposed for the genus and its monophyly has never been demonstrated. Poll (1971) provides the most recent revision of the genus and a key to the species. The geographic distribution of *Synodontis* is similar to that of the family as a whole; they are found in many rivers and lakes throughout Africa.

Joannis (1835) described a second genus, *Mochokus*, but did not ally it with *Synodontis*. Joannis was justified in missing or ignoring a relationship to *Synodontis* because, unlike most mochokids, *Mochokus* does not have S-shaped teeth or a highly modified jaw. Today there are just two valid species in the genus *Mochokus*. Their geographic distribution is limited to northern and western Africa, including the Nile River.

Bleeker (1862-1863) reviewed several species of *Synodontis* that had been described in the intervening years and created four new genera to accommodate certain species. *Leiosynodontis* and *Pseudosynodontis* (both monotypic) were never widely used and were effectively synonymized by Günther (1864). *Brachysynodontis* and *Hemisynodontis* remain today as monotypic genera. The validity of these two genera is questionable at best. Some authors have already suggested that the two species, *H. membranaceous* and *B. batensoda*, belong in the genus *Synodontis* (Willoughby, 1994). The status of *Hemisynodontis* and *Brachysynodontis* will be effectively settled in this work. Both species are found in northern and western Africa.

The genus *Rhinoglanis*, now considered a junior synonym of *Mochokus*, was described by Günther (1864). Günther recognized that *Rhinoglanis* and *Mochokus* were allied to, but separate from *Synodontis* by placing each of them in his family Siluridae Stenobranchiae, but in different “groups.” He placed *Rhinoglanis* and *Mochokus* in his “group Rhinoglanina,” with a member of the Asian family Sisoridae. He placed *Synodontis* in the “group Doradina,” which also contained members of the South American families Cetopsidae, Auchenipteridae and Doradidae. Günther’s placement of *Synodontis* is noteworthy because the Auchenipteridae and Doradidae have been recovered as close relatives of the Mochokidae in more recent works (Chardon, 1968; Mo, 1991; de Pinna, 1993; Lundberg, 1993; Diogo, 2005). Günther’s “group Doradina” may constitute the first hypothesis of a close relationship between mochokids and these Neotropical families. One significant aspect of this relationship lies in the implied biogeographical scenario. Among catfishes, this is the only trans-Atlantic clade with solid

support, morphological or otherwise. Lundberg (1993) suggested that this relationship is the result of an African-South American vicariance event.

Peters (1868) described the sucker-mouthed genus *Chiloglanis* and allied it to Günther's "group Doradina." Today *Chiloglanis* is the second largest mochokid genus, with approximately 45 valid species. Several undescribed species are known to exist. Again, no substructure within the genus has been proposed. The geographic distribution of *Chiloglanis* is similar to that of the family as a whole, although they are strictly riverine species and absent from lakes.

When Sauvage (1879) described a second sucker-mouthed genus, *Atopochilus*, he incorrectly allied it to Günther's "group Ariina" in the family Siluridae Proteropterae. Today there are seven valid species of *Atopochilus*. The distribution of *Atopochilus* species is peculiar. The type species is described from the Lower Guinea ichthyofaunal province. Five of the remaining species are restricted the Congo basin and the final species is described from eastern Africa, in the Wami River of Tanzania.

Boulenger (1900) made an effort to bring all of the components, described thus far, together in a paper concerning the so-called subfamily Doradinae. He allied *Chiloglanis*, *Atopochilus*, and *Mochokus* with *Synodontis*, and synonymized *Rhinoglanis* with *Mochokus*. He also described and allied *Euchilichthys*, a new sucker-mouthed genus, to the group. Today there are five valid species in the genus *Euchilichthys*, though the distinction between *Euchilichthys* and *Atopochilus* has always been unclear. Between the two, a small number of undescribed species are known to exist. *Euchilichthys* species are limited to the Congo basin.

In a few short years Boulenger (1903) described the first species in the genus *Microsynodontis*, immediately allying it with *Synodontis*. Today there are 11 valid species in the genus *Microsynodontis*; eight of those species were described recently (Ng, 2004). At least one undescribed species is known and the genus is probably significantly larger than expected. *Microsynodontis* species can be found in the Congo basin, the Lower Guinea ichthyofaunal province and western Africa.

In his classification of teleostean fishes, Regan (1911) placed the mochokid genera into their own family for the first time, the Synodontidae. He also noted the fundamental differences between the sucker-mouthed 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.

Nichols and Griscom (1917) described the first and only species in the genus *Acanthocleithron*. They recognized it as being within Boulenger's and Regan's mochokid groups, and allied it with *Mochokus*. A total of ten specimens are known for this very distinct species, yet it has a surprisingly large geographical range throughout the Congo basin.

In a detailed review of anatomy, myology and osteology of the genus *Synodontis*, Taverne and Aloulou-Triki (1974) created a subfamily, the Simuldentinae, containing *Synodontis*, *Brachysynodontis*, and *Hemisynodontis*. While there is no obvious reason to question the monophyly of this group, the act is curious because they did not treat any

other genera within the family. According to Ferraris (2007) the Simuldentinae is not a valid subfamily or ‘family-group name’ because it is not based on an available genus name.

Another family group is recognized from a name proposed in the aquarium literature (Riehl and Baensch, 1990). The subfamily name Chiloglanidinae is applied to two species of *Chiloglanis* in that work, but the name is most appropriate for a group composed of all sucker-mouthed species. This subfamily name and the term ‘chiloglanidin’ will be used throughout the text to refer to a group composed of *Chiloglanis*, *Atopochilus*, *Euchilichthys*, and *Atopodontis*. The monophyly of this group will be tested by the analyses in this work.

Howes (1980) described the first and only species in the genus *Mochokiella* from Sierra Leone. Howes was unwilling to make any specific statement about the placement of this new genus, but allied it most closely with *Microsynodontis*. *Mochokiella* remains a monotypic genus. As far as known, *Mochokiella* is limited to small coastal drainages in Sierra Leone.

The newest mochokid genus, *Atopodontis* (Friel and Vigliotta, 2008), is described in this volume. *Atopochilus adriaensi* is a sucker-mouthed species that shares a number of features with species of *Chiloglanis*, but also *Atopochilus* and *Euchilichthys*. The placement and validity of the genus is tested in this work. Thus far, *Atopodontis* is known from the Ogôoué and Nyanga Rivers in Gabon.

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. Recent work suggests that the

Mochokidae are related to several African catfish families and that they are most closely related to the Amphiliidae (loach catfishes) and Malapteruridae (electric catfishes) (Sullivan et al., 2006). These relationships are well supported by the molecular data, but they greatly conflict with the phylogenetic scheme supported by morphology.

To summarize, the intrafamilial relationships for the Mochokidae have never been sufficiently examined. Original authors have allied genera based on gross morphological similarities, but never in a discrete phylogenetic context. Molecular 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 relationship of the Mochokidae to other catfishes is also unclear. Morphological and molecular phylogenies have not recovered the same group(s) as sister to the Mochokidae and, in fact, the hypotheses are drastically different.

## MATERIALS AND METHODS

### **Materials and Preparations**

Materials examined in this study were prepared as cleared and stained specimens, dry skeletons, or fluid specimens. Appendix 1 lists the material examined and denotes the family, species, catalog number, number of specimens by each preparation type, country and specific locality. For preparation type, C&S = cleared and stained, DS = dry skeleton and ALC = alcoholic, fluid specimen. The materials are listed alphabetically by family, genus and species. 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 at least some variation within a species, to examine sexually dimorphic characters and to rule out anomalous features. Dry skeletons were prepared with a dermestid beetle colony after cleaning by hand. External morphological features were examined on fluid specimens, but also on cleared and stained specimens when appropriate. Fluid specimens and cleared and stained specimens were usually available from the same lot.

Because material for the genus *Acanthocleithron* is exceedingly rare, other techniques were required to glean the necessary 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 completely nondestructive technique for visualizing features in the interior of opaque solid objects, and for obtaining digital information on their 3-D geometries and properties. It is useful for a wide range of materials, including bone and soft tissue. Individual slices and video reconstructions of the three-dimensional specimen allowed me to visualize many of the internal features not otherwise accessible in this rare species.

### **Delimitation of Taxa**

The ingroup considered in this work is the family Mochokidae, which includes nearly 200 valid species. Fifty-five ingroup species were initially examined (at least three undescribed), with at least one species from all of the valid genera within the family. The following taxa were considered valid genera within the family; numbers in parentheses

represent the number of species examined: *Acanthocleithron* (1 valid species), *Atopochilus* (1 valid species), *Atopodontis* (1 valid species), *Brachysynodontis* (1 valid species), *Chiloglanis* (8 valid species, 3 undescribed, 1 unidentified), *Euchilichthys* (2 valid species, 2 unidentified), *Hemisynodontis* (1 valid species), *Microsynodontis* (2 valid species, 1 unidentified), *Mochokiella* (1 valid species), *Mochokus* (2 valid species), *Synodontis* (28 valid species). For *Synodontis* and *Chiloglanis*, the large number of described species required careful selection. In both instances, species were chosen to maximize the range of morphological variation within the genus and to cover as much of the known geographic range as possible. Type species were examined for all of the ingroup genera except *Chiloglanis*, *Euchilichthys* and *Microsynodontis*; suitable material for those type species was not available. All type species examined were included in the most comprehensive analysis. A small number of undescribed and otherwise unidentifiable species were included in the analyses because of their unique morphologies. Within this work, 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 alleged to be closely related to the Mochokidae. Thirty-seven species from the following families or genera were examined for the reasons provided:

**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 family was recently established as sister to all siluroid catfishes, with loricarioids as sister to that group (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** – The Ictaluridae is a relatively plesiomorphic group, with at least one phylogeny supporting a close relationship to the Mochokidae, though support is admittedly weak (Hardman, 2005). The molecular data of this work suggests that the Mochokidae are sister to a group composed of the Ictaluridae plus the Cranoglanididae. *Cranoglanis* was not examined in this study. The relatively plesiomorphic nature of the Ictaluridae is key to its choice as an outgroup.

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

**Ariidae** – The Ariidae is the basal group of Lundberg's (1993) 'arioid' clade, which included the Mochokidae as a more derived member. 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 considerably rare and was not readily available for use in this study.

**Auchenipteridae and Doradidae** – These families were long ago established as a potential sister group of the Mochokidae based on morphology. The affinity of the Mochokidae to these families was known at least as far back as Günther (1864). 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*, *Chrysiichthys* and *Parauchenoglanis*** – Each genus represents a separate family or subfamily in the ‘Big Africa’ group of Sullivan et al. (2006). ‘Big Africa’ is a group comprised of six large African clades, including the Schilbeidae (African only), Claroteinae, Auchenoglanidinae, Amphiliidae, Malapteruridae and Mochokidae.

**Amphiliidae and Malapteruridae** – Within the ‘Big Africa’ group 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. Data were entered into a matrix (Appendix 2) using Mesquite, version 1.11 (Maddison and Maddison, 2006). In the matrix unknown or missing data were entered as ‘?’ and data that were inapplicable for a given taxon was entered as ‘-’; both of these were recognized as missing data and treated as such in parsimony analysis. All characters were left unweighted and all characters were left unordered unless otherwise noted. Characters

were ordered only when it was reasonable to infer a priori the nature of a transformational series. As such, ordered characters are limited to those pertaining to the counts of discrete elements. The data were subjected to parsimony analysis in PAUP (Phylogenetic Analysis Using Parsimony), version 4.0b10 (Swofford, 2002). Of the 92 taxa initially examined (55 ingroup, 37 outgroup), two subsets were chosen to make searching with various algorithms reasonably time-efficient.

In the first and most inclusive analysis (Analysis 1), 61 taxa were included; 42 of these were part of the ingroup (refer to matrix, Appendix 2). The taxa included in Analysis 1 were chosen for completeness of data, as well as utility in achieving the objectives. For example, some *Synodontis* were ultimately excluded due to a lack of cleared and stained material, which was necessary for scoring a considerable number of characters. 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.

In a more restricted analysis (Analysis 2), 24 taxa were included; 17 of these were part of the ingroup; all taxa were part of the larger subset in Analysis 1. Here, only examples of unique morphotypes from the ingroup genera were used. As such, species of similar morphology with similar ranges were excluded. Given the smaller number of taxa, a branch-and-bound search was now convenient for finding the single set of most parsimonious trees.

For both analyses, outgroup and ingroup relationships were resolved simultaneously, using global parsimony analysis as outlined by Nixon and Carpenter (1993). In each, the root was placed in the Diplomystidae, which is widely regarded 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). In either case, the Diplomystidae are sufficiently basal with respect to all of the other taxa considered. To assess possible synapomorphies for the various subgroups, trees were optimized under both ACCTRAN and DELTRAN. Under ACCTRAN, reversals are maximized with respect to convergences; the opposite is true under DELTRAN.

To test the robustness of the trees recovered, Bremer decay indices were determined for the nodes in the consensus trees from each analysis. Decay indices were calculated for both trees using TreeRot, v.2 (Sorenson, 1999). Bootstrap values were evaluated in PAUP for the branch and bound tree only, because calculation of bootstrap values for the TBR search was not time-efficient. Bootstrap values are calculated from 1000 replicates.

### **Illustrations and Terminology**

Anatomical illustrations were produced digitally using Adobe Photoshop and Adobe Illustrator. Objects for illustration were chosen carefully from the materials listed in Appendix 1 and photographed at the proper angle to maximize the utility of the resulting figure. Digital photographs were then 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 throughout 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 and medial nuchal plate, fused; **a.p.e.**, anterior pterygoid element; **a.prp.c.c.**, anterior paraporphysis of the compound centrum; **ahy**, anterohyal or anterior ceratohyal; **al.pr.lv.gr.**, anterolateral process of the pelvic girdle; **am.pr.plv.gr.**, anteromedial process of the pelvic girdle; **ang-art**, angulo-articular; **apa**, autopalatine; **ar.co.neuro.**, articulating condyle for the neurocranium; **ar.fa.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.plv.gr.**, cartilage of the anterior processes of the pelvic girdle; **cbr**, ceratobranchial; **cl**, cleithrum; **cl.pr.**, cleithral process; **cmk**, coronomeckalian; **cor.pr.**, coronoid process; **d.pr.cl.**, dorsal processes of the cleithrum;

**d.pr.r.**, dorsal-fin proximal 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.**, medial 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.prp.c.c.**, posterior parapophysis of the complex centrum; **p.sp.**, pectoral spine; **pa-so**, parieto-supraoccipital; **pa-so.for.**, parieto-supraoccipital foramen; **pasp**, parasphenoid; **phbr**, pharyngobranchial; **phpu**, parhypural; **phy**, posterohyal 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**, uroneural; **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 61 rows for the total number of taxa in Analysis 1 and 92 columns for as many characters, which are described below. This section is divided into several subsections that correspond to various osteological and morphological systems.

Each character description is formatted in the same manner. Each listing starts with a character number. These correspond with the numbers at the top of each column in the matrix. After the character number is a descriptive title for the character. Next, in parentheses, the consistency index (CI) and retention index (RI) for the character are given from the consensus in Analysis 1. The indices from Analysis 2 are not given; they are inflated because there are fewer taxa included. The consistency index for a character is calculated by dividing the minimum number of steps ( $m$ ) by the observed number of steps ( $s$ ). The consistency index is a measure of how well a character fits a phylogenetic tree. The retention index is also a measure of how well a character fits the tree and is calculated as  $(g-s)/(g-m)$ , where  $m$  and  $s$  are as for the consistency index, and  $g$  is the maximum number of steps. The retention index for an autapomorphic state is mathematically indeterminate and labeled as 'AUT'. Following the indices is a list of references that contain information pertinent to the character. When a reference includes a similar character, the reference is followed by a bracketed number corresponding to the character number used in that reference.

The entire header is followed by a short 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 the previous use of similar characters will also be included here. Comments on convergences, reversals and the adaptive nature of certain character states are held for the discussion, where they can be placed in the context of the resulting phylogeny.

After the descriptive paragraph, each character state is listed in a shorter form. Each character state has a character state number, **CS-X**, where the X corresponds with the codes used in the matrix. The character state number is followed by the state itself. A telegraphic writing style was generally employed to keep them as short as possible. Typically, the distribution for each derived character state follows the state itself. When distributions are exceedingly complex, the reader is referred to the matrix. The distribution for CS-0 is generally not given. It should be assumed that the state occurs in all taxa not listed as showing the derived state(s). When taxa are listed, they are listed in as short a form as possible. When all taxa of a higher group (genus or family) share the same state, the higher-group name is listed in the distribution. 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 group is followed by a bracketed character state number to indicate which state it does show.

A small number of characters have a state called ‘inapplicable’ which will be listed last. The text for this state lists taxa that cannot be coded for and gives specific reasons for assigning this character state. As noted above, the code for inapplicable (-) is treated the same as missing data (?) by PAUP.

## **Neurocranium and Nuchal Shield**

**1. Ventral process of the mesethmoid. (CI = 1.000, RI = 1.000)** (Starks, 1926; Mo, 1991 [1]; Diogo, 2005 [61])

In most Siluriformes the mesethmoid supports the premaxillary tooth plates ventrally without any well-developed process between them (Fig. 1A, B). In *Atopodontis*, *Atopochilus* and *Euchilichthys* there is a well-developed process on the ventral surface of the mesethmoid between the premaxillary tooth plates (Fig. 1C). Mo (1991) and Diogo (2005) recognized a similar process in certain loricarioids, but make no mention of such a structure in the Mochokidae.

**CS-0:** Mesethmoid without ventral process.

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

**2. Anterolateral cornua of the mesethmoid. (CI = 0.400, RI = 0.909)**

In the Siluriformes the anterior end of the mesethmoid is often formed by two laterally directed cornua. These cornua can be nearly double the width of the more posterior portion of the bone (Fig. 2A). In the derived conditions, the mesethmoid lacks truly well-developed anterolateral cornua. In several mochokids and some of the outgroup taxa the cornua are poorly developed; the anterior end of the mesethmoid is only slightly wider than the rest of the bone (Fig. 2B). In *Zaireichthys* and the chiloglanidins the mesethmoid is entirely without anterolateral cornua (Fig. 2C).

**CS-0:** Mesethmoid with well-developed anterolateral cornua.

**CS-1:** Mesethmoid with modestly or poorly developed cornua. (*Doumea*; *Phractura*; *Doradidae*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*)

**CS-2:** Mesethmoid entirely without anterolateral cornua. (*Zaireichthys*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

[Insert Figures 1 and 2 near here.]

**3. Relative width of ventral and dorsal portions of the mesethmoid at articulation with the lateral ethmoids. (CI = 0.200, RI = 0.846) (Mo, 1991 [1])**

In most of the siluriform taxa considered here the dorsal ridge of the mesethmoid is just as wide as the ventral portion where it joins to the lateral ethmoids synchondrally (Fig. 2A, B). In several mochokids, as well as the Amphiliidae and Malapteruridae, the dorsal ridge of the mesethmoid is much narrower than the ventral portion. In these taxa the wider ventral portion tends to form a base to the nasal cavity (Fig. 2C).

**CS-0:** Ventral portion of mesethmoid not much wider than the dorsal portion.

**CS-1:** Ventral portion of mesethmoid much wider than the dorsal portion. (*Amphiliidae*; *Malapteruridae*; *Mochokus*; *Mochokiella*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

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

In several of the outgroup taxa considered the lateral ethmoids are rather short and wide, being sutured to the frontals nearly transversely and being laterally expanded to form a

large portion of the orbit (Fig. 2A). In the derived state, shared by several mochokid genera and a few of the outgroup taxa, the lateral ethmoids are relatively elongate, sutured to the lateral edge of the frontals and without obvious lateral expansion. They form only a small portion of the orbit, if at all (Fig. 2B, C).

**CS-0:** Lateral ethmoids short and wide, with a transverse suture to frontals.

**CS-1:** Lateral ethmoids elongate and narrow, with a longitudinal suture to the frontals.

(*Parauchenoglanis*; Amphiliidae; *Centrodoras*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

#### **5. Laminar curtain of lateral ethmoids. (CI = 1.000, RI = 1.000) (Starks, 1926)**

In the vast majority of Siluriformes the anterolateral edge of the lateral ethmoid is roughly horizontal (Fig. 1A, B and Fig. 3A, B). In *Atopodontis*, *Atopochilus* and *Euchilichthys* the lateral ethmoid is suddenly bent to a vertical position at the anterolateral edge, forming a thin, hanging, laminar curtain (Fig. 1C and Fig. 3C).

**CS-0:** Lateral edge of lateral ethmoid relatively horizontal.

**CS-1:** Lateral edge of lateral ethmoid vertical. (*Atopodontis*; *Atopochilus*; *Euchilichthys*)

[Insert Figures 3 and 4 near here.]

#### **6. Posterior fontanelle. (CI = 0.200, RI = 0.500)**

Plesiomorphically, among catfishes, the posterior fontanelle is formed as a gap between the posterior portions of the frontals (beyond the epiphyseal bar), and as a hole along the

midline of the parieto-supraoccipital (Fig. 2A and Fig. 4B). In CS-1 the typical posterior fontanelle is absent; openings beyond the epiphyseal bar, when present, are restricted to gaps between the frontals and do not extend deep onto parieto-supraoccipital (Fig. 2B); most mochokids lack a truly well-formed posterior fontanelle and more often than not the posterior fontanelle is entirely absent (Fig. 2C). In CS-2 the typical posterior fontanelle is also absent but the parieto-supraoccipital is marked by a small centrally located circular foramen (Fig. 4A). Such a foramen is found in several of the smaller mochokid species and may represent a pedomorphic condition. Nevertheless, this state is shared, and probably represents a synapomorphy for some of taxa which show it. The exact distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Posterior fontanelle extending well onto parieto-supraoccipital.

**CS-1:** Posterior fontanelle as a gap between the frontals only.

**CS-2:** Posterior fontanelle as a gap between the frontals only. Parieto-supraoccipital perforated by small centrally located foramen.

## **7. Posterolateral corners of neurocranium. (CI = 1.000, RI = 1.000)**

In all of the outgroup taxa and most of the ingroup taxa considered, the posterolateral corners of the neurocranium are formed by the exoccipital, epioccipital and pterotic; the posttemporo-supracleithrum is often tightly joined at this corner of the neurocranium as well (Fig. 3A). In the chiloglanidins the epioccipital plays little or no role in forming the posterolateral corner of the neurocranium; here, the epioccipital is continuous with the ossified transcapular ligament to form a nearly complete wall between the neurocranium

and the post-cranial skeleton. In addition, the posterior border of the pterotic has subsided anteriorly, creating a large cavity below the fused posttemporo-supracleithrum. In these taxa the posterolateral corner of the neurocranium is formed by the prootic, exoccipital, pterotic and sphenotic (Fig. 3C and Fig. 5).

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

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

### **8. Reduced epioccipital. (CI = 1.000, RI = 1.000)**

In most Siluriformes the epioccipital is present as a substantial element which helps to close the posterolateral corner of the neurocranium, with only modest amounts of cartilage between neighboring elements (Fig. 6A). In most of the Mochokidae the epioccipital is greatly reduced and the posterolateral corner of the neurocranium is largely formed by cartilage joining this greatly reduced bone to its neighbors (Fig. 6B).

**CS-0:** Epioccipital not greatly reduced.

**CS-1:** Epioccipital greatly reduced, crescent shaped and delicate. (all *Synodontis* except *S. acanthoperca* [0]; *Hemisynodontis*; *Brachysynodontis*)

**Inapplicable:** In *Chiloglanis*, *Atopodontis*, *Atopochilus* and *Euchilichthys* because the epioccipital plays such a drastically different role in these taxa.

[Insert Figures 5 and 6 near here.]

**9. Articulating facet for hyomandibula. (CI = 0.333, RI = 0.900) (Mo, 1991 [21])**

Among some putatively basal catfishes (Diplomystidae, and also the loricarioids), the hyomandibula inserts on the underside of the neurocranium between the sphenotic and prootic and often extends to the faces of the pterotic and pterosphenoid (Fig. 3B, C). This is also the case in the Mochokidae, with the exception of *Acanthocleithron* and *Mochokus*. However, in most catfishes the main portion of the facet for the hyomandibula is on the face of the sphenotic and does not include the prootic (CS-1); here, the facet may also extend to the pterotic and pterosphenoid (Fig. 3A). Mo (1991) did not recognize that the prootic plays a role in this articulation in most members of the Mochokidae.

**CS-0:** Hyomandibula inserting at border between the sphenotic and prootic.

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

**CS-1:** Hyomandibula inserting on the face of the sphenotic. (All taxa not showing state CS-0)

**10. Pterotic spine. (CI = 0.500, RI = 0.957)**

Among the Siluriformes the ventral face of the pterotic is generally without a well-formed anteroventrally-directed spinous projection that envelopes the posterior edge of the hyomandibula (Fig. 1A, C). In several mochokids the pterotic possesses a spinous projection ventrally that acts to accept and envelope the posterior edge of the hyomandibula (Fig. 1B).

**CS-0:** Pterotic spine absent.

**CS-1:** Pterotic spine present. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*; *Chiloglanis macropterus*; *C. sp.* 'burundi')

**11. Basioccipital pit. (CI = 0.333, RI = 0.778)**

In many of the outgroup taxa 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 some instances the pit is filled by a small bony plug, but is still distinguishable as a pit. In all of the Mochokidae and some of the outgroup taxa this pit is not present on the ventral surface of the basioccipital (Fig. 3B, C). It seems likely that the small bony plug, seen in some of the outgroup taxa, is totally fused with the surrounding bone.

**CS-0:** Basioccipital pit present.

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

**12. Lateral expansions of the basioccipital. (CI = 0.500, RI = 0.909)**

In many of the outgroup taxa, including *Diplomystes* and *Ictalurus*, the basioccipital is without obvious lateral expansions. Here, the basioccipital is never much wider than the anterior centra (Fig. 3A). In all mochokids as well as several of the outgroup taxa the basioccipital has obvious lateral expansions/arms that join the ossified transcapular ligaments. In these taxa the lateral expansion makes 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*.

**CS-0:** Basioccipital without distinct lateral expansions.

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

**13. Extrascapular. (CI = 0.500, RI = 0.889) (Mo, 1991 [88])**

Plesiomorphically, among catfishes, there is a distinct and separate extrascapular near the posterolateral corner of the neurocranium (Fig. 2A). In mochokids as well as some of the outgroup families the extrascapular is not present as a separate element. It is either lost or wholly fused to the elements surrounding it (Fig. 2B, C and Fig. 4B).

**CS-0:** Extrascapular as separate, unfused element.

**CS-1:** Extrascapular not present as separate element. (Amphiliidae; Auchenipteridae; Doradidae; Mochokidae)

**14. Posttemporo-supracleithrum. (CI = 0.500, RI = 0.857) (Mo, 1991 [89])**

In some of the outgroup taxa the posttemporo-supracleithrum is set rather loosely between the extrascapular anteriorly and the epioccipital posteriorly (Fig. 2A). In all mochokids and several of the outgroup taxa the posttemporo-supracleithrum is tightly sutured to the posterolateral corner of the neurocranium (Fig. 2B, C and Fig. 4B). This derived condition can be correlated with increased stabilization of the pectoral girdle through increased ossification, fusion and tighter articulations.

**CS-0:** Posttemporo-supracleithrum set loosely in neurocranium.

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

**15. Ventral process of transcapular ligament. (CI = 0.333, RI = 0.857) (Diogo, 2005 [151 and 154])**

In most of the taxa presented here the ventral extremities of the ossified transcapular ligament are simple. They are primarily formed laterally, to tightly accept the upper arm of the cleithrum. There are no complex ornamentations or processes medially (Fig. 6A). In several mochokids the ventral extremities of the transcapular ligament are complex, with ventrally-expansive ornamentations and processes directed medially as well as laterally (Fig. 6B).

**CS-0:** Ventral process of transcapular ligament simple.

**CS-1:** Ventral process of ossified transcapular ligament complex. (*Microsynodontis* sp. 'odzala'; all *Synodontis* except *S. acanthoperca* [0], *S. nigriventris* [0] and *S. contractus* [0]; *Hemisynodontis*; *Brachysynodontis*)

NOTE: The next three characters refer to nuchal plates. Nuchal plates are modified homologs of certain dorsal-fin elements. I have taken the following to be true: the anterior nuchal plate is a modified and greatly enlarged homolog of a supraneural; the medial or middle nuchal plate is an enlarged homolog of the first dorsal-fin pterygiophore, which acts to enclose the dorsal spinelet anteriorly and laterally; the posterior nuchal plate is the enlarged homolog of the second dorsal-fin pterygiophore,

which acts to enclose the dorsal spinelet posteriorly and supports the dorsal spine on its dorsal surface. The term nuchal shield refers to the complete bridge of three bones as a unit.

**16. Nuchal plates. (CI = 0.400, RI = 0.824) (Mo, 1991 [64 and 99])**

In many of the outgroup taxa the nuchal plates, formed from supraneurals and the first two dorsal-fin pterygiophores, are very narrow. In these taxa the supraneural barely joins the dorsal-fin elements to the neurocranium, if at all (Fig. 2A). In certain species of *Chiloglanis* and some of the outgroup taxa the supraneural and first two dorsal-fin pterygiophores are much more developed, creating a solid bridge between the dorsal-fin elements and the supraoccipital spine. However, in this state, the supraoccipital spine and nuchal shield are not nearly as wide as the main body of the parieto-supraoccipital (Fig. 4B). In the Auchenipteridae, Doradidae and the great majority of the Mochokidae the nuchal shield is well developed and remains wide (as wide as the main body of the parieto-supraoccipital) along its entire length (Fig. 2B, C and Fig. 4A).

**CS-0:** Nuchal shield poorly formed.

**CS-1:** Nuchal shield moderately formed. (Pangasiidae; *Chrysichthys*; Ariidae;

*Chiloglanis* sp. 'igamba'; *C. niloticus*; *C. micropogon*; *C. polypogon*; *C. cf. neumanni*)

**CS-2:** Nuchal shield well formed. (Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*;

*Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*;

*Chiloglanis disneyi*; *C. macropterus*; *C. congicus*; *C. carnosus*; *C. sp. 'kalungwishi'*; *C.*

*sp. 'ntumbachusi'*; *C. sp. 'burundi'*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

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

**17. Dorsal suture between posttemporo-supracleithrum and nuchal plates. (CI = 0.333, RI = 0.600)**

In the great majority of the taxa presented here the posttemporo-supracleithrum does not reach posteriorly to join the nuchal plates (Fig. 2A, B, C and Fig. 4B). In the Doradidae as well as *Mochokus* and *Mochokiella*, the posttemporo-supracleithrum joins the nuchal plates at the dorsal surface (Fig. 4A). Lundberg (1993) suggested that this derived state was a synapomorphy for a group composed of the ‘doradoids’ and the fossil *Titanoglanis*. He notes a reversal in some mochokids but, in fact, the only members of the family to show this derived state are *Mochokus* and *Mochokiella*.

**CS-0:** Posttemporo-supracleithrum not joined to nuchal plates.

**CS-1:** Posttemporo-supracleithrum joined to nuchal plates. (Doradidae; *Mochokus*; *Mochokiella*)

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

**18. Number of nuchal plates. (CI = 0.333, RI = 0.895)**

In all of the outgroup taxa and many of the ingroup taxa the two anterior elements of the nuchal shield are present as separate elements (Fig. 2A, B and Fig. 4A). In *Chiloglanis*, *Atopodontis*, *Euchilichthys* and some species of *Synodontis* the two anterior elements of the nuchal shield are not visible as separate elements dorsally; the suture between these

elements, which can take various forms (see character 19), is not visible and the elements may be entirely fused (Fig. 2C and Fig. 4B).

**CS-0:** Anterior nuchal plate and medial nuchal plate separate.

**CS-1:** Anterior nuchal plate and medial nuchal plate not separate. (*Synodontis nigriventris*; *S. batesii*; *S. contractus*; *S. albolineatus*; *Chiloglanis*; *Atopodontis*; *Euchilichthys*)

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

**19. Configuration of Anterior and Medial Nuchal Plates. (CI = 0.333, RI = 0.882)**

(Lundberg, 1993; Diogo, 2005 [142])

Plesiomorphically, among catfishes, the medial nuchal plate is fully posterior to the anterior nuchal plate and does not reach forward on each side to join elements of the neurocranium (Fig. 2A and Fig. 4A). In the Auchenipteridae, the Doradidae and some mochokids the medial nuchal plate is bridge-shaped, wherein it surrounds the anterior nuchal plate laterally to join certain elements of the neurocranium (Fig. 2B).

**CS-0:** Medial nuchal plate simple.

**CS-1:** Medial nuchal plate bridge-shaped. (Auchenipteridae; Doradidae; *Mochokus brevis*; all *Synodontis* except *S. acanthoperca* [0] and those listed in 'Inapplicable' below; *Hemisynodontis*; *Brachysynodontis*)

**Inapplicable:** In the Malapteruridae, because most dorsal-fin elements are totally absent in the family. In *Synodontis nigriventris*, *S. contractus*, *S. batesii*, *S. albolineatus*,

*Chiloglanis*, *Atopodontis* and *Euchilichthys*, because in these taxa the anterior nuchal plate and medial nuchal plate are not visible as separate elements.

**20. Dorsal-fin proximal radials. (CI = 0.143, RI = 0.769)**

In several of the outgroup and ingroup taxa presented here the dorsal-fin proximal radials, beyond the second (which forms the posterior nuchal plate), are without conspicuous dorsolateral expansion (Fig. 2A, C and Fig. 4B). In CS-1, some or all of the dorsal-fin proximal radials are expanded dorsolaterally, though expansion decreases moving posteriorly (Fig. 2B and Fig. 4A).

**CS-0:** Dorsal-fin proximal radials not expanded dorsolaterally.

**CS-1:** Dorsal-fin proximal radials expanded dorsolaterally. (Pangasiidae; Schilbeidae; Ariidae; all Doradidae except *Agamyxis* [0]; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*)

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

**21. Third dorsal-fin proximal radial. (CI = 0.333, RI = 0.882)**

In nearly all of the outgroup taxa considered and most of the ingroup taxa the third dorsal-fin proximal radial does not join or otherwise touch the second proximal radial near the dorsal surface (Fig. 4A). In CS-1 the third dorsal-fin proximal radial is laterally expanded dorsally; further, these expansions are tightly joined to the expansions of the second dorsal-fin proximal radial/posterior nuchal plate (Fig. 2B).

**CS-0:** Third proximal radial not joined to second proximal radial.

**CS-1:** Third proximal radial joined to second proximal radial. (*Bagre*; *Mochokiella*; all *Synodontis* except *S. acanthoperca* [0]; *Hemisynodontis*; *Brachysynodontis*)

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

**22. Number of Infraorbitals (ORDERED). (CI = 0.429, RI = 0.867) (Mo, 1991 [56])**

Among catfishes the number of infraorbitals is quite variable. In many putatively basal catfishes the number of infraorbitals is rather high. In *Diplomystes*, for example, there are eight or more infraorbitals. Here CS-0 is taken to be the presence of six or more infraorbitals. In various groups considered here, the number of infraorbitals has been greatly reduced (Fig. 2 and Fig. 4) to as few as three infraorbitals. In all mochokids there are four or five infraorbitals. In all instances the lachrymal was included as the first infraorbital in this work. The nature of this feature, being a count of discrete elements, allowed for a hypothesis of transformational series. The transformational series here assumes that there would be a loss or gain of one element at a time. As such, this character is treated as ordered in the analyses.

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

**CS-1:** Five infraorbitals. (*Chrysichthys*; *Schilbeidae*; *Amphilius*; *Doumea*; *Malapteruridae*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

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

**CS-3:** Three infraorbitals. (*Centrodoras*)

## Splanchnocranium

**23. Ascending Meckel's cartilage. (CI = 0.250, RI = 0.786)** (Mo, 1991 [35]; de Pinna, 1993 [22]; Diogo, 2005 [419])

Plesiomorphically among catfishes the ascending Meckel's cartilage is present as a sheath running vertically, just lateral to the coronomeckalian and medial to the dentary (Fig. 7A). In *Amphilius*, *Doumea*, *Phractura*, the Malapteruridae and the Mochokidae there is no obviously separate ascending branch of Meckel's cartilage; cartilage in the lower jaw is limited to the horizontal sheath of Meckel's cartilage (Fig. 7B).

**CS-0:** Ascending branch of Meckel's cartilage present.

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

[Insert Figure 7 near here.]

**24. Size of horizontal Meckel's cartilage. (CI = 0.500, RI = 0.923)** (Mo, 1991 [35]; de Pinna, 1993 [43 and 44]; Diogo, 2005 [423])

In many of the outgroup taxa the horizontal branch of Meckel's cartilage is many times longer than it is thick. 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 length (Fig. 7B).

**CS-0:** Horizontal branch of Meckel's cartilage elongate.

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

**25. Coronomeckalian. (CI = 0.500, RI = 0.941)** (Mo, 1991 [36]; de Pinna, 1993 [23]; Diogo, 2005 [424])

Plesiomorphically, among catfishes, the coronomeckalian is 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; when present it is miniscule and it is not joined to the dentary, but is largely incorporated into the horizontal branch of the Meckel's cartilage (Fig. 7B).

**CS-0:** Coronomeckalian present.

**CS-1:** Coronomeckalian absent. (Malapteruridae; Mochokidae)

**26. Coronoid process. (CI = 1.000, RI = 1.000)** (de Pinna, 1993 [50]; Diogo, 2005 [400])

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

**CS-0:** Coronoid process well formed.

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

**27. Intermandibular angle. (CI = 0.500, RI = 0.957)**

In most catfishes, two points at the articulations of the mandible and a point at the symphysis (vertex) will form an angle of about 90 degrees (Fig. 8A). In most mochokids these points form an angle that is much closer to 180 degrees and certainly no less than 135 degrees (Fig. 8B).

**CS-0:** Intermandibular angle near 90 degrees.

**CS-1:** Intermandibular angle greater than 135 degrees and sometimes approaching 180 degrees. (*Microsynodontis*; *Synodontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

[Insert Figure 8 near here.]

**28. Angulo-articular facet for the quadrate. (CI = 1.000, RI = 1.000) (de Pinna, 1993 [48]; Diogo, 2005 [410])**

In all of the outgroup taxa the angulo-articular facet for the quadrate is saddle-shaped (a hyperbolic paraboloid) (Fig. 7A and Fig. 8A). In all mochokids except *Mochokus* this facet is shaped as a cup with a raised rim along the entire edge (Fig. 7B and Fig. 8B). 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 quadrate in most mochokids is ball-shaped for articulation with the cup-shaped facet of the angulo-articular.

**CS-0:** Articulating facet saddle-shaped.

**CS-1:** Articulating facet cup-shaped. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**29. Dentary tooth cup. (CI = 1.000, RI = 1.000)** (de Pinna, 1993 [49]; Diogo, 2005 [396])

Among putatively basal siluroid catfishes and the Diplomystidae the dentary supports teeth on its relatively flat dorsal surface and does not support teeth in any sort of cup anteriorly (Fig. 7A and Fig. 8A). In many mochokids, as in various loricarioid catfishes, the anterior face of the dentary is formed as a pocket that supports teeth, herein referred to as the tooth cup (Fig. 9A, B).

**CS-0:** Dentary tooth cup absent.

**CS-1:** Dentary tooth cup present. (*Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

[Insert Figure 9 near here.]

NOTE: The next two characters refer to mandibular teeth. It is well known that most mochokids bear specialized S-shaped teeth in an anteriorly directed cup of the dentary. It was quite surprising, therefore, when I found several species (including *Brachysynodontis*, *Hemisyndontis*, *Microsynodontis* and some *Synodontis*) that bear

more typical conical and gently recurved teeth on the dorsal surface of the aforementioned tooth cup. Based largely on position and shape, I decided that the conical teeth on the dorsal surface of the dentary should be interpreted as the homologs of the teeth on the dorsal surface of dentary in other catfishes. Further, the S-shaped teeth of most mochokids (which could themselves be derived from the more typical teeth of the dorsal surface) are considered here a separate synapomorphy for the taxa that exhibit them.

### **30. Dentary surface teeth. (CI = 0.286, RI = 0.848)**

In most catfishes, including nearly all of the outgroup taxa presented here, the dorsal surface of the dentary supports gently recurved conical teeth in a continuous patch across the symphysis (Fig. 7A and Fig. 8A). In CS-1 the dentary does support teeth on its dorsal surface, but they are in separate patches on each side of the symphysis (Fig. 7B, Fig. 8B and Fig. 9A). In CS-2 there are no teeth on the dorsal surface of the dentary (Fig. 9B).

**CS-0:** Dentary teeth on dorsal surface in single patch across symphysis.

**CS-1:** Dentary teeth on dorsal surface in separate patches, divided at symphysis.

(*Phractura*; *Microsynodontis*; some *Synodontis* (see matrix for details); *Hemisyndontis*;

*Brachysynodontis*)

**CS-2:** Dentary teeth on dorsal surface absent. (*Acanthocleithron*; some *Synodontis* (see matrix for details); *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

### **31. Dentary auxiliary S-shaped teeth. (CI = 1.000, RI = 1.000)**

In all of the outgroup taxa teeth of the lower jaw are restricted to the relatively flat dorsal surface of the dentary. In all of the derived states here, the lower jaw also holds S-shaped teeth of various sorts set in the cavity or tooth cup (see character 29). The S-shaped teeth in these taxa exist in at least three forms, differing in shape of the tooth tip (Fig. 10). The precise shape of these teeth in lateral view is quite variable, but in all cases the teeth have an S shape. In most mochokids the tips of the auxiliary S-shaped teeth are pointed. In *Atopodontis*, *Atopochilus* and *Euchilichthys* the tips of the S-shaped teeth are either spatulate or trowel-shaped.

**CS-0:** S-shaped teeth not present.

**CS-1:** S-shaped teeth present, tips pointed. (*Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*; *Chiloglanis*)

**CS-2:** S-shaped teeth present, tips spatulate. (*Atopochilus*; *Euchilichthys dybowskii*)

**CS-3:** S-shaped teeth present, tips trowel-shaped. (*Atopodontis*; all *Euchilichthys* except *E. dybowskii* [2])

[Insert Figure 10 near here.]

### **32. Size of maxilla. (CI = 0.500, RI = 0.944)**

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 the chiloglanidins the maxilla is massive, being much longer than the mesethmoid is wide (Fig. 4B).

**CS-0:** Maxilla relatively small.

**CS-1:** Maxilla relatively large. (*Zaireichthys*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

### **33. Laminar expansion of maxilla. (CI = 1.000, RI = 1.000)**

Plesiomorphically, among catfishes, the proximal portion of the maxilla is composed of two bulbous heads that articulate with the anterior autopalatine cartilage. In most of the taxa presented here there is no well-formed horizontal lamina extending anteriorly from the proximal portion of the maxilla (Fig. 4A). In certain species of *Chiloglanis* the dorsal articulating head is continuous with a large horizontal lamina along the anterior side of the element (Fig. 4B).

**CS-0:** Maxilla without laminar expansions proximally.

**CS-1:** Maxilla with laminar expansions proximally. (*Chiloglanis* sp. 'igamba'; *C. disneyi*; *C. niloticus*; *C. micropogon*; *C. polypogon*; *C. cf. neumanni*; *C. sp.* 'ntumbachusi')

### **34. Shape of premaxillary tooth plates. (CI = 1.000, RI = 1.000)**

In all of the outgroup taxa presented here the premaxillae support numerous teeth on an expansive ventral surface. The premaxillae themselves 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 the most mochokids there are multiple faces for the support of premaxillary teeth and the premaxillae themselves are more block-like in shape. In each case the premaxilla support teeth on a vertical posterior face in addition to

the ventral face. In *Microsynodontis*, *Synodontis*, *Hemisyndontis* and *Brachysynodontis* the premaxillae are generally rectangular and support teeth on both the ventral and posterior face of a single solid element (Fig. 12). In *Atopodontis*, *Atopochilus*, *Euchilichthys* and some species of *Chiloglanis* the teeth are again supported by a ventral and posterior face, but these faces are joined to each other by a transverse swath of porous bone. The element is still block-like in shape (Fig. 13). In other species of *Chiloglanis* the two faces are even more disjunct, being attached to each other only near the midline; in this instance the premaxillae are claw-shaped (Fig. 14).

**CS-0:** Premaxillary tooth plate flat, with ventrally directed face only.

**CS-1:** Premaxillary tooth plates block-like and solid, with posterior and ventral faces.

(*Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*)

**CS-2:** Premaxillary tooth plates block-like, with posterior and ventral faces joined by swath of porous bone. (*Chiloglanis disneyi*; *C. macropterus*; *C. congicus*; *C. carnosus*; *C. sp. 'kalungwishi'*; *C. sp. 'burundi'*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**CS-3:** Premaxillary tooth plates claw-shaped, with posterior and ventral faces joined medially only. (*Chiloglanis sp. 'igamba'*; *C. niloticus*; *C. micropogon*; *C. polypogon*; *C. cf. neumanni*; *C. sp. 'ntumbachusi'*)

[Insert Figures 11, 12, 13 and 14 near here.]

### **35. Differentiation of premaxillary teeth. (CI = 1.000, RI = 1.000)**

Plesiomorphically, among catfishes, the premaxillary tooth plates hold teeth in a single patch; the teeth may gently decrease in size from front to back, but do not present as

being part of discrete patches by shape or drastic changes in size (Fig. 11). In all mochokids except *Mochokus*, *Mochokiella* and *Acanthocleithron* the teeth of the premaxillary tooth plates are in discrete patches by size from front to back. In these mochokids there are teeth of at least two distinct sizes, the most posterior of these small and often needle-like (Fig. 12, Fig. 13 and Fig. 14).

**CS-0:** Teeth uniform.

**CS-1:** Teeth differentiated. (*Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

### **36. Premaxillary tooth shape. (CI = 1.000, RI = 1.000)**

Shape of the premaxillary teeth in catfishes is fairly conserved. In *Diplomystes* 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).

**CS-0:** Premaxillary teeth cylindrical and gently recurved.

**CS-1:** Premaxillary teeth cylindrical and S-shaped. (*Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

[Insert Figure 15 near here.]

### **37. Premaxillary tooth tips. (CI = 0.333, RI = 0.600)**

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 teeth are flattened at the tip, having a spatulate shape (Fig. 15A). In *Tetracamphilius* the teeth are bicuspid.

**CS-0:** Tips of premaxillary teeth conical and pointed.

**CS-1:** Tips of premaxillary teeth spatulate. (*Acanthocleithron*; *Chiloglanis disneyi*; *C. micropogon*; *C. congicus*; *C. carnosus*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

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

## **Suspensorium**

**38. Autopalatine facet for the lateral ethmoid. (CI = 0.200, RI = 0.636)** (Diogo, 2005 [298])

Plesiomorphically, among catfishes, the autopalatine rests on the lateral ethmoid without any well-formed facet. In most of the outgroup taxa the articulating surface is at most a raised area along the medial or dorsal surface of the autopalatine (Fig. 16A). In the great majority of mochokids and a few of the outgroup taxa the autopalatine has a well-developed articulating facet with a concave surface, characterized by a raised ridge anteriorly, for cupping the anterolateral corner of the lateral ethmoid (Fig. 16B).

**CS-0:** Autopalatine without ornamentation or concave facet.

**CS-1:** Autopalatine with concave facet. (*Parauchenoglanis*; Amphiliidae; *Bagre*; all Mochokidae except *Mochokus brevis* [0])

[Insert Figure 16 near here.]

**39. Dimensions of the autopalatine. (CI = 1.000, RI = 1.000)**

Plesiomorphically, among catfishes, the autopalatine is an elongate bone, being several times longer than wide (Fig. 16A, B). In *Chiloglanis* the autopalatine is relatively short, still cylindrical, but only up to three times as long as wide (Fig. 17A). The autopalatine is further shortened in *Atopodontis*, *Atopochilus* and *Euchilichthys*, where the element is block-like and only slightly longer than wide (Fig. 17B).

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

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

(*Chiloglanis*)

**CS-2:** Autopalatine block-like, length less than 2X width or depth. (*Atopodontis*;  
*Atopochilus*; *Euchilichthys*)

[Insert Figure 17 near here.]

**40. Posterior cartilage of autopalatine. (CI = 0.250, RI = 0.864)** (Mo, 1991 [29]; de

Pinna, 1993 [21]; Diogo, 2005 [283])

Plesiomorphically, among catfishes, the posterior end of the autopalatine is capped by a small plug of cartilage (Fig. 16A, B). In all chiloglanidins, most amphiliids and *Malapterurus* the posterior end of the autopalatine is without cartilage (Fig. 17A and Fig. 17B).

**CS-0:** Posterior end of the autopalatine with a small cap of cartilage.

**CS-1:** Posterior end of the autopalatine entirely without cartilage. (*Amphilius*; *Tetracamphilius*; *Zaireichthys*; *Phractura*; Malapteruridae; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**41. Hyomandibular process. (CI = 0.500, RI = 0.952)**

In most of the outgroup taxa considered the medial edge of the hyomandibula is relatively smooth, or at least without any well-developed, elongate processes (Fig. 18A). In all mochokids except *Mochokus* and the chiloglanidins there is a well-formed elongate process along the medial edge of the hyomandibula (Fig. 18B).

**CS-0:** Hyomandibular process absent.

**CS-1:** Hyomandibular process present. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*)

[Insert Figure 18 near here.]

**42. Dorsal articulation of the hyomandibula. (CI = 0.333, RI = 0.892) (de Pinna, 1993 [100])**

In all of the outgroup taxa examined the dorsal condyle of the hyomandibula (for articulation with the underside of the neurocranium) is elongate, many times longer than wide (Fig. 18A). In *Mochokiella*, *Microsynodontis*, *Hemisyndontis*, *Brachysynodontis* and some *Synodontis* the condyle is much shorter, being oval in dorsal view (Fig. 18B). In the chiloglanidins and some *Synodontis* the condyle is rounded and often spherical, like a ball (Fig. 18C).

**CS-0:** Dorsal surface of the hyomandibula elongate.

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

**CS-2:** Dorsal surface of the hyomandibula spherical. (*Synodontis acanthomias*; *S. pleurops*; *S. clarias*; *S. sorex*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

### **43. Anterior pterygoid element. (CI = 0.400, RI = 0.900)**

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 most mochokids, however, there is also a tiny spherical or boomerang-shaped element anterior to the metapterygoid (Fig. 18B, C). By the standards of Arratia (1992) these elements may be considered a sesamoid entopterygoid, being somewhat medial to the palatoquadrate and formed as mineralizations within a ligament (also referred to as a ‘tendon bone’). With which of the various plate-like bones in other catfishes this element may be homologous is still unclear. A much reduced or absent ‘anterior pterygoid element’ is nonetheless a useful diagnostic character for the Mochokidae. Furthermore, the shape of this ‘tendon bone’ is predictably variable within the family, making it phylogenetically informative. For these reasons, CS-0 is taken to be the absence of the tendon bone, either by total absence of any anterior pterygoid element or by the presence of a more typical plate-like element in its place.

**CS-0:** Greatly reduced anterior pterygoid element absent.

**CS-1:** Greatly reduced anterior pterygoid element present, spherical or ovoid.

(*Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*; all *Chiloglanis* except

*C. sp. 'igamba'* [2], *C. niloticus* [2] and *C. congicus* [2])

**CS-2:** Greatly reduced anterior pterygoid element present, elongate and rod-like.

(*Chiloglanis sp. 'igamba'*; *C. niloticus*; *C. congicus*; *Atopodontis*; *Atopochilus*;

*Euchilichthys*)

## **Opercular Series**

### **44. Opercular ornamentation/spines. (CI = 0.500, RI = AUT)**

In the great majority of the taxa presented here the posterior vertex of the roughly triangular operculum is gently rounded and not formed as a sharp spine. In *Mochokiella* and *Synodontis acanthoperca* there is a well-developed spine at the rear of the operculum (see figures in Friel and Vigliotta, 2006). In each case this feature is sexually dimorphic, where males have a much larger spine than found in females. A sexually dimorphic opercular spine is also found in a related undescribed species of *Synodontis* (Vreven, personal communication).

**CS-0:** Rear of the operculum without a well-developed spine.

**CS-1:** Rear of the operculum with a well-developed spine, larger in males than in

females. (*Mochokiella*; *Synodontis acanthoperca*)

## **Hyoid and Branchial Arches**

**45. Reduction of parurohyal. (CI = 1.000, RI = 1.000)** (Mo, 1991 [39]; Diogo, 2005 [388])

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

**CS-0:** Parurohyal not reduced.

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

[Insert Figure 19 near here.]

**46. Dorsohyal/Venterohyal. (CI = 0.200, RI = 0.692)** (Mo, 1991 [43])

In most of the taxa presented here the dorsohyal and venterohyal are present as separate elements (Fig. 20A). In some amphiliids and mochokids the dorsohyal and venterohyal are not present as separate elements and are wholly fused to each other (Fig. 20B).

Contrary to Mo's (1991) assertion, these elements are not fused in all amphiliids.

**CS-0:** Dorsohyal and venterohyal separate.

**CS-1:** Dorsohyal and venterohyal fused. (*Tetracamphilius*; *Zaireichthys*; *Phractura*; *Chiloglanis*; *Atopodontis*)

[Insert Figure 20 near here.]

**47. Shape of the posterohyal. (CI = 0.500, RI = 0.947)**

Plesiomorphically, among catfishes, the posterohyal is roughly triangular, tapering distally to a point (Fig. 21A). In *Doumea*, *Phractura* and the chiloglanidins the posterohyal is oddly shaped, the distal end being much wider than the proximal end (Fig. 21B).

**CS-0:** Posterohyal triangular.

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

[Insert Figure 21 near here.]

**48. Interhyal. (CI = 0.333, RI = 0.867) (Mo, 1991 [45])**

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

**CS-0:** Interhyal present.

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

**49. Shape of basibranchials. (CI = 1.000, RI = 1.000)**

In the majority of the taxa presented here there are two roughly cylindrical and elongate basibranchials (Fig. 20B). In *Atopochilus* and *Euchilichthys* the basibranchials are flattened dorsoventrally and rounded or many-sided in ventral or dorsal view (Fig. 20A).

**CS-0:** Basibranchials cylindrical and elongate.

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

**50. Length of branchiospines. (CI = 1.000, RI = 1.000)**

In the great majority of the taxa presented here the branchiospines are rather short, from only slightly longer than the width of their bases up to a few times as long as the width of their bases. In *Hemisynodontis* and *Brachysynodontis* the branchiospines are extremely elongated, being several times longer than the width of their bases (certainly greater than 10X).

**CS-0:** Branchiospines short.

**CS-1:** Branchiospines extremely elongated. (*Hemisynodontis*; *Brachysynodontis*)

**51. Number of branchiostegal rays (ORDERED). (CI = 0.150, RI = 0.528) (Mo, 1991 [54])**

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, like *Diplomystes* and *Ictalurus*, have a minimum of eight rays. The taxa of CS-1 to CS-3 show various states with fewer than eight rays. Members of the Mochokidae possess anywhere between five and eight branchiostegal rays. The nature of this feature, being a count of discrete elements, allowed for a hypothesis of

transformational series. As such, this character is treated as ordered. The exact distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Eight or more branchiostegal rays.

**CS-1:** Seven branchiostegal rays.

**CS-2:** Six branchiostegal rays.

**CS-3:** Five branchiostegal rays.

### **Pectoral Girdle and Fins**

#### **52. Size of cleithral process. (CI = 0.333, RI = 0.867) (Mo, 1991 [91])**

Plesiomorphically, among catfishes, a posteriorly directed cleithral/humeral process is found just above the pectoral spine articulation. It is triangular and relatively small, reaching only slightly past the posterior extremity of the dorsal processes of the cleithrum (Fig. 22A). In CS-1 the cleithral process is generally pointed and triangular, but sometimes blunt-ended; in all cases the humeral process is quite massive, extending to well beyond the posterior extremities of the dorsal processes of the cleithrum (Fig. 22B). In some amphiliids and all malapterurids the cleithral process is altogether absent. I do not consider the small dorsally located processes found on the cleithrum of some amphiliids to be homologous with the more ventrally placed cleithral processes found in other catfishes.

**CS-0:** Cleithral processes small.

**CS-1:** Cleithral processes large. (*Zaireichthys*; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*)

**CS-2:** Cleithral processes altogether absent. (*Amphilius*; *Doumea*; *Phractura*; Malapteruridae)

[Insert Figure 22 near here.]

**53. Shape of cleithral process. (CI = 0.667, RI = 0.750)**

In most of the taxa presented here the cleithral process is acutely pointed in lateral view (Fig. 22A, B). In *Acanthocleithron* and some species of *Synodontis* the cleithral process is rounded or truncate in lateral view, with a more or less blunt posterior end (Fig. 22C). In certain *Chiloglanis* the shape of the cleithral process is sexually dimorphic. Females display the plesiomorphic pointed cleithral process and males possess an enlarged, rounded process (Fig. 22C).

**CS-0:** Cleithral process pointed.

**CS-1:** Cleithral process rounded or truncate. (*Acanthocleithron*; *Synodontis pleurops*; *S. congicus*; *S. decorus*)

**CS-2:** Cleithral process shape sexually dimorphic, being pointed in females and rounded in males. (*Chiloglanis niloticus*; *C. micropogon*; *C. polypogon*)

**Inapplicable:** In *Amphilius*, *Doumea* and *Phractura*, because I do not consider the more dorsally placed cleithral process in these taxa to be homologous to that found in other catfishes. In the Malapteruridae, because the cleithral process is absent.

**54. Mesocoracoid arch. (CI = 0.500, RI = 0.800)** (Mo, 1991 [94]; Diogo, 2005 [185])

In many of the outgroup taxa and all of the ingroup taxa the mesocoracoid arch is a bridge of bone on the posterior side of the vertical scapulo-coracoid lamina that surrounds the adductor profundus muscle (Fig. 23A, B, C). In the Ariidae, Auchenipteridae Doradidae the mesocoracoid arch is entirely absent.

**CS-0:** Mesocoracoid arch present.

**CS-1:** Mesocoracoid arch absent.

(Ariidae; Auchenipteridae; Doradidae)

[Insert Figure 23 near here.]

**55. Dorsal terminus of mesocoracoid arch. (CI = 0.333, RI = 0.917)**

In many of the taxa possessing a mesocoracoid arch the dorsal terminus of the arch ends by attaching 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 the chiloglanidins the mesocoracoid arch does not terminate solely at the dorsal edge, but is very broadly connected to the vertical lamina of the scapulo-coracoid. There is no dorsally directed prominence near the dorsal terminus of the arch in these taxa (Fig. 23C).

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

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

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

**56. Pectoral locking foramen. (CI = 0.333, RI = 0.926)**

In many catfishes, there is a foramen of 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). In most chiloglanidins, as well as some of the outgroup taxa, this pectoral locking foramen is altogether absent (Fig. 23C).

**CS-0:** Pectoral locking foramen present.

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

**57. First pectoral-fin proximal radial. (CI = 0.250, RI = 0.829) (Mo, 1991 [95])**

In several of the outgroup taxa considered the first proximal radial of the pectoral fin is narrow along its entire length, without any ventrally or dorsally directed processes (Fig. 23A). In several chiloglanidins and the Ariidae the proximal portion of this element has both ventrally and dorsally directed processes (Fig. 23B). In CS-2 the proximal portion of

the element shows a very large ventral process, but only slight expansion dorsally (Fig. 23C).

**CS-0:** First pectoral-fin proximal radial without processes.

**CS-1:** First pectoral-fin proximal radial with dorsal and ventral processes. (Ariidae; *Chiloglanis disneyi*; *C. macropterus*; *C. congicus*; *C. carnosus*; *C. cf. neumanni*; *C. sp. 'kalungwishi'*; *C. sp. 'burundi'*; *Atopochilus*; *Euchilichthys*)

**CS-2:** First pectoral-fin proximal radial with ventral process only. (*Chrysichthys*; *Parauchenoglanis*; Schilbeidae; *Mochokiella*; *Microsynodontis*; all *Synodontis* except *S. contractus* [0]; *Hemisynodontis*; *Brachysynodontis*)

#### **58. Anterior pectoral-spine serrae. (CI = 0.250, RI = 0.889)**

In some putatively basal catfishes, including *Diplomystes* and the Ictaluridae, the anterior edge of the pectoral spine is keeled, but without well-formed serrae. In CS-1 well-formed serrae are present.

**CS-0:** Anterior edge of pectoral spine without serrae.

**CS-1:** Anterior edge of pectoral spine with well-formed serrae. (Pangasiidae; *Chrysichthys*; Schilbeidae; Ariidae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*)

#### **59. Posterior pectoral-spine serrae. (CI = 0.250, RI = 0.727)**

In some putatively basal catfishes, including Diplomystes, the posterior edge of the pectoral spine has well-formed serrae. This is true for most mochokids as well. In CS-1 serrae are present as small denticulations only. In CS-2 serrae are altogether absent.

**CS-0:** Posterior edge of pectoral spine with serrae.

**CS-1:** Posterior edge of pectoral spine with small denticulations. (Ictaluridae; *Synodontis contractus*; *Chiloglanis macropterus*; *C. sp. 'burundi'*; *Atopodontis*; *Euchilichthys*)

**CS-2:** Posterior edge of pectoral spine without any serrae. (*Amphilius*; *Tetracamphilius*; *Doumea*; *Phractura*; all *Chiloglanis* except *C. macropterus* [1] and *C. sp. 'burundi'* [1])

**60. Number of pectoral-fin rays (ORDERED). (CI = 0.200, RI = 0.628)**

The number of pectoral-fin rays is highly variable among catfishes, but does characterize certain higher-level groups. In some basal catfishes there are nine or more soft pectoral-fin rays behind the pectoral spine (CS-0). In some derived groups (CS-1 through CS-4) the number of rays has been reduced to as few as five. The nature of this feature, being a count of discrete elements, allowed for a hypothesis of transformational series. As such, this character is treated as ordered. The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Nine or more pectoral-fin rays.

**CS-1:** Eight pectoral-fin rays.

**CS-2:** Seven pectoral-fin rays.

**CS-3:** Six pectoral-fin rays.

**CS-4:** Five pectoral-fin rays.

## Dorsal, Pelvic, Anal and Adipose Fins

### 61. Anterior dorsal-spine serrae. (CI = 0.250, RI = 0.500)

In the majority of the taxa presented here the anterior side of the dorsal spine is without any conspicuous serrae. In the Auchenipteridae, the Doradidae, *Mochokus* and some *Synodontis* the anterior side of the dorsal spine has very well-formed and pointed serrae.

**CS-0:** Anterior side of dorsal spine without well-formed serrae.

**CS-1:** Anterior side of dorsal spine with well-formed serrae along entire face.

(Auchenipteridae; Doradidae; *Mochokus niloticus*; *Synodontis clarias*; *S. batesii*; *S. albolineatus*)

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

### 62. Posterior dorsal-spine serrae. (CI = 0.143, RI = 0.778)

In many of the outgroup taxa the posterior side of the dorsal spine is without any conspicuous serrae. In CS-1 the posterior side of the dorsal spine has very well-formed and pointed serrae.

**CS-0:** Posterior side of dorsal spine without well-formed serrae.

**CS-1:** Posterior side of dorsal spine with well-formed serrae along entire face.

(Ariidae; *Centrodoras*; *Platydoras*; *Mochokiella*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*; *Chiloglanis macropterus*; *C. niloticus*; *C. polypogon*; *C. sp. 'burundi'*)

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

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

Among catfishes, the number of dorsal-fin rays is quite variable. In some putatively basal taxa there are seven or more soft rays in the dorsal fin. In CS-1 and CS-2 the number of rays is reduced to six and five respectively. In the Malapteruridae (CS-3) there are no dorsal-fin rays or other typical dorsal-fin elements. The nature of this feature, being a count of discrete elements, allowed for a hypothesis of transformational series. As such, this character is treated as ordered. In this instance, one of the states required the use of a user-defined step matrix. The matrix expressed the idea that it was possible to move from any state to the state CS-3 in a single step and vice versa. The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Seven or more dorsal-fin rays.

**CS-1:** Six dorsal-fin rays.

**CS-2:** Five dorsal-fin rays.

**CS-3:** NO dorsal-fin rays.

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

Among catfishes, the number of pelvic-fin rays is modestly variable, but quite conserved among higher-level groups. There are six pelvic-fin rays plus a bony splint in *Diplomystes* and many of the outgroup taxa. In states CS-1 and CS-2 the number of pelvic-fin rays is seven and eight respectively. The nature of this feature, being a count of discrete elements, allowed for a hypothesis of transformational series. As such, this character is treated as ordered.

**CS-0:** Six pelvic-fin rays.

**CS-1:** Seven pelvic-fin rays. (*Centrodoras*; *Platydoras*; all Mochokidae except *Chiloglanis* sp. 'ntumbachusi' [2])

**CS-2:** Eight pelvic-fin rays. (Ictaluridae; Pangasiidae; *Chiloglanis* sp. 'ntumbachusi')

**65. Pelvic splint. (CI = 0.125, RI = 0.682) (Mo, 1991 [107])**

Among various ingroup and outgroup taxa, regardless of the number of pelvic-fin rays, a small splint-like element is present just lateral to the base of the outermost pelvic-fin ray (Fig. 24A, C). In CS-1 this splint is entirely absent (Fig. 24B). The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Pelvic splint present.

**CS-1:** Pelvic splint absent.

[Insert Figure 24 near here.]

**66. Anterior processes of the pelvic girdle. (CI = 0.750, RI = 0.952)**

In most outgroup taxa and many of the ingroup taxa the anterolateral process of the pelvic girdle extends further forward than the anteromedial process (Fig. 24B). In the Malapteruridae the opposite is true, wherein the anteromedial process of the pelvic girdle extends further forward than the anterolateral process. In all *Amphilius*, *Tetracamphilius*, *Zaireichthys* and the chiloglanidins the anterior processes terminate at about the same level (Fig. 24C). In *Doumea* and *Phractura* the individual processes are indistinguishable, joined to each other by lamina in between.

**CS-0:** Anterolateral process extending further forward.

**CS-1:** Anteromedial process extending further forward. (Malapteruridae)

**CS-2:** Anterolateral and anteromedial processes terminating at roughly same point.

(*Amphilius*; *Tetracamphilius*; *Zaireichthys*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**CS-3:** Anterolateral and anteromedial processes of pelvic girdle indistinguishable.

(*Doumea*; *Phractura*)

**67. Cartilage of anterior processes of pelvic girdle. (CI = 0.500, RI = 0.950)** (de Pinna, 1993 [212])

In most of the taxa presented here the anterior processes of the pelvic girdle are capped by small lengths of cartilage that terminate without joining the cartilage of the neighboring processes (Fig. 24A, B). In *Amphilius*, *Tetracamphilius*, *Zaireichthys* and the chiloglanidins these lengths of cartilage are continuous with each other, forming arcs and joining the tips of the anterior processes (Fig. 24C).

**CS-0:** Cartilage of anterior processes not continuous.

**CS-1:** Cartilage of anterior processes continuous. (*Amphilius*; *Tetracamphilius*; *Zaireichthys*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

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

**68. Form of the first anal-fin pterygiophore. (CI = 0.500, RI = 0.938)**

In most of the taxa presented here the first anal-fin pterygiophores is developed as a slender, elongate element like all of the succeeding pterygiophores. In all chiloglanidins

except *Chiloglanis micropogon* the first pterygiophore is flattened and rounded when viewed ventrally. It appears as plate-like element just below the surface of the skin.

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

**CS-1:** First anal-fin pterygiophore developed as flat, rounded, plate-like element just below skin surface. (all *Chiloglanis* except *C. micropogon* [0]; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

### **69. Adipose fin. (CI = 1.000, RI = 1.000)**

In most of the taxa presented here the posterior dorsal fin is a fleshy adipose fin, without any rays for support. In *Mochokus* the posterior dorsal fin has rays similar to those found in the anterior dorsal fin. There are no radial elements associated with the rays.

**CS-0:** Posterior dorsal fin without rays.

**CS-1:** Posterior dorsal fin with rays. (*Mochokus*)

## **Caudal Fin**

### **70. Lower hypurals. (CI = 0.333, RI = 0.692)**

In many of the outgroup taxa presented here the parhypural, hypural one and hypural two are completely autonomous (Fig. 25). In CS-1 hypurals one and two are fused, but the parhypural is autonomous (Fig. 26). In CS-2 the parhypural and hypurals one and two are wholly fused (Fig. 27).

**CS-0:** Parhypural, hypural one and hypural two autonomous.

**CS-1:** Parhypural autonomous, hypurals one and two fused. (*Amphilius*; Ariidae; *Centrodoras*; *Agamyxis*; *Euchilichthys* sp. 'zambia'; *E. sp.* 'congo'; *E. royauxi*)

**CS-2:** Parhypural, hypural one and hypural two fused. (*Tetracamphilius*; *Zaireichthys*; *Doumea*; *Phractura*; Malapteruridae; Auchenipteridae; *Platydoras*; all Mochokidae except *Euchilichthys* sp. 'zambia' [1], *E. sp.* 'congo' [1] and *E. royauxi* [1])

[Insert Figures 25, 26 and 27 near here.]

### **71. Upper hypurals. (CI = 0.250, RI = 0.714)**

In many of the outgroup taxa presented here the upper hypurals (three through five OR three through six) are totally autonomous (Fig. 25). In CS-1 some of the upper hypurals are fused, but at least one is autonomous (Fig. 26). In CS-2 the upper hypurals are wholly fused (Fig. 27).

**CS-0:** All upper hypurals autonomous.

**CS-1:** Hypurals fusion pattern intermediate. (*Doumea*; Malapteruridae; Ariidae; Auchenipteridae; Doradidae; *Chiloglanis* sp. 'igamba'; *C. sp.* 'ntumbachusi'; *Atopochilus*; *Euchilichthys*)

**CS-2:** Upper hypurals completely fused. (*Tetracamphilius*; *Zaireichthys*; *Phractura*; all Mochokidae except *Chiloglanis* sp. 'igamba' [1], *C. sp.* 'ntumbachusi' [1], *Atopochilus* [1] and *Euchilichthys* [1])

### **72. Border of upper and lower hypurals. (CI = 0.333, RI = 0.500)**

In the great majority of the taxa presented here the upper and lower hypurals are separated by an obvious space (Fig. 25, Fig. 26 and Fig. 27). 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. 28).

**CS-0:** Hypurals two and three divided by obvious space.

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

[Insert Figure 28 near here.]

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

Among catfishes the number of principal caudal-fin rays is highly variable. It is fairly variable within the Mochokidae, but comparatively conserved within certain higher-level taxa. In *Diplomystes* the principal caudal-fin ray count is 9 + 9. For a great number of catfishes the count is reduced by one in the upper lobe, 8 + 9 (CS-1); this represents the highest caudal-fin ray count for any mochokid. For CS-2 through CS-5 the principal caudal-fin count is further reduced as described below. The nature of this feature, being a count of discrete elements, allowed for a hypothesis of transformational series. As such, this character is treated as ordered. The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** 9 + 9 principal caudal-fin rays.

**CS-1:** 8 + 9 principal caudal-fin rays.

**CS-2:** 7 + 8 principal caudal-fin rays.

**CS-3:** 7 + 7 principal caudal-fin rays.

**CS-4:** 6 + 7 principal caudal-fin rays.

**CS-5:** 6 + 6 principal caudal-fin rays.

#### **74. Shape of caudal fin. (CI = 0.100, RI = 0.250)**

In the majority of the taxa considered here the caudal fin is forked. In CS-1 the caudal fin is best described as truncate or rounded.

**CS-0:** Caudal fin forked.

**CS-1:** Caudal fin truncate or rounded. (*Ameiurus*; *Parauchenoglanis*; *Zaireichthys*; Malapteruridae; Auchenipteridae; *Microsynodontis*; *Chiloglanis* sp. 'igamba'; *C. disneyi*; *C. macropterus*; *C. carnosus*; *C. sp.* 'kalungwishi')

#### **Vertebrae, Weberian Apparatus and associated structures**

#### **75. Freedom of the anterior parapophyses of the compound centrum. (CI = 0.333, RI = 0.920) (Mo, 1991 [76]; Lundberg, 1993; de Pinna, 1993 [192])**

In many of the outgroup taxa 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 in the literature.

**CS-0:** Anterior parapophyses of the compound centrum not free.

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

**76. Elaboration of the anterior parapophyses of the compound centrum. (CI = 0.333, RI = 0.840)** (Mo, 1991 [76]; Lundberg, 1993; de Pinna, 1993 [192])

In most of the outgroup taxa considered the anterior parapophyses of the compound centrum are unspecialized, angular and without enlarged plates or expansions distally (Fig. 3A). In CS-1 the anterior parapophyses of the compound centrum are elaborated as enlarged plates distally (Fig. 3B, C). In CS-2 the anterior parapophyses of the compound centrum are elaborated as enlarged flap-like structures distally. The flap-like structures protect a portion of the gas bladder anteroventrally (Fig. 5).

**CS-0:** Anterior parapophyses not elaborated distally.

**CS-1:** Anterior parapophyses plate-like distally. (Malapteruridae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisynodontis*; *Brachysynodontis*; *Atopochilus*; *Euchilichthys*)

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

**77. Anterior process of the anterior parapophyses of the compound centrum. (CI = 0.250, RI = 0.760)**

In most of the outgroup taxa the anterior parapophyses of the compound centrum are without any obvious bends along their length. They do not possess any well-formed

anteriorly directed processes either. In CS-1 the anterior parapophysis has an obvious bend along its length, but there are no well-formed anteriorly directed processes at this bend (Fig. 3C). In CS-2 a bend is present and further ornamented by a large anteriorly directed process (Fig. 3B and Fig. 29). The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Anterior parapophysis of the compound centrum without well-formed anterior process or obvious bend.

**CS-1:** Anterior parapophysis of the compound centrum with an obvious bend, no process.

**CS-2:** Anterior parapophysis of the compound centrum with an obvious bend and a well-formed anteriorly directed process.

[Insert Figure 29 near here.]

**78. Development of posterior parapophyses of the compound centrum. (CI = 0.500, RI = 0.923) (Mo, 1991 [67])**

In most of the outgroup taxa the posterior parapophyses of the compound centrum are broadly joined to the anterior parapophyses, creating a dorsal shield over the gas bladder (Fig. 3A and Fig. 5). In CS-1 the parapophyses of the compound centrum are deeply divided to their bases, or nearly so. In CS-2 the posterior parapophyses are very poorly developed or entirely absent (Fig. 3B, C).

**CS-0:** Posterior parapophyses broadly joined to anterior.

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

*Brachysynodontis*; *Chiloglanis macropterus*; *C. sp. 'burundi'*; *Atopodontis*; *Atopochilus*;  
*Euchilichthys*)

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

**79. Development of the parapophyses of the 5<sup>th</sup> centrum. (CI = 0.250, RI = 0.600)**

(Mo, 1991 [79])

In a fair number of the outgroup taxa and many of the ingroup taxa the parapophyses of the 5<sup>th</sup> centrum are formed as elongate lateral projections which are deeply divided and separate from the parapophyses of the compound centrum (Fig. 3A, B, C). In CS-1 the parapophyses of the 5<sup>th</sup> centrum are broadly joined to the posterior parapophyses of the compound centrum (Fig. 5). In CS-2 the parapophyses of the 5<sup>th</sup> centrum are entirely absent.

**CS-0:** Parapophyses of the 5<sup>th</sup> centrum deeply divided from those of compound centrum.

**CS-1:** Parapophyses of the 5<sup>th</sup> centrum broadly joined to those of compound centrum.

(*Amphilius*; *Phractura*; Ariidae; *Acanthocleithron*; most *Chiloglanis* (see matrix for details))

**CS-2:** Parapophyses of the 5<sup>th</sup> centrum entirely absent. (*Tetracamphilius*; *Zaireichthys*;  
Doradidae)

**80. Development of the parapophyses of the 6<sup>th</sup> centrum. (CI = 1.000, RI = 1.000)**

In all of the outgroup taxa and most of the ingroup taxa the parapophyses of the 6<sup>th</sup> centrum is formed as a moderately elongate, laterally directed process for supporting the first pleural rib (Fig. 3A, B). In the chiloglanidins the parapophyses of the 6<sup>th</sup> centrum are

incorporated into an elongate venterolaterally directed strut that does not support a pleural rib (Fig. 3C and Fig. 5). The rib supported by the 6<sup>th</sup> parapophysis in other catfishes may be lost or incorporated into the bony strut in these taxa.

**CS-0:** Parapophyses of the 6<sup>th</sup> centrum simple.

**CS-1:** Parapophyses of the 6<sup>th</sup> centrum formed as enlarged struts. (*Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**81. Fusion of anterior centra (ORDERED). (CI = 0.375, RI = 0.792) (Mo, 1991 [60])**

In most of the outgroup taxa presented relatively few of the anterior centra are fused to each other. In *Diplomystes* the second through fourth centra are deeply sutured and fused (CS-0). In some putatively basal siluroids the second through fifth centra are fused as such (CS-1) (Fig. 3A). In CS-2 the sixth centrum is tightly fused to this complex (Fig. 3B and Fig. 5). In CS-3 the sixth and seventh centra are tightly fused to the complex (Fig. 3C). The nature of this feature, being the successive fusion of elements, allowed for a hypothesis of transformational series. As such, this character is treated as ordered.

**CS-0:** Fusion of centra two through four. (*Diplomystes*)

**CS-1:** Fusion of centra two through five. (Ictaluridae; Pangasiidae; *Chrysichthys*; *Parauchenoglanis*; Schilbeidae; Amphiliidae; Malapteruridae; *Agamyxis*)

**CS-2:** Fusion of centra two through six. (Ariidae; *Mochokus*; *Mochokiella*; *Acanthocleithron*; *Microsynodontis*; all *Synodontis* except *S. contractus* [3]; *Hemiosynodontis*; *Brachysynodontis*; all *Chiloglanis* except *C. congicus* [3] and *C. sp. 'burundi'* [3])

**CS-3:** Fusion of centra two through seven. (Auchenipteridae; *Centrodoras*; *Platydoras*; *Synodontis contractus*; *Chiloglanis congicus*; *C. sp. 'burundi'*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**82. Os suspensoria. (CI = 0.667, RI = 0.800)**

In all of the outgroup taxa and most of the ingroup taxa the ventral extremity of the os suspensoria are formed as rounded or angular nodules that lies tightly against the compound centrum (Fig. 3A). In derived states the ventral extremity is flattened and relatively free of the compound centra. Some species of *Chiloglanis* exhibit a flattened extremity shaped as a hammer. In the remaining species of *Chiloglanis* the extremity is an enlarged flap-like, paddle-shaped structure (Fig. 5).

**CS-0:** Ventral extremity of os suspensorium angular.

**CS-1:** Ventral extremity of os suspensorium flattened and hammer shaped. (*Chiloglanis disneyi*; *C. carnosus*; *C. sp. 'kalungwishi'*; *C. sp. 'ntumbachusi'*)

**CS-2:** Ventral extremity of os suspensorium flattened, greatly enlarged and flap-like. (*Chiloglanis niloticus*; *C. micropogon*; *C. polypogon*)

**83. Pleural rib articulations. (CI = 1.000, RI = 1.000)** (Mo, 1991 [85 and 86]; de Pinna, 1993 [193 and 198]; Roberts, 2003)

In all of the ingroup taxa and many of the outgroup taxa the pleural ribs articulate on the ventral surface or the posteroventral surface of the parapophyses. In the Doradidae the ribs articulate on the dorsal surfaces of the parapophyses. In the Auchenipteridae the ribs

articulate with the posterior face of the parapophyses. In the Amphiliidae the ribs have a complex articulation, in which the rib wraps around the parapophysis.

**CS-0:** Ribs articulating with ventral or posteroventral face of the parapophyses.

**CS-1:** Ribs articulating with dorsal face. (Doradidae)

**CS-2:** Ribs articulating with posterior face. (Auchenipteridae)

**CS-3:** Ribs articulating largely on dorsal face, but wrapping around the posterior face to touch ventral surface as well. (Amphiliidae)

#### **84. Anterior pleural ribs. (CI = 0.250, RI = 0.812)**

In many of the outgroup taxa the pleural ribs vary by length but are generally of similar thickness from anterior to posterior (Fig. 3A). In CS-1 the pleural ribs are greatly enlarged anteriorly. In many of these taxa the first rib is particularly enlarged (Fig. 3B). The ribs are modestly enlarged beyond the first and decrease in size moving posteriorly.

**CS-0:** Anterior pleural ribs not particularly enlarged.

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

**Inapplicable:** In the *Chiloglanis*, *Atopodontis*, *Atopochilus* and *Euchilichthys*, as the first rib might be absent or fully incorporated into a strut-like process as described in character 80.

### **Lateralis System**

#### **85. Proliferation of sensory-canal pores. (CI = 0.333, RI = 0.714)**

In most of the taxa considered there is one pore (occasionally two or three) at each site along the cephalic sensory canals. In some species of *Euchilichthys*, as well as several of the 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.

**CS-0:** One pore at each site along cephalic sensory canals.

**CS-1:** Multiple pores at each site along cephalic sensory canals. (*Chrysichthys*; *Parauchenoglanis*; Schilbeidae; Ariidae; *Euchilichthys* sp. 'zambia'; *E. sp.* 'congo'; *E. royauxi*)

**86. Pores of the mandibular sensory canal. (CI = 0.556, RI = 0.882)**

In many of the outgroup taxa there is a sensory canal running through each half of the mandible which opens at the skin surface by five or more pores. On each side, only those pores emanating from a hole in the lower jaw are counted. That is, I do not count pores emanating from the canal at the interface of the mandible and quadrate. In CS-1 through CS-5 there are fewer than five pores.

**CS-0:** Mandibular sensory canal with at least five pores.

**CS-1:** Mandibular sensory canal with four pores. (*Centrodoras*; *Platydoras*)

**CS-2:** Mandibular sensory canal with three pores. (*Mochokiella*; *Acanthocleithron*; *Microsynodontis*; all *Synodontis* except *S. congicus* [3]; *Hemisyndontis*; *Brachysynodontis*)

**CS-3:** Mandibular sensory canal with two pores. (*Tetracamphilius*; *Zaireichthys*; *Mochokus*; *Synodontis congicus*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**CS-4:** Mandibular sensory canal with one pore. (*Doumea*; *Phractura*)

**CS-5:** No mandibular sensory canal. (*Chiloglanis*)

### **Barbels, Lips and Mouth**

**87. Outer mandibular barbels. (CI = 0.571, RI = 0.919)** (Diogo, 2005 [1 and 3])

The nature of the outer mandibular barbels is quite variable among catfishes, but in the outgroup taxa considered the outer mandibular barbels are generally simple and unbranched. In *Diplomystes* the outer mandibular barbels are absent. Among basal siluroid catfishes, like the Ictaluridae, the outer mandibular barbels are straight, slender and unbranched (CS-1). In CS-2 the outer mandibular barbels have single branches at each point along their lengths (Fig. 30A). In CS-3 the outer mandibular barbels have two branches at various points along their lengths, directly opposing each other basally and closely alternating distally. These barbels often show secondary branching (Fig. 30B). In CS-4 the outer mandibular barbels are largely incorporated into the lower lip of an oral sucker, only extending a small distance beyond the rim of the sucker and unbranched along that portion. The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Outer mandibular barbels absent.

**CS-1:** Outer mandibular barbels without branches.

**CS-2:** Outer mandibular barbels with single branches.

**CS-3:** Outer mandibular barbels with two branches.

**CS-4:** Outer mandibular barbels incorporated into oral sucker.

[Insert Figure 30 near here.]

**88. Inner mandibular barbels. (CI = 1.000, RI = 1.000)** (Diogo, 2005 [1 and 3])

The nature of the inner mandibular barbels is quite variable among catfishes, but in the outgroup taxa considered the inner mandibular barbels are generally simple and unbranched. In *Diplomystes* the inner mandibular barbels are absent. Among basal siluroid catfishes, like the Ictaluridae, the inner mandibular barbels are straight, slender and unbranched (CS-1). In CS-2 the inner mandibular barbels have single branches at each point along their lengths (Fig. 30A). In CS-3 the inner mandibular barbels have two branches at various points along their lengths, directly opposing each other basally and closely alternating distally. These barbels often show secondary branching (Fig. 30B). In CS-4 the inner mandibular barbels are largely incorporated into the lower lip of an oral sucker, only extending a small distance beyond the rim of the sucker and unbranched along that portion. The distribution of states for this character is rather complex. Please refer to the matrix for details.

**CS-0:** Inner mandibular barbels absent. (Diplomystidae)

**CS-1:** Inner mandibular barbels without branches. (Ictaluridae; *Chrysichthys*; *Parauchenoglanis*; Schilbeidae; Amphiliidae; Malapteruridae; *Sciades*; Auchenipteridae; Doradidae)

**CS-2:** Inner mandibular barbels with single branches. (*Mochokus*; *Mochokiella*)

**CS-3:** Inner mandibular barbels with two branches. (*Acanthocleithron*; *Microsynodontis*; *Synodontis*; *Hemisyndontis*; *Brachysynodontis*)

**CS-4:** Inner mandibular barbels incorporated into oral sucker. (*Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**89. Basal membrane of maxillary barbels. (CI = 0.500, RI = 0.875)**

In most of the taxa presented here the base of the maxillary barbels is rounded in cross section and without any obvious flap-like membrane along the posterior/medial margin. In *Hemisynodontis*, *Brachysynodontis* and some species of *Synodontis* the base of the barbel has a membranous flap along the medial/posterior margin.

**CS-0:** Maxillary barbels without basal membrane.

**CS-1:** Maxillary barbels with prominent basal membrane.

(*Synodontis longirostris*; *S. schall*; *S. pleurops*; *S. nigrita*; *S. congicus*; *S. clarias*; *S. sorex*; *Hemisynodontis*; *Brachysynodontis*)

**Inapplicable:** In the *Chiloglanis*, *Atopodontis*, *Atopochilus* and *Euchilichthys*, because the state is obscured by the fact that the maxillary barbel is largely incorporated into the enlarged oral sucker.

**Miscellaneous**

**90. Free orbit. (CI = 0.167, RI = 0.808)**

Among many of the outgroup taxa, including the Ictaluridae and *Diplomystes*, there is a groove around the perimeter of the eye, generally referred to as a free orbit. In CS-1 the orbit is not free; the skin over the eye is entirely confluent with the skin surrounding the eye.

**CS-0:** Free orbit present.

**CS-1:** Free orbit absent. (Amphiliidae; Malapteruridae; Auchenipteridae; *Agamyxis*; *Platydoras*; *Mochokus*; *Mochokiella*; *Microsynodontis*; *Chiloglanis*)

**91. Gill openings. (CI = 0.250, RI = 0.800) (Mo, 1991 [123])**

In many of the outgroup taxa considered the gill openings run from the isthmus ventrally to the level of the eye dorsally. In CS-1 the gill openings are restricted to the sides of the head, from near the base of the pectoral spine to the level of the eye. Among mochokids, *Brachysynodontis* shows an intermediate state where the lower end of the gill opening extends to the ventral surface, below the base of the pectoral spine. Still, I view the openings here as largely restricted to the sides of the head; they do not extend all the way to the isthmus.

**CS-0:** Gill openings not restricted to sides of head.

**CS-1:** Gill openings largely restricted to sides of head. (Malapteruridae; Auchenipteridae; Doradidae; *Mochokus*; *Mochokiella*; *Microsynodontis*; *Synodontis*; *Brachysynodontis*; *Chiloglanis*; *Atopodontis*; *Atopochilus*; *Euchilichthys*)

**92. Gas bladder. (CI = 0.400, RI = 0.842) (Mo, 1991 [120])**

In many of the taxa presented here the gas bladder is formed as a large, roughly heart-shaped chamber, occupying a position just ventral to the fused vertebrae of the compound centrum. The posterior chambers of the gas bladder are large, extending well beyond the fused vertebrae and are generally shielded by the anterior ribs both dorsally and laterally. The gas bladder is generally longer than wide (Fig. 3B). In some chiloglanidins the gas

bladder is somewhat reduced in size with smaller posterior chambers, occupying a similar position, but only reaching to near the end or slightly past the compound centra. In these taxa the gas bladder slightly shorter than it is wide (Fig. 3C). In the remaining chiloglanidins the posterior chambers of the gas bladder are drastically reduced. The gas bladder is formed as two bulbs on each side of the compound centrum, protected by the parapophyses of the 4<sup>th</sup> and 5<sup>th</sup> vertebrae dorsally. In some instances the parapophyses and other processes of the compound centra almost completely surround the bulbs of the gas bladder (Fig. 5).

**CS-0:** Gas bladder large.

**CS-1:** Gas bladder somewhat reduced. (*Chiloglanis* sp. 'kalungwishi'; *C. sp.* 'burundi'; *Atopochilus*; *Euchilichthys*)

**CS-2:** Gas bladder greatly reduced. (all *Chiloglanis* except *C. macropterus* [0], *C. sp.* 'kalungwishi' [1] and *C. sp.* 'burundi' [1]; *Atopodontis*)

## RESULTS AND DISCUSSION

### Phylogenetic Analyses

Analysis 1, using the TBR heuristic search algorithm to recover a set of most parsimonious trees, resulted in six trees of 394 steps, CI = .3680 and RI = .8537. Here, CI, the consistency index for the tree, is calculated as the average of CI for all characters. Likewise, retention index for the tree is the average of RI for all characters. The recovered trees differ in the placement of certain species of *Synodontis*, in the placement of the genus *Microsynodontis* and in the relationship of certain outgroup taxa. The strict

consensus of the trees (406 steps, CI = .3571, RI = .8467) is shown with decay indices in Figure 31. Bootstrap values could not be calculated due to the extensive search time required.

A second analysis was used to confirm the relationships recovered by the heuristic search. Analysis 2, using the branch and bound method to find the set of most parsimonious trees, resulted in two trees of 269 steps, CI = .5056 and RI = .7746. The two trees differ with regards to the position of the genus *Microsynodontis* only. The strict consensus of the trees (270 steps, CI = .4924, RI = .7729) is shown with bootstrap values and decay indices in Figure 32. Branch lengths for this tree are referenced below, in the discussion.

The results of analyses 1 and 2 are largely in agreement. For the ingroup taxa considered in both analyses, the topology is largely the same. Below, clades and synapomorphies are discussed having considered the results of both analyses, but support values are given for the labeled nodes from Analysis 2 only (Fig. 32). Synapomorphies are listed below following bold-faced character state numbers. Synapomorphies were universally recovered under both ACCTRAN and DELTRAN optimizations, unless specifically noted.

[Insert Figure 31 and 32 near here.]

### **The relationship of the Mochokidae to other catfishes**

Because it is easiest to consider synapomorphies in order of successively smaller groups, higher-level relationships will be discussed first. Characters state changes and possible synapomorphies for nodes outside of the Mochokidae are discussed below.

### **The ‘arioids’: Node Y**

This group includes the Mochokidae, the Doradidae, the Auchenipteridae and the Ariidae. The group receives poor to fair support from the tests for robustness including a bootstrap value of 62, a decay index of 3 and a branch length of 9 in the consensus tree optimized under ACCTRAN. Two of the synapomorphies recovered were already hypothesized to characterize the group. These synapomorphies include:

**(12-1):** Venterolateral expansions of the basioccipital that join the ossified transcapular ligament (Lundberg, 1993). This state is also found in *Zaireichthys*, but is independently derived in that case. In both cases, the derived state helps to stabilize the pectoral girdle in these heavily armed catfishes.

**(75-1):** A free and movable anterior parapophyses of the compound centrum (Mo, 1991; Lundberg, 1993; de Pinna, 1993). This free parapophysis is generally referred to as an elastic spring apparatus. However, the shape and form of this process varies greatly in those taxa where it is free. In the Ariidae it is angular and looks a lot like those found in other catfishes where the parapophysis is not free. It is most highly modified in the Doradidae, Auchenipteridae and many, but not all, mochokids (see ‘doradoid’ synapomorphy (76-1) below). Within the Mochokidae, freedom of the anterior parapophyses is lost in the chiloglanidin group and subsequently regained in *Atopochilus* and *Euchilichthys*.

Previously unknown synapomorphies for the group include:

**(11-1):** The absence of a basioccipital pit. The ventral surface of the basioccipital is not marked by a pit in this group. The only other taxa examined that lack a pit on the ventral surface of the basioccipital are members of the Leptoglaninae (Amphiliidae). The absence of a basioccipital pit in the Leptoglaninae is independently derived. All other outgroup taxa have a pit on the ventral surface of the basioccipital. As far as known, this character has not been thoroughly examined among other catfishes; it deserves further inspection at a higher level.

**(22-2):** Four infraorbitals. The number of infraorbitals is reduced in some species of Doradidae and increased to five in all chiloglanidins.

**(58-1):** The presence of moderate or strong serrae along the anterior edge of the pectoral spine. Anterior pectoral-spine serrae are lost in all members of the chiloglanidin group. The reality of this synapomorphy is questionable because many catfishes not considered also possess such serrae. In this work, *Chrysichthys*, *Schilbe* and *Pangasius* are the only other outgroup taxa possessing anterior pectoral-spine serrae.

**(81-2):** Sixth centrum fused or deeply suture to the compound centrum. In some chiloglanidins the seventh centrum is also fused to this complex. In the Doradidae fusion can continue to the seventh centrum and beyond.

In addition to these, the basal members of this group lack a mesocoracoid arch (54-1). However, this state change is not recovered as a synapomorphy for the group under DELTRAN because all members of the Mochokidae possess the mesocoracoid arch. The distribution of states here is notable because, in fact, it seems to reject the idea that the Mochokidae is a derived member of the group. Among catfishes the

mesocoracoid arch is rarely absent (see character 94 in Mo (1991) or character 185 in Diogo (2005) for details). In addition, the recovered topology requires that the Mochokidae regain a mesocoracoid arch, which seems somewhat unlikely.

### **The ‘doradoids’: Node Z**

This group includes the Mochokidae, the Doradidae and the Auchenipteridae. The group receives poor to fair support from the tests for robustness including a bootstrap value of 66, a decay index of 3 and a branch length of 13 in the consensus tree optimized under ACCTRAN. All of the synapomorphies recovered were already hypothesized to characterize the group. The synapomorphies include:

**(13-1):** A fused extrascapular. A fused extrascapular is common in other groups of catfishes, including the Amphiliidae here (Mo, 1991). This state might be characteristic of some larger group, but that conclusion was not within the scope of this work. 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 its basal position within the family.

**(16-2):** A well-formed and wide nuchal shield (Mo, 1991). Within the Mochokidae, several species of *Chiloglanis* sensu stricto (sensu stricto: excluding *C. macropterus* and *C. sp. ‘burundi’*; see Figure 31) show reversal to a modestly formed nuchal shield (16-1).

**(45-1):** A reduced and oddly shaped parurohyal (Mo, 1991). A greatly reduced parurohyal was not observed in any of the remaining outgroup taxa.

**(52-1):** A greatly enlarged cleithral process (Mo, 1991; Diogo, 2005). Within this group, the cleithral process is reduced in size among all chiloglanidins. A large cleithral process is independently derived in *Zaireichthys*. In general, the most impressive cleithral processes are found in those taxa that also have large and intensely serrated pectoral spines.

**(76-1):** An anterior parapophysis of the compound centrum with a plate-like elaboration at its distal end (Mo, 1991; Lundberg, 1993; de Pinna, 1993). A well-developed elastic spring apparatus is lost in the basal members of the chiloglanidin group and regained in *Atopochilus* and *Euchilichthys*. A plate-like distal end to the elastic spring apparatus is independently acquired in the Malapteruridae.

**(91-1):** Restricted gill openings (Mo, 1991). Within the Mochokidae, only *Hemisynodontis* and *Acanthocleithron* have gill openings open to the isthmus. Both instances represent a reversal to the plesiomorphic state within the Siluriformes. The presence of larger gill openings in *Hemisynodontis* might be expected given its feeding ecology. *Hemisynodontis* has few oral teeth, extremely long branchiospines and highly modified pharyngeal jaws as compared to other *Synodontis*-like mochokids. This species is filtering large amounts of water to extract food items and enlarged gill openings are an obvious advantage to that end. The presence of a larger gill opening in *Acanthocleithron* is not so easily explained, although this species possesses unusually large pharyngeal teeth. Restricted gill openings are independently acquired in the Malapteruridae.

Great effort was made to include all reasonable outgroups in hopes of recovering the sister group to the Mochokidae. As with several previous works, this analysis

recovered the South American Doradidae + Auchenipteridae as sister to the Mochokidae. In addition, the Ariidae are recovered as the sister group to the Mochokidae + (Doradidae + Auchenipteridae). These results agree with Lundberg's (1993) hypothesis of an 'arioid' clade and a nested 'doradoid' clade. In light of mounting molecular evidence (Hardman, 2005; Sullivan et al., 2006), these relationships are being seriously questioned for the first time. While the results here agree with previous morphological works, the support values for the 'arioid' and 'doradoid' clades are admittedly weak. The inclusion of newly hypothesized sister groups, Amphiliidae and Malapteruridae (Sullivan et al., 2006), may partially account for those weak values. Several of the mochokid synapomorphies (below) are independently derived for amphiliid and malapterurid taxa. They could, in fact, represent synapomorphies for groups composed of the Amphiliidae, Mochokidae and Malapteruridae.

If we consider the results of the higher-level phylogenetic work in Sullivan et al. (2006), the morphological similarities between the Mochokidae and other 'doradoids' would represent an exceptional example of extensive homoplasy. In truth, most of the morphological evidence for the 'arioid' and 'doradoid' groups are related to a small number of systems like the nuchal shield, the Weberian apparatus 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 group 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. 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.

#### **Monophyly of the Mochokidae: Node A**

The family Mochokidae, as currently delimited, is a monophyletic group. Node A (Fig. 32) includes all of the Mochokidae to the exclusion of all other taxa and receives good support from the tests for robustness including a bootstrap value of 88, a decay index of 8 and a branch length of 16 in the consensus tree optimized under ACCTRAN. Of the hypothesized character state changes supporting the monophyly of the Mochokidae, several were already hypothesized to be synapomorphies for the group. These include:

**(23-1):** The absence of an ascending Meckel's cartilage (Mo, 1991; de Pinna, 1993; Diogo, 2005). The ascending Meckel's cartilage is independently lost in the Amphiliidae (in part) and the Malapteruridae.

**(24-1):** A shortened horizontal Meckel's cartilage (Mo, 1991; de Pinna, 1993; Diogo, 2005). A shortened horizontal Meckel's cartilage is independently acquired in the Amphiliidae.

**(25-1):** The absence or extreme reduction of the coronomeckalian (Mo, 1991; de Pinna, 1993; Diogo, 2005). The coronomeckalian is independently lost in the Malapteruridae. 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. The much reduced nature of the element is somewhat variable and, as such, was not utilized as a separate character state.

**(26-1):** The absence or extreme reduction of the coronoid process (de Pinna, 1993; Diogo, 2005). This state was not seen in any of the outgroups considered.

**(48-1):** The absence of the interhyal (Mo, 1991). The interhyal is independently lost in some members of the Amphiliidae.

**(64-1):** Seven pelvic-fin rays (Mo, 1991). In a single undescribed species of *Chiloglanis* there are eight pelvic-fin rays. Seven pelvic-fin rays are also found in some of the Doradidae, but must be independently derived.

**(87-2):** Ramified outer mandibular barbels. The outer mandibular barbels are slender and unbranched in a single mochokid species, *Mochokus brevis*. The absence of ramified outer mandibular barbels in *M. brevis* probably represent a reversal because its sister species at the base of the mochokid tree, *M. niloticus*, does show ramification. In the chiloglanidins, the outer mandibular barbels are wholly incorporated into the oral disc. Some members of the Doradidae also possess branched outer mandibular barbels (Higuchi, 1992). This state is probably independently derived in the Doradidae.

**(88-2):** Ramified inner mandibular barbels. The inner mandibular barbels are wholly incorporated into the oral disc in the chiloglanidins. As with the outer mandibular

barbels, some members of the Doradidae have independently acquired branched inner mandibular barbels (Higuchi, 1992).

Of the remaining, previously unknown, character state changes occurring at node A, a few are noteworthy and represent new synapomorphies for the family. They include: **(56-0):** The presence of a pectoral locking foramen. The pectoral locking foramen is subsequently lost in all chiloglanidins except *Chiloglanis macropterus*. The pectoral locking foramen is absent in the Doradidae, the Auchenipteridae and the Ariidae. The pectoral locking foramen is also absent in the Malapteruridae and the Amphiliidae. The distribution of the character states for this character needs broader examination within the Siluriformes.

**(71-2):** Complete fusion of the upper caudal-fin elements. In most mochokids, fusion has proceeded to the point where individual hypurals are indistinguishable. In *Atopochilus* and *Euchilichthys* the outer or marginal elements of the caudal fin are unfused (71-1). Extensive fusion of the upper hypurals is independently derived in some of the Amphiliidae.

**(86-2 to 86-5):** A reduced number of mandibular sensory-canal pores. The greatest number found in any mochokid is 3 (86-2) and in *Chiloglanis* sensu lato (all *Chiloglanis* included) there are no mandibular sensory-canal pores (86-5). In most of the outgroup taxa presented here the number of mandibular sensory-canal pores is five or more. The number of mandibular sensory-canal pores is modestly reduced in certain Doradidae and more extremely reduced in certain Amphiliidae. The reduced number of mandibular sensory canal pores must be independently derived in each case.

In addition to these, the presence of an elongate and discrete posterior parapophysis of the compound centrum (78-1) is probably a synapomorphy for the Mochokidae, but it is recovered under DELTRAN optimization only because the posterior parapophysis is greatly reduced or totally absent in the Doradidae and Auchenipteridae. Within the Mochokidae, a discrete parapophysis is subsequently lost in *Chiloglanis* sensu stricto. An elongate posterior parapophysis is independently acquired in the Malapteruridae.

Monophyly of the Mochokidae is fairly well supported in this work. The previously known synapomorphies for Mochokidae are largely restricted to the oral jaws, suspensorium and mouth. This is not unexpected, considering the specialization seen in the mochokid mouth. Changes in the mouth and jaws are a recurring theme in mochokid evolution; the synapomorphies that characterize the family make up the first of three major shifts (at nodes A, D and G) in jaw and mouth morphology. This first shift consists of the reduction of Meckel's cartilage, the reduction of the coronomeckalian, the reduction of the coronoid process, the ramification of the barbels and a reduced number of mandibular sensory-canal pores. The adaptive nature, if any, behind these changes is unclear, though I expect that these changes are related to a shift in feeding ecology.

My work suggests that features of the pectoral girdle, caudal fin and mandibular sensory canals are also synapomorphies for the family. In addition, features of the nuchal shield and Weberian apparatus might be synapomorphies for the group if the higher-level relationships are not correctly resolved. It is important to reiterate that, in fact, many of the previously known and newly proposed synapomorphies for the Mochokidae are

shared with members of the Amphiliidae and Malapteruridae. If we adopt the higher level relationships of Sullivan et al. (2006), many of these features could represent synapomorphies for clades composed of these three families.

### **Clades within the Mochokidae**

With the expectation that there will be a large amount of taxonomic and systematic work pertaining to the Mochokidae in the immediate future, I have chosen to leave the newly recovered groups within the Mochokidae unnamed at this point. Several pieces of information suggest this is prudent. For example, within the genus *Chiloglanis* several (15+) undescribed species are already known to exist and await formal description; extensive research on the genus has also revealed some definite substructure. In addition, further study of the Mochokidae (after this thesis work was completed) has revealed unforeseen morphological diversity and novelty, which needs to be taken into consideration. Lastly, new and exciting material is still being collected from Africa. The new genus *Atopodontis* (Friel and Vigliotta, 2008) is proof of that. At this point, flooding mochokid taxonomy with new names seems ill advised. Comprehensive revisions of smaller scope are better suited for the introduction of new names, and will follow this work. Still, major clades within the Mochokidae are discussed below.

### ***Mochokus***

The genus *Mochokus* contains only two valid species. The following are recovered as synapomorphies for the genus:

**(55-1):** A mesocoracoid arch that is straight and that joins the posterior face of the vertical scapulo-coracoid lamina without any dorsal prominence. This state is independently derived in the chiloglanidins.

**(60-3):** 6 or fewer pectoral-fin rays. Among mochokids this small number of pectoral-fin rays is only matched by *Microsynodontis*, where it is independently derived.

**(69-1):** A rayed adipose fin. A rayed adipose fin is exceedingly rare among catfishes and was only seen in *Mochokus* in this work.

**(72-1):** The absence of a space between the upper and lower hypurals. In this work the only other taxa showing this state were *Phractura*, *Doumea* and *Malapterurus*.

**(86-3):** Two mandibular sensory-canal pores on each side of the mandible. Two mandibular sensory-canal pores are also found in *Atopochilus*, *Euchilichthys* and *Atopodontis*, but are independently derived in that instance.

Both species of *Mochokus* are considered in Analysis 1 and they form a monophyletic group, sister to all other mochokids. The unique set of characteristics described above and a decay index of 3 in Figure 31 lends support to the monophyly of the group.

#### **Unnamed group: Node B**

This group includes all mochokids with the exception of *Mochokus*. The group receives poor support from the tests for robustness including a bootstrap value of 62, a decay index of 2 and a branch length of 9 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(10-1):** A spinous projection on the ventral side of the pterotic. Most chiloglanidins have lost the pterotic spine; only *Chiloglanis macropterus* and *C. sp. 'burundi'*, which present as basal members of the chiloglanidin group, have a pterotic spine. In the taxa possessing a pterotic spine the hyomandibula is still quite firmly joined to the underside of the neurocranium, despite the fact that the articulation is relatively short compared to other catfishes (see character 42). In this respect, the pterotic spine probably serves to strengthen the articulation by enclosing the hyomandibula along its posterolateral edge. *Mochokus* lacks a pterotic spine altogether.

**(28-1):** A cup-shaped facet of the angulo-articular for the quadrate. The precursor of this 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.

**(41-1):** A spinous projection along the medial edge of the hyomandibula. The hyomandibular process is lost 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. I do not consider this small flange to be equivalent to the process seen in other mochokids.

**(57-2):** Ventral processes at the proximal end of the first pectoral-fin proximal radial. In most chiloglanidins the ventral process is accompanied by a dorsal process (57-1). In *Synodontis contractus*, *Atopodontis* and some species of *Chiloglanis* sensu stricto the proximal end of the first pectoral-fin proximal radial is without processes altogether (57-0). The same is true for *Mochokus*.

The exclusion of *Mochokus* with respect to the members of this group seems dubious, and the relative positions of *Mochokiella* and *Acanthocleithron* at the base of this group are also poorly resolved. Each presents a unique set of seemingly plesiomorphic features, which accounts for the poor support in this region of the tree.

### *Mochokiella*

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

**(21-1):** Third dorsal-fin proximal radial joined by dorsolateral expansion to the posterior nuchal plates (second dorsal-fin proximal radial). This state is independently derived for all species of *Synodontis*, except *S. acanthoperca*.

**(44-1):** A well-formed opercular spine. The opercular spine is sexually dimorphic, wherein males possess a much larger spine than females. The presence of the opercular spine was previously unknown for *Mochokiella paynei*. A well-formed and sexually dimorphic opercular spine is also found in *Synodontis acanthoperca* and another species of *Synodontis* that is still undescribed (personal commun., Dr. Emmanuel Vreven). Given the recovered topology, this feature must be independently derived in the two groups, but the basal position of *S. acanthoperca* within its genus is certainly intriguing.

**(51-2):** The presence of 6 branchiostegal rays. This reduced number of branchiostegal rays is independently derived in a large number of species of *Chiloglanis* sensu stricto and a smaller number of *Synodontis* species.

### Unnamed group: Node C

This group includes all mochokids with the exception of *Mochokus* and *Mochokiella*. The group receives poor support from the tests for robustness including a bootstrap value of 56, a decay index of 1 and a branch length of 8 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(2-1):** The absence of well-formed anterolateral cornua of the mesethmoid. In the chiloglanidins anterolateral cornua are entirely absent (2-2). *Mochokus* and *Mochokiella* show fairly well formed anterolateral cornua.

**(29-1):** The presence of a tooth cup. In the basal member of this group, *Acanthocleithron*, the tooth cup is only modestly formed and the cup is more anterodorsally directed. *Mochokus* and *Mochokiella* do not possess a tooth cup.

**(73-1):** A count of 8 + 9 principal caudal-fin rays. The caudal-fin ray count is consistently reduced in *Microsynodontis* and occasionally reduced in species of *Synodontis* and *Chiloglanis* sensu stricto. In *Mochokus* and *Mochokiella* the caudal-fin ray count is always less than 8 + 9.

**(88-3):** Two branches at each branching point along the length of the inner mandibular barbel. The inner mandibular barbels have been incorporated into the lower lip in the chiloglanidins (88-4). In *Mochokus* and *Mochokiella* there are only single branches at each point along the inner mandibular barbels.

Again, exclusion of *Mochokus* and *Mochokiella* with respect to the members of this group is dubious because support for the group at node C is rather poor. It is most

proper to think of *Acanthocleithron*, *Mochokiella* and *Mochokus* as independent lineages outside of the group at node D, each with its own set of plesiomorphic features. The relationships between these three lineages and the group at node D are not satisfactorily resolved.

### ***Acanthocleithron***

*Acanthocleithron* is a monotypic genus. Based on the recovered topology, the following are autapomorphies for this species:

**(37-1):** Spatulate premaxillary teeth. Spatulate teeth are also found in some members of the chiloglanidin group.

**(53-1):** Blunt or rounded cleithral processes. Some species of *Synodontis* and males of certain sexually dimorphic species of *Chiloglanis* sensu stricto display blunt cleithral processes.

**(79-1)** Parapophyses of the 5<sup>th</sup> centrum broadly joined to those of compound centrum. Within the Mochokidae, this state is independently derived for several species of *Chiloglanis* sensu stricto.

**(90-0)** A free orbit. Within the Mochokidae this state is independently derived in *Synodontis* and the group composed of *Atopodontis*, *Atopochilus* and *Euchilichthys*.

**(91-0):** Gill openings open to the isthmus. All other mochokids except *Hemisynodontis membranaceous* have gill openings that are largely restricted to the side of the head.

### **Unnamed group: Node D**

This group includes all mochokids with the exception of *Mochokus*, *Mochokiella* and *Acanthocleithron*. The group receives fair to good support from the tests for robustness including a bootstrap value of 77, a decay index of 4 and a branch length of 8 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(4-1):** An anteroposteriorly elongated lateral ethmoid, without any great lateral prominence and a relatively straight lateral edge.

**(27-1):** A rather large intermandibular angle, no less than 135 degrees. In *Hemisynodontis*, there is a reversal to approximately 90 degrees as seen in *Acanthocleithron*, *Mochokiella* and *Mochokus*.

**(31-1 to 31-3):** S-shaped auxiliary dentary teeth. The tooth tips vary within this group, but are S-shaped in all instances.

**(34-1 to 34-3):** Premaxillary tooth plates with ventral and posterior faces supporting teeth. The shape of premaxillary tooth plates differs within this group, but all possess ventral and posterior faces.

**(35-1):** The differentiation of premaxillary teeth by size and shape from front to back.

**(36-1):** S-shaped teeth on the premaxilla.

**(43-1):** A greatly reduced anterior pterygoid element. In some chiloglanidins this element is elongate and boomerang shaped, though still reduced in size (43-2).

In addition to these synapomorphies, the following were recovered under DELTRAN only for the group at node D. In each instance the derived state for the group is also found in *Mochokiella*. Given the uncertain relationships of the putatively basal mochokids, these should be considered possible synapomorphies for the group.

**(9-0):** Articulating facet for the hyomandibula at the border of the prootic and the sphenotic. In most siluroid catfishes, the articulating facet for the hyomandibula is found on the ventral face of the sphenotic and does not involve the prootic. Among mochokids this state is found in *Mochokus* and *Acanthocleithron* only. In all other mochokids, including *Mochokiella*, the articulating facet is located at the interface of the sphenotic and prootic (as in *Diplomystes* and the loricarioids). The nature of this character within the Mochokidae, and among catfishes in general, suggests that it may be rather important and that it deserves further review. Within the Mochokidae, it is most accurate to say that some, but not all, ‘basal’ mochokids possess an articulating facet similar to most siluroid catfishes. All other mochokids possess a facet similar to loricarioids and *Diplomystes*. The plesiomorphic nature of this character in most mochokids is puzzling. In most respects the Mochokidae are highly derived catfishes.

**(42-1):** A compact articulating condyle on the dorsal edge of the hyomandibula. A compact articulating condyle is also found in *Mochokiella*. The condyle is particularly shortened and spherical in the chiloglanidins and in some species of *Synodontis* (42-2).

**(62-1):** The presence of serrae along the posterior margin of the dorsal spine. Posterior dorsal-spine serrae are lost in most chiloglanidins. Serrae are also found along the posterior margin of the dorsal spine in *Mochokiella*.

**(84-1):** The presence of greatly enlarged ribs anteriorly. Greatly enlarged anterior ribs are also found in *Mochokiella*.

Support for the group at node D is better than for that at B and C and exclusion of *Acanthocleithron*, *Mochokiella* and *Mochokus* with respect to the members of the group

seems reasonably well founded. The morphological support for the group at D is overwhelmingly biased towards the jaws and suspensorium. The synapomorphies supporting the group at node D represent the second major shift in jaw and mouth morphology within the Mochokidae. The most compelling of these are the large intermandibular angle, the presence of S-shaped auxiliary dentary teeth, the presence of premaxillary tooth plates with multiple faces and the differentiation of premaxillary teeth by shape and size. Again, these morphological changes are most likely correlated with a shift in feeding ecology. Most members of this group display a ventrally directed mouth for feeding either at the waters surface (as in the upside-down catfishes) or along the bottom. Members of this group are feeding selectively on invertebrates and smaller food items; piscivory is very uncommon. For feeding on these items along the bottom it is obviously advantageous to have a ventrally directed mouth.

#### ***Microsynodontis*: Node E**

The members of this group belong to the genus *Microsynodontis*. The group receives poor to fair support from the tests for robustness including a bootstrap value of 69, a decay index of 1 and a branch length of 4 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(60-3):** Six pectoral-fin rays. This reduced number of rays is, otherwise, only found in *Mochokus*, where the count may be even lower.

**(73-3):** 7 + 7 caudal-fin rays. In one species this character was polymorphic and some individuals showed a count of 6 + 6. Among mochokids, such low counts are only matched by *Mochokus niloticus* and the enigmatic *Synodontis contractus*.

**(74-1):** A rounded caudal fin. A rounded caudal fin is also found in some species of *Chiloglanis* sensu lato (including *C. macropterus*), though I predict it is independently derived with respect to *Microsynodontis*.

*Microsynodontis* is a group defined largely by plesiomorphic features. As a result, *Microsynodontis* was the only higher-level mochokid group to vary in its placement within the sets of most parsimonious trees. Grouping with *Synodontis* and the chiloglanidins 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* would be aided by a comprehensive taxonomic revision of the group, because, like many small African fishes, the actual breadth of diversity in *Microsynodontis* is poorly known. At least one undescribed species is known. The recent description of eight new species (Ng, 2004) suggests that many species remain uncollected and that cryptic species exist.

***Synodontis* (including *Hemisynodontis* and *Brachysynodontis*): Node F**

This group includes *Synodontis*, *Hemisynodontis* and *Brachysynodontis*. The group receives good support from the tests for robustness including a bootstrap value of 86, a decay index of 3 and a branch length of 7 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(6-1):** The total absence of a posterior fontanelle. *Synodontis acanthoperca*, not included in Analysis 2, is a notable exception. Like several smaller mochokid species, *S. acanthoperca* has a small centrally-located foramen on the parieto-supraoccipital (6-2).

This, among other traits, accounts for its basal position in Analysis 1. The posterior fontanelle is also totally absent in *Mochokus brevis*, *Mochokiella*, and a majority of the chiloglanidins.

**(8-1):** A reduced epioccipital. *Synodontis acanthoperca*, not included in Analysis 2, is a notable exception. The epioccipital is reasonably well-formed in this species (8-0).

**(19-1):** The presence of a bridge-shaped medial nuchal plate and a small, scale-shaped anterior nuchal plate. *Synodontis acanthoperca*, not included in Analysis 2, is a notable exception. *S. acanthoperca*, unlike any other species of *Synodontis*, has simple anterior and medial nuchal plates that span the entire width of the nuchal shield (19-0). For some *Synodontis* this character cannot be applied, because they lack separate anterior and medial nuchal plates. A bridge-shaped medial nuchal plate and scale-shaped anterior nuchal plate are independently derived in *Mochokus brevis*.

**(21-1):** Third dorsal-fin proximal radial joined by dorsolateral expansion to the posterior nuchal plates (second dorsal-fin proximal radial). *Synodontis acanthoperca*, not included in Analysis 2, is a notable exception. The third dorsal-fin proximal radial does not touch the posterior nuchal plate in this species (21-0). However, the joining of these elements is independently derived in *Mochokiella*.

**(77-2):** An anteriorly directed process on the elastic spring apparatus. A small number of *Synodontis* species show an obvious bend in the parapophyses, but no well-formed anteriorly directed process (77-1).

**(90-0):** A free orbit. This state is independently derived for *Acanthocleithron* as well as a group composed of *Atopodontis*, *Atopochilus* and *Euchilichthys* (node I).

Further investigation of this rather large group (over 120 species) is necessary to determine if the genus *Synodontis* is truly monophyletic. The attempt here has led to a couple of conclusions. First, the genus *Synodontis* cannot be monophyletic without the inclusion of *Brachysynodontis batensoda* and *Hemisynodontis membranaceous*. The taxonomy of these two species has wavered for decades, but I find no evidence to suggest they represent anything more than uniquely derived members of the group. To maintain the monophyly of *Synodontis*, these two species should be considered members of the genus.

More interesting is the placement of *Synodontis acanthoperca* which, from the synapomorphies discussed above, seems to be a basal member of the group. It is recovered as such in Analysis 1, though the support is low. *Synodontis acanthoperca* shows a number of seemingly plesiomorphic features. Other features are simply unique and not necessarily plesiomorphic. Some of these features probably signify a paedomorphic body plan. The small size of this species is interesting, because *Microsynodontis*, basal chiloglanidins and the ‘basal’ mochokids all share a small body size. Small body size may be the plesiomorphic condition for *Synodontis* and the family as a whole. These interesting points can be most appropriately addressed in a phylogenetic work specific to the genus *Synodontis*.

### **Subfamily Chiloglanidinae: Node G**

This group includes *Chiloglanis* sensu lato, *Atopochilus*, *Euchilichthys* and *Atopodontis*. The group receives excellent support from the tests for robustness including a bootstrap value of 100, a decay index of 19 and a branch length of 31 in the consensus

tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(2-2):** The total absence of anterolateral cornua of the mesethmoid.

**(3-1):** A mesethmoid that is much wider ventrally. This state is independently derived in *Mochokus* and *Mochokiella*.

**(7-1):** Posterolateral corners of the neurocranium formed by the prootic, exoccipital, pterotic and sphenotic.

**(18-1):** The presence of only two nuchal plates because the anterior and medial nuchal plates are fused. This state is independently derived in some species of *Synodontis*.

**(22-1):** The presence of five infraorbitals. All other mochokids possess four infraorbitals, wherein the lachrymal and second infraorbital are fused. These elements are unfused in the chiloglanidins.

**(30-2):** The total absence of teeth on the dorsal surface of the tooth cup. This state is independently derived in *Acanthocleithron* and some *Synodontis*.

**(32-1):** A very large maxilla.

**(34-2):** Multiple faces of the premaxillary tooth plates loosely joined to each other; in some species of *Chiloglanis* sensu stricto the tooth bearing faces are joined to each other only at the medial edge and the element is claw-shaped (34-3).

**(39-1):** A shortened autopalatine; in *Atopodontis*, *Atopochilus* and *Euchilichthys* the autopalatine is extremely shortened and block-like (39-2).

**(40-1):** The absence of cartilage at the posterior end of the autopalatine.

**(41-0):** The absence of a process along the medial edge of the hyomandibula. The hyomandibular process is also absent in *Mochokus*, which may be the plesiomorphic state for the Mochokidae.

**(42-2):** A round or spherical condyle along the dorsal edge of the hyomandibula. This state is independently derived in some species of *Synodontis*. Despite the shorter articulations seen in these taxa, the hyomandibula is still quite firmly attached. The ball-and-socket-like articulation in these taxa may serve to strengthen the articulation in the absence of a lengthy articulation or a pterotic spine (character 10).

**(46-1):** Fusion of the dorsohyal and ventrohyal. A reversal occurs in *Atopochilus* and *Euchilichthys*, where these elements are, in fact, separate.

**(47-1):** A posterohyal whose distal end is wider than the proximal end.

**(52-0):** A relatively small cleithral process.

**(55-1):** A mesocoracoid arch with no obvious bend along its length, which joins the posterior face of the vertical scapulo-coracoid lamina without any dorsal prominence.

This state is independently derived in *Mochokus*.

**(57-1):** A first pectoral-fin proximal radial whose proximal end shows both ventral and dorsal expansion. In some species of *Chiloglanis* sensu stricto there is no expansion at the proximal end of this element.

**(58-0):** A total lack of serrae along the anterior edge of the pectoral spine. Strong serrae are found along the anterior edge in all other mochokids.

**(59-1):** A marked reduction of serrae along the posterior edge of the pectoral spine.

*Atopochilus savorgnani* and *Euchilichthys dybowskii* show a reversal to strong serrae

along the posterior margin. In *Chiloglanis* sensu stricto serrae are totally absent along the posterior edge of the pectoral spine (59-2).

**(63-1):** A reduced number of dorsal-fin rays. Most members of this group possess six or five flexible rays in the dorsal fin. *Atopochilus savorgnani* and *Euchilichthys dybowskii* show a reversal to seven dorsal rays, as seen in most other mochokids. A reduced number of dorsal rays is independently derived in some *Microsynodontis* and *Mochokus brevis*.

**(65-0):** The presence of a pelvic splint. The pelvic splint is lost in *Atopodontis* and several species of *Chiloglanis* sensu stricto. Among mochokids, the pelvic splint is also found in some species of *Synodontis*.

**(66-2):** Anterior processes of the pelvic girdle, which terminate at approximately the same point.

**(67-1):** Anterior processes of the pelvic girdle joined by cartilage.

**(68-1):** A plate-like first anal-fin pterygiophore. A plate-like first anal-fin pterygiophore is lacking in *Chiloglanis micropogon* only.

**(75-0):** Anterior parapophyses of the compound centrum tightly joined to the ossified transcapular ligament. The anterior parapophysis is free and formed as an elastic spring apparatus in *Atopochilus* and *Euchilichthys*.

**(80-1):** An enlarged strut-like parapophysis of the 6<sup>th</sup> centrum without a free-floating rib.

**(86-5):** A greatly reduced number of mandibular canal pores. *Chiloglanis* sensu lato have no mandibular sensory-canal pores and the canal itself is absent. *Atopodontis*, *Atopochilus* and *Euchilichthys* have a canal and two pores on each side of the mandible (86-4).

**(87-4):** The incorporation of the outer mandibular barbels into an oral sucker.

**(88-4):** The incorporation of the inner mandibular barbels into an oral sucker.

The monophyly of the Chiloglanidinae is almost certain with regards to the taxa examined here. This group receives the strongest character support of any clade on the tree. A number of the synapomorphies for the group are related to the mouth. These synapomorphies represent the third and most significant shift in jaw and mouth morphology seen in the Mochokidae. This shift, however, is accompanied by changes throughout the body. I attribute changes throughout the body to an increased benthic existence and the dorsoventral depression seen in members of the group. The impetus behind this shift was probably not feeding ecology, but adaptation to living in fast-flowing water. Depression of the body and a sucker-like mouth are found in many benthic stream fishes (e.g. – balitorid loaches and loricariid catfishes). As a result of adaptations to benthic life, a shift in diet would be expected, but it was probably not the driving force behind the evolution of the oral disc. Not surprisingly, the largest chiloglanidins, which live in the fastest flowing waters and possess the most well-formed oral discs, have shifted to grazing.

#### **Unnamed group: Node H**

This group includes *Atopochilus*, *Euchilichthys*, *Atopodontis* and all *Chiloglanis* except *C. macropterus* and *C. sp. 'burundi'*. The group receives fair support from the tests for robustness including a bootstrap value of 71, a decay index of 4 and a branch length of 9 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(10-0):** The absence of a spinous projection on the ventral side of the pterotic. Within the Mochokidae the pterotic spine is also absent in *Mochokus*.

**(37-1):** Premaxillary teeth with spatulate tips. In some species of *Chiloglanis* sensu stricto there is a reversal to premaxillary teeth with pointed tips. Premaxillary teeth with spatulate tips are also found in *Acanthocleithron*.

**(62-0):** The absence of posterior dorsal-spine serrae. In at least two species of *Chiloglanis* sensu stricto posterior dorsal-spine serrae are present. Within the Mochokidae, posterior dorsal spine serrae are also absent in *Mochokus* and *Acanthocleithron*.

**(76-1):** Flap-like elaborations of the anterior parapophyses of the compound centrum. In *Atopochilus* and *Euchilichthys* the anterior parapophyses of the compound centrum are disc-shaped. In one species of *Chiloglanis* sensu stricto the anterior parapophyses are not at all elaborated.

The reality of the group at node H is tentative, but it presents some interesting results. The exclusion of *Chiloglanis macropterus* and *C. sp. 'burundi'* from this group is more interesting than the group itself. The obvious result of excluding these species is that *Chiloglanis* sensu lato is not recovered as monophyletic. At first glance *C. macropterus* presents as a very *Synodontis*-like *Chiloglanis*, so it is not surprising that aspects of the osteology and gross morphology have borne this out. Its basal position within the chiloglanidins was suspected from the outset. The placement of *C. sp. 'burundi'* was somewhat unexpected because it appears to be more similar to other *Chiloglanis*. Further research on the chiloglanidin group may require a new genus for

these species, given the nested position of *Atopodontis*, *Atopochilus* and *Euchilichthys* within *Chiloglanis* sensu lato.

### **‘Larger chiloglanidins’: Node I**

This group includes *Atopodontis*, *Atopochilus* and *Euchilichthys*. The group receives good support from the tests for robustness including a bootstrap value of 84, a decay index of 5 and a branch length of 8 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(1-1):** A distinct ventral mesethmoid process for articulation with the premaxillary tooth plates. None of the other taxa considered in this entire work possess such a process. Mo (1991), among others, recognized a similar process of the mesethmoid in various sucker-mouthed loricarioids. It seems likely that a ventral mesethmoid process (in both groups) is functionally correlated with a relatively mobile premaxilla for conforming to surfaces and rasping during feeding or clinging to surfaces. A ventral process of the mesethmoid was not found in any of the smaller sucker-mouthed mochokids of the genus *Chiloglanis*.

**(5-1):** A ventrally-hanging, laminar curtain along the anterolateral edge of the lateral ethmoid. This portion of laminar bone probably surrounds the muscle extensor tentaculi (De Puyselier, 2006). It seems likely that this curtain provides attachment for muscle and helps enhance muscular control of the oral disc.

**(31-3):** The presence of trowel-shaped tips on the auxiliary dentary teeth. The teeth are slightly different in *Atopochilus savognani* and *Euchilichthys dybowskii*; in these two species the tooth tips are simply spatulate (31-2). All other mochokids possessing S-

shaped teeth have tooth tips that are more or less pointed. The flattened nature of the tooth tips is most certainly correlated with diet.

**(39-2):** A block-like autopalatine.

**(86-3):** Two pores emanating from the mandibular canal on each side. All other chiloglanidins lack pores along the mandible and lack the mandibular canal altogether. The presence of a mandibular sensory canal represents a reversal to the plesiomorphic state for Mochokidae.

**(90-0):** A free orbit. Within the Mochokidae this state is independently derived in *Synodontis* and *Acanthocleithron*.

The monophyly of this group is well supported. All members of this group are fairly large when compared to species in the genus *Chiloglanis* sensu lato. In addition to the synapomorphies above, members of this group possess a rather large oral disc that is probably used for grazing. Stomach contents reveal that they consume large amounts of silt, algae and detritus; species of *Chiloglanis* sensu lato have a more variable diet. As a result of their grazing habits, species in this group possess rather long guts (up to 7 times TL) compared to other mochokids. Gut length is generally correlated with diet and the feature deserves further review throughout the Mochokidae.

### *Atopodontis*

*Atopodontis* is a monotypic genus. Based on the recovered topology, the following are autapomorphies for this species:

**(57-0)** Middle pectoral-fin radial without any expansions proximally. Within the Chiloglanidinae, proximal expansions are also absent in some species of *Chiloglanis* sensu stricto.

**(65-1)** Pelvic splint absent. Within the Chiloglanidinae, a pelvic splint is also absent in some species of *Chiloglanis* sensu stricto.

Consult Friel and Vigliotta (2008) for a complete diagnosis of the genus and discussion of its placement within the family.

### ***Atopochilus* + *Euchilichthys*: Node J**

This group includes species of *Atopochilus* and *Euchilichthys* only. The group receives very good support from the tests for robustness including a bootstrap value of 89, a decay index of 5 and a branch length of 8 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(46-0):** A separate dorsohyal and ventrohyal. Basal members of the chiloglanidin group show fusion of these elements. The separate nature of the elements here represents a reversal to the plesiomorphic state for the Mochokidae.

**(49-1):** Flattened, many-sided and laterally expansive basibranchials.

**(71-1):** Marginal, upper hypurals autonomous and not totally fused. This state is independently derived in a couple species of *Chiloglanis* sensu stricto. In the great majority of mochokids, including *Atopodontis*, the hypurals show complete fusion.

**(75-1):** A free and movable anterior parapophysis of the compound centrum or elastic spring apparatus. Basal members of the chiloglanidin do not have a free anterior

parapophysis. Freedom of the anterior parapophysis in this group represents a reversal to the plesiomorphic state for the Mochokidae.

**(76-1):** Elaborations at the distal end of the anterior parapophyses of the compound centrum. Among chiloglanidins, members of this group are the only ones to show plate-like elaborations distally, which represents a reversal to the plesiomorphic state for the Mochokidae.

**(77-1):** An obvious bend in the elastic spring apparatus, without any well-formed anteriorly directed processes.

**(92-1):** A moderately reduced gas bladder. Most chiloglanidins show extreme reduction of the gas bladder. The moderate size of the gas bladder in these taxa is independently derived in two species of *Chiloglanis* sensu lato.

Support for this group is very strong, but the monophyly of the genera involved is less likely. Nested placement of *Atopochilus savorgnani* makes *Euchilichthys* a paraphyletic group. The monophyly of *Atopochilus* was not testable here, because only one species was included. The distinction between *Atopochilus* and *Euchilichthys*, if any, is subtle. In a treatment of the larger chiloglanidins, *Atopochilus* and *Euchilichthys* will need to be redescribed because one or both is paraphyletic.

The exclusion of *Atopodontis adriaensi* with respect to the members of this group is an important result. *Atopodontis* shares several features with *Atopochilus* and *Euchilichthys*, but it also shows many of the characteristics seen in *Chiloglanis* species. Its placement as sister to *Atopochilus* + *Euchilichthys* supports the idea that this species should belong to a distinct genus.

### **Unnamed group: Node K**

This group includes *Atopochilus savorgnani* and *Euchilichthys dybowskii*. The group receives good support from the tests for robustness including a bootstrap value of 81, a decay index of 2 and a branch length of 3 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(31-2):** Auxiliary dentary teeth with spatulate tips. None of the other taxa possessing auxiliary dentary teeth show spatulate tips.

**(59-0):** Posterior edge of the pectoral spine with well-developed serrae. Among the chiloglanidins, these are the only two species possessing well developed posterior pectoral spine serrae. Well developed serrae along the posterior edge of the pectoral spine are also found in many species of mochokids outside of the chiloglanidin group.

**(63-0):** The presence of 7 or more dorsal-fin rays. Among chiloglanidins, these are the only taxa consistently possessing this relatively high number of rays.

Having examined most species of *Atopochilus* and *Euchilichthys*, I expect that *Euchilichthys dybowskii* is mistakenly included in the genus *Euchilichthys*. Movement to the genus *Atopochilus* would resolve the paraphyly of *Euchilichthys* here. The generic identity of this species will be most effectively handled in a review of all larger chiloglanidins.

### **‘*Chiloglanis sensu stricto*’: Node L**

This group includes all *Chiloglanis* except *C. macropterus*. In considering Analysis 1, the species called *C. sp. 'burundi'* may be excluded as well. The group receives poor support from the tests for robustness including a bootstrap value of 57, a decay index of 1 and a branch length of 3 in the consensus tree optimized under ACCTRAN. The following are recovered as synapomorphies for the group:

**(51-2):** A reduced number of branchiostegal rays. Members of this group display 5 or 6 branchiostegal rays. This reduced number of branchiostegal rays is independently derived in a few species of *Synodontis*, in *Mochokiella* and in *Mochokus niloticus*.

**(59-2):** A total lack of serrae along the posterior edge of the pectoral spine.

**(78-0):** Posterior parapophysis of the compound centrum broadly joined to the anterior parapophysis, such that they form a shield dorsally over the gas bladder.

The reality of this grouping to the exclusion of *Chiloglanis macropterus* and *C. sp. 'burundi'* is tentative at best. Despite the topology that was recovered, members of the genus *Chiloglanis* sensu lato do share a small number of derived features. The most compelling of these is the total lack of a mandibular sensory canal. According to the current topology, the canal would have to be lost for all chiloglanidins and then regained in the group composed of *Atopodontis*, *Atopochilus* and *Euchilichthys*; this seems somewhat unlikely.

The genus *Chiloglanis* sensu lato requires much revision. As shown, a new genus may be required to accommodate *C. macropterus* and related species. In addition, several undescribed species that would be most appropriately placed in this genus are already

known. These facts, and the rather large number of valid species, will most likely require the description of new genera. Studies and revisions of *Chiloglanis* are being undertaken.

## CONCLUSIONS

Mochokid catfishes are most often exemplified by the genus *Synodontis*. Its members are widespread, numerous and fairly large. Furthermore, among catfishes, species of *Synodontis* are rather charismatic. Yet, despite these qualities, the genus shows surprisingly little morphological evolution relative to other mochokids. And so, having *Synodontis* as the ‘stand-in’ for the Mochokidae gives a false sense of the group’s diversity. The extensive morphological evolution in the Mochokidae becomes much more evident and impressive when they are examined as a whole.

In examining the group as a whole, one thing becomes clear; morphological evolution in the Mochokidae is dominated by changes in the oral jaws, mouth and suspensorium. From the results here, I perceive three major shifts in the evolution of the mochokid mouth. The first of these helps to define the family (node A); the second defines a group consisting of *Microsynodontis*, *Synodontis* and the chiloglanidins (node D); the third defines the chiloglanidins alone (node G). Not surprisingly, the nodes corresponding to these shifts in jaw morphology are well supported in the analyses.

Despite support for these groups, from characters of the jaw (and beyond), it is evident that the systematics of the Mochokidae are 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 that will require the

description of at least one new genus; substructure within the large genus *Synodontis* is still largely unknown, but for now, *Hemisynodontis membranaceous* and *Brachysynodontis batensoda* should be placed within *Synodontis*; *Euchilichthys* is paraphyletic and will need to be redescribed along with *Atopochilus*; the relationship of *Microsynodontis* to other mochokids is unresolved; and finally, the relationships of *Mochokus*, *Mochokiella* and *Acanthocleithron* at the base of the mochokid group are best described as unresolved. In short, taxonomy and systematics of the Mochokidae remain incomplete. Several new species are already awaiting description and many more are likely to be discovered. 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*. Results of this work agree with prior studies in the relationship of the Mochokidae to the Doradidae and Auchenipteridae, but support is rather low. This is due, in part, to the inclusion of the newly hypothesized sister groups to the Mochokidae, the Amphiliidae and Malapteruridae. There seems to be abundant evidence for a possible relationship between these families and the Mochokidae. 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

- 1a.** Lips and barbels modified into oral sucker; cleithral process small (Fig. 22C); 5 infraorbitals (Fig. 2C and Fig. 4B); posterior pectoral-spine serrae large, small or altogether absent; head and body depressed .....**2**
- 1b.** Lips and barbels not modified into oral sucker; cleithral process quite large (Fig. 22B); 4 infraorbitals (Fig. 2B and Fig. 4A); posterior pectoral-spine serrae usually large; head and body depressed or not .....**6**
- 2a.** Mandibular teeth bunched (in bouquet) or in one or two discrete rows; S-shaped auxiliary dentary teeth pointed (Fig. 10D, E, F); eyes without free border; mandibular sensory-canal pores absent; usually less than 10cm TL; 5 or 6 dorsal-fin rays; posterior dorsal-spine serrae present or absent; caudal fin rounded, truncate or forked .....**3**
- 2b.** Mandibular teeth in more than two discrete rows; S-shaped auxiliary dentary teeth spatulate or trowel-shaped (Fig. 10A, C); eyes with free border; 2 mandibular sensory-canal pores present on each side; attaining lengths greater than 10cm TL; 6 or 7 dorsal-fin rays; posterior dorsal-spine serrae absent; caudal fin gently forked .....**4**
- 3a.** Wide nuchal shield; small posterior pectoral-spine serrae present; 7 branchiostegal rays; 7 or 8 pectoral-fin rays .....***Chiloglanis* in part (*C. macropterus* and *C. sp. 'burundi'*)**
- 3b.** Wide or narrow nuchal shield (Fig. 4B); posterior pectoral-spine serrae absent; 5 or 6 branchiostegal rays; 8 or 9 pectoral-fin rays .....***Chiloglanis* in part (all other *Chiloglanis*)**

**4a.** Small anteriorly-directed pocket underneath lower lip produced by folds of skin

.....*Atopodontis*

**4b.** Small anteriorly-directed pocket underneath lower lip absent .....**5**

**5a.** Mandibular teeth spatulate and unicuspid (Fig. 10C); large posterior pectoral-spine serrae; 8 pectoral rays; 7 dorsal rays; one or only a few pores at sites along the cephalic sensory canals .....*Atopochilus*

**5b.** Mandibular teeth with lengthwise keel creating trowel shape and sometimes bicuspid from wear (Fig. 10A); small posterior pectoral-spine serrae; 8 or 9 pectoral rays; 6 or 7 dorsal rays; several pores at various sites along the cephalic sensory canals

.....*Euchilichthys*

**6a.** S-shaped auxiliary dentary teeth present (Fig. 10A, C, D, E, F); premaxillary teeth differentiated by shape and size front to back .....**7**

**6b.** S-shaped auxiliary dentary teeth absent (Fig. 10B); premaxillary teeth showing little, if any, differentiation from front to back .....**8**

**7a.** From 8cm up to 80cm TL; eyes with free border; 17 principal caudal-fin rays (only 13 in *Synodontis contractus*); tail forked; 7, 8 or 9 pectoral-fin rays (usually 8); outer mandibular barbels with single, gracile branches at each point along length or not (Fig.

30A, B) .....*Synodontis*

**7b.** Usually less than 8cm TL; eyes without free border; 12 or 14 principal caudal-fin rays; tail truncate or rounded; 6 or 7 pectoral-fin rays (usually 6); outer mandibular barbels with single, gracile branches at each point along length (Fig. 30A)

.....*Microsynodontis*

**8a.** Rayed adipose fin; 5 or 6 pectoral-fin rays; 2 mandibular sensory-canal pores on each side; 6 or 7 dorsal-fin rays; inner mandibular barbels with single, gracile branches at each point along length (Fig. 30A) .....*Mochokus*

**8b.** Adipose fin without rays; 7 or 8 pectoral-fin rays; 3 mandibular sensory-canal pores on each side; 7 dorsal-fin rays; inner mandibular barbels with single, gracile branches at each point along length (*Mochokiella*) or with multiple, thick branches at each point along length (Fig. 30A, B) .....**9**

**9a.** Seven pectoral-fin rays; posterior dorsal-spine serrae present; 7 + 8 principal caudal-fin rays; tips of mandibular teeth conical and pointed; inner mandibular barbels with single, gracile branches at each point along length (Fig. 30A); dorsal surface of the head and nuchal shield smooth; opercle bearing obvious spine in males; pointed cleithral process; cleithrum without spine in males; free orbit absent; gill openings restricted to sides of the head .....*Mochokiella*

**9b.** Eight pectoral-fin rays; posterior dorsal-spine serrae absent; 8 + 9 principal caudal-fin rays; tips of mandibular teeth spatulate (Fig. 10B); inner mandibular barbels with multiple, thick branches at each point along length (Fig. 30B); dorsal surface of the head and nuchal shield covered by large ridges and spinous projections, opercle without obvious spine in males; rounded or blunt cleithral process; cleithrum bearing spine in males; free orbit present; gill openings open to isthmus .....*Acanthocleithron*

#### ACKNOWLEDGEMENTS

This work was conducted at the Cornell University Museum of Vertebrates for a Master's thesis at Cornell University. That being said, I must first thank my committee members, J. Friel, A. McCune and W. Bemis. Without their support this work would not have been possible.

Next, I thank the institutions that provided materials and services to complete this research. From the American Museum of Natural History I thank M. Stiassny, B. Brown R. Schelly. From the Academy of Natural Sciences I thank M. Sabaj Pérez, J. Lundberg and K. Luckenbill. From the British Museum of Natural History I thank J. Maclaine and O. Crimmen. From the California Academy of Sciences I thank D. Catania. From the Museum of Comparative Zoology I thank K. Hartel. From the Royal Museum for Central Africa I thank M. Parrent, E. Vreven and J. Snoeks. From the South African Institute of Aquatic Biodiversity I thank R. Bills and S. Terry. From the University of Michigan, Museum of Zoology I thank D. Nelson. From the National Museum of Natural History I thank J. Williams, S. Raredon and K. Murphy. From the University of Texas at Austin and the NSF-funded Digimorph project, for the very successful CT-scans of three specimens, I thank J. Maisano and J. Humphries. I would be remiss if I did not thank the entire staff at the Cornell University Museum of Vertebrates. In particular, I must thank C. Dardia, who was abundantly patient with my use of museum space and resources.

Finally, this work was supported by a research assistantship from the All Catfish Species Inventory (ACSI), which was funded by the National Science Foundation (NSF DEB 0315963). I am extremely grateful for the support from the ACSI project during my time as a student and beyond.

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## APPENDIX 1: MATERIALS EXAMINED

### AMPHILIIDAE

*Amphilius cryptobullatus*, CU 91076, 1 DS, 6 ALC, Zambia, Itabu River at bridge on Nkoshya-Mukunsa road; CU 91067, 2 C&S, 77 ALC, Zambia, Lufubu River Falls below bridge at Chipili on Mansa-Mununga road; CU 91075, 44 ALC, Zambia, Kundabwika Falls on Kalunguishi River. *Amphilius jacksonii*, CU 90468, 2 C&S, 40 ALC, Tanzania, Moyowosi River at bridge near Nyantwiga; CU 91055, 2 C&S, 27 ALC, Zambia, Luongo River at Mukonshi Bridge on Mwenda-Kawambwa road. *Amphilius longirostris*, CU 89988, 5 ALC, Cameroon, Ngonebok Creek on road from Ebolowa to Lolodorf; CU 86325, 2 C&S, 16 ALC, Gabon, Okano River on rapids ~0.5 km south of the village of Na. *Amphilius nigricaudatus*, CU 80203, 2 C&S, 20 ALC, Gabon, Okoloville--Route from Franceville to Oroudja. *Amphilius uranoscopus*, CU 90470, 2 C&S, 11 ALC, Tanzania, Malagarasi River at Igamba Falls and below falls. *Andersonia leptura*, CU 91440, 1 C&S, 8 ALC, Central African Republic, Gribingui River at Kanga Bando. *Belonoglanis tenuis*, CU 91536, 2 C&S, 54 ALC, Central African Republic, Tomi River at bridge in Sibut; CU 91534, 8 ALC, Central African Republic, Oubangui River downriver from Mobaye. *Doumea alula*, CU 91611, 1 DS, Central African Republic, Rapids on Mbourou River within AXMIN Ndassima mine concession area; CU 91472, 2 ALC, Central African Republic, Rapids on Kotto River north of Mingala; CU 91046, 2

C&S, 69 ALC, Zambia, Kapuma Falls on Mutoloshi River near Mporokoso. *Doumea gracila*, CU 89991, 2 C&S, 34 ALC, Cameroon, Lobé rapids between ocean and bridge. *Doumea typica*, CU 80360, 1 DS, Gabon, Ntem River at confluence with Nyé River, under bridge near Bikondom. *Phractura lindica*, CU 91606, 4 C&S, 181 ALC, Central African Republic, Rapids on Kotto River north of Mingala; CU 91607, 16 ALC, Central African Republic, Liwa River; CU 88356, 2 C&S, 17 ALC, Republic of Congo, Large Rapids on Mambili River, Odzala National Park. *Phractura longicauda*, CU 80273, 1 C&S, 7 ALC, Gabon, Okoloville--Creek crossing road, downstream of road crossing. *Tetracamphilius notatus*, CU 91422, 1 C&S, 5 ALC, Central African Republic, Tomi River at bridge in Sibut. *Zaireichthys sp. 'tanzania'*, CU 90475, 3 C&S, 42 ALC, Tanzania, Moyowosi River at bridge near Nyantwiga. *Zaireichthys sp. 'zambia'*, CU 91036, 4 C&S, 165 ALC, Zambia, Luongo River at Mukonshi Bridge on Mwenda-Kawambwa road; CU 91040, 61 ALC, Zambia, Kanchibiya Stream at bridge on Kasama-Mpika road.

#### 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 & 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, Small cove on S side of river, SW of Pta. Cabrian, bet. Pt. Ordaz & Barrancas, 152.4 nm from sea buoy. *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.

#### AUSTROGLANIDIDAE

*Austroglanis sclateri*, CU 90981, 1 C&S, 1 DS, 7 ALC, South Africa, Kraai River at the Barkly East-Lady Grey road bridge (Lappa Munik Bridge).

#### CLARIIDAE

*Clarias stappersii*, CU 91880, 1 DS, Zambia, Bridge at Musola on Musola River; just outside Kasanka National Park.

#### CLAROTEIDAE

*Auchenoglanis occidentalis*, CU 90832, 1 DS, Republic of Congo, Lékoli River just above Lékénie River, Odzala National Park. *Chrysichthys mabusi*, CU 91695, 2 C&S, 30 ALC, Zambia, Mambilima Falls on Luapula River. *Chrysichthys nigrodigitatus*, CU 53958, 2 C&S, 38 ALC Ghana, Mouth of Volta R. *Parauchenoglanis balayi*, CU 80552, 1 DS, Gabon, Mevam Creek just West of Miong Creek Between Edama III and Agnizok

II; CU 83280, 2 C&S, 30 ALC, Gabon, Lower Balé Creek below bridge; CU 80654, 15 ALC, Gabon, Mevam Creek just West of Miong Creek Between Edama III and Agnizok II. *Parauchenoglanis punctatus*, CU 91865, 1 DS, Central African Republic, Mbourou River at AXMIN Ndassima Camp; CU 80568, 2 C&S, 18 ALC, Gabon, Motoboi Village; Kiené Creek; CU 90232, 1 DS, Republic of Congo, Lékoli River, Odzala National Park

#### DORADIDAE

*Agamyxis albomaculatus*, CU 91905, 1 DS, unspecified, unspecified; CU 80966, 2 C&S, 13 ALC, Venezuela, Cano Anabata mouth in Rio Orinoco near buoy mile 117 to 250 m upstream where Cano forks north of Isla Portuguesa. *Centrodoros brachiatus*, CU 79413, 1 DS, Brazil, Unspecified; CU 81225, 1 DS, Brazil, Rio Solimões below confluence with Rio Japura; CU 81235, 4 ALC, Brazil, Amazonas above Para. *Centrodoros sp.*, CU 81181, 1 C&S, Brazil, Rio Negro. *Hemidoros sp.*, CU 90916, 1 DS, Brazil, Rio Negro below Branco. *Leptodoros sp.*, CU 90915, 1 DS, Brazil, Rio Branco above Rio Negro. *Oxydoros niger*, CU 73180, 1 ALC, Brazil, unspecified; CU 81237, 1 DS, Brazil, Solimoes R. below Jura; CU 79380, 1 DS, unspecified, unspecified; CU 81207, 1 C&S, unspecified, unspecified. *Platydoros costatus*, CU 81198, 1 C&S, unspecified, unspecified. *Pterodoros rivasi*, CU 79376, 1 DS, unspecified, unspecified; CU 79407, 1 DS, Venezuela, unspecified. *Rhinodoros sp.*, CU 81184, 3 C&S, Brazil, unspecified. *Trachydoros 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, Oneida Lake, Shackelton Point, Billington Bay (exposed cove). *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. mi. point 203.9; at Belleville Locks and Dam. *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, Small creek crossing road to Hevecam Rubber Plantation at Nyé été, Ndingui creek; CU 80551, 1 DS, Gabon, Diengué Creek near village of St. Martin; CU 81646, 1 ALC, Gabon, Ogouee R. *Malapterurus microstoma*, CU 91879, 1 DS, Central African Republic, Baïdou River, above and below pontoon crossing. *Malapterurus monsembeensis*, CU 90839, 1 DS, Republic of Congo, Lékoli River, Odzala National Park; CU 90961, 1 DS, Republic of Congo, Lékoli River, Odzala National Park. *Malapterurus sp.*, AMNH 90265, 1 DS, unspecified, unspecified.

#### MOCHOKIDAE

*Atopodontis adriaensi*, CU 92320, 1 C&S, 6 ALC, Gabon, Rapids at Loa-Loa; MRAC 049-P-0334, 1 ALC, Gabon, Loa Loa, Makokou, Ivindo riv. *Acanthocleithron chapini*, AMNH 6548, 1 ALC, Congo, volta R. backwater pond of Fishery Dept. at Agorkpo; AMNH 6575, 1 ALC, Congo, Avakubi, Ituri River; MRAC 138179, 1 ALC, Congo Belge, riv. Litorumbu. *Atopochilus savorgnani*, CU 86329, 1 C&S, 1 DS, 5 ALC, Gabon, Okano River on rapids ~0.5 km south of the village of Na; CU 80738, 4 ALC, Gabon, Ntem River just in front of Auberge d'Ayengbe; MRAC 95-030-P-1411-1427, 1 C&S, 16 ALC, Cameroon, riv. Ntem, chutes de Memve'élé. *Brachysynodontis batensoda*, USNM 230106, 1 C&S, 6 ALC, Nigeria, Nigeria: Argungu. Main Sokoto R. At Festival Site; MRAC P.168272-168276, 1 C&S, 5 ALC, Senegal, Mbane, lac de Guiers. *Chiloglanis carnosus*, MCZ 50541, 3 C&S, Zaire, Zaire River mainstream near Inga hydroelectric dam; MCZ 50241, 21 ALC, Zaire, Zaire River mainstream near Bulu, W of Luozi. *Chiloglanis congicus*, MCZ 50149, 2 ALC, Zaire, Zaire River at Gombe or Ngombe, about 20 km W of Kinshasa. Rapids in the mainstream; MCZ 50540, 3 C&S, 10 ALC, Zaire, Zaire River mainstream near Inga hydroelectric dam. *Chiloglanis disneyi*, USNM 303505, 2 C&S, 8 ALC, Cameroon, Cameroon: Akpa-Yafe System: Streams and Rivers of South-West Korup; Cataracts 200 m Below Origin of 'R' (Transect). *Chiloglanis macropterus*, CU 91007, 2 C&S, 111 ALC, Zambia, Luongo River at Mukonshi Bridge on Mwenda-Kawambwa road. *Chiloglanis micropogon*, CAS 60803, 2 C&S, 33 ALC, Congo, Trib. to Riviere Luala, 26 km north of Kibunzi; USNM 303409 10 ALC, 2 C&S, Cameroon, Cameroon: Upper Ndian System: Streams and Rivers of South-East Boundary of Korup; Main Ndian R. At Bridge Crossing Into Korup; CU 91434, 3 C&S, 81 ALC, Central African Republic, Gribingui River at Kanga

Bandoro. *Chiloglanis cf. neumanni*, UMMZ 199975, 1 C&S, Zambia, Trib to Lwombe River, 50 mi SSW of Mbala on road to Kasama, 9 mi S Senga Hill, 5 mi N of Nondo; Lwonde-\*\* *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, Points on Southern Munaya River draining Northern Korup; Basep River junction with Munaya River Station P10; USNM 304263, 1 C&S, Cameroon, Cameroon: Cross System: Collecting Points On Southern Munaya R. Draining Northern Korup; Basep R. Junction With Munaya. *Chiloglanis sp. 'burundi'*, CU 90387, 1 C&S, 10 ALC, Burundi, River Rugoma; at point South of route from Kinyinya to Rumpungwe. *Chiloglanis sp. 'igamba'*, CU 90576, 2 C&S, 39 ALC, Tanzania, Malagarasi River at Igamba Falls and below falls. *Chiloglanis sp. 'kalungwishi'*, CU 91005, 1 C&S, 10 ALC, Zambia, Below Kabwelume Falls on Kalungwishi River. *Chiloglanis sp. 'ntumbachushi'*, CU 91017, 1 C&S, 24 ALC, Zambia, Below Ntumbachushi Falls on Ng'ona River. *Euchilichthys dybowskii*, CU 91376, 1 C&S, 2 ALC, Central African Republic, Baïdou River, above and below pontoon crossing. *Euchilichthys geuntheri*, MCZ 50538, 1 C&S, 26 ALC, Zaire, Zaire River mainstream near Inga hydroelectric dam; SU 54221, 1 DS, Democratic Rep. of the Congo, Kisangani (Stanleyville). *Euchilichthys royauxi*, CU 91612, 1 DS, Central African Republic, Fishes purchased in fish markets in Bangui; CU 91614, 1 DS, Central African Republic, Fishes purchased in fish markets in Bangui; CU 91764, 1 DS, Central African Republic, Purchased from fishermen in Mobaye; CU 91828, 1 DS, Central African Republic, Purchased from fishermen in Mobaye; CU 91380, 2 C&S, 50 ALC, Central African Republic, Oubangui

River shoreline at uncompleted bridge at Mobaye; CU 91379, 4 ALC, Central African Republic, Kotto River at Mingala. *Euchilichthys sp.*, AMNH 6472, 1 DS, Congo, Stanleyville, Junction Lualaba River with Congo River. *Euchilichthys sp. 'congo'*, SAIAB 74306, 2 C&S, 13 ALC, Congo, Lower Congo Rapids at Brazzaville.

*Euchilichthys sp. 'zambia'*, SAIAB 40150, 2 C&S, 16 ALC, Zambia, Rapids near Chinsala pontoon. *Hemisynodontis membranaceous*, CU 51996, 1 ALC, Ghana, Volta R. backwater pond of Fishery Dept. at Agorkpo; SU 63500, 2 ALC, Ghana, Bosua-Atimpoku-Senchi Ferry; CU 89007, 1 ALC, 1 DS, unspecified, unspecified; USNM 313584, 1 C&S, Ghana, Lanto, Ghana; USNM 086639, 1 ALC, Niger, Mouth of Guran River. *Microsynodontis emarginatus*, CU 80567, 1 C&S, 28 ALC, Gabon, Motoboi I Village; Kiené Creek. *Microsynodontis vigilis*, CU 80133, 1 C&S, 16 ALC, Gabon, Branch of Nzorbang creek N. of village of some name, ~ 12 km N. of Lambaréné.

*Microsynodontis sp. 'odzala'*, CU 88266, 2 C&S, 42 ALC, Republic of Congo, Lékénie River at Mboko dock, Odzala National Park. *Mochokiella paynei*, AMNH 215709, 1 ALC, Sierra Leone, River Kasini (Kasenay Stream), Taiama Region; BMNH 1979.8.22.1, 1 ALC, Sierra Leone, Kassewe Forest Reserve; CU 91904, 1 ALC, Sierra Leone, Specific Locality Unknown; BMNH 1979.8.22.2-3, 2 ALC, Sierra Leone, Kassewe Forest Reserve; CU 91903, 2 C&S, 4 ALC, Sierra Leone, Specific Locality Unknown; AMNH 58398, 2 C&S, unspecified, unspecified. *Mochokus brevis*, BMNH 1981.2.17.1941-1947, 5 of 7 ALC, Niger, Malamfatori, northwest shore of Lake Chad; BMNH 1907.12.2.2529-2542, 1 C&S, 14 ALC, Sudan, Fashoda, White Nile. *Mochokus niloticus*, AMNH 228532, 1 ALC, Central African Republic, Control zone of Sangba, Bamingui River confluence avec la Ivingou River, 60 kilometers aval of Sangba Base;

AMNH 228721, 1 ALC, Central African Republic, Control of Sangba, N'goumbiri River;  
AMNH 230647, 1 ALC, Central African Republic, Manovo-Gounda Saint Floris  
National Park, Vakaga River, Tributary to Bahr Kameur; CU 91384, 1 ALC, Central  
African Republic, Gribingui River at bridge in Kanga Bandoro; CU 91385, 4 ALC,  
Central African Republic, Gribingui River at Kanga Bandoro; CU 91386, 2 C&S, 5 ALC,  
Central African Republic, Gribingui River at Kanga Bandoro; AMNH 55403, 2 ALC,  
Egypt, Regulators at Luxor; AMNH 55113, 2 ALC, Guinea, Kankan, Milo River; MRAC  
P.119455-119456, 2 C&S, Guinea, Kankan, riv. Milo. *Synodontis acanthomias*, CU  
91613, 1 DS, Central African Republic, Purchased from fishermen in Mobaye; CU  
91388, 4 ALC, Central African Republic, Oubangui River shoreline at uncompleted  
bridge at Mobaye; AMNH 235705, 1 C&S, Republic of Congo, Downstream from  
Brazzaville, shallow pool, channel leading to Congo River; CU 89763, 1 DS, Republic of  
Congo, Mambili River, Odzala National Park; CU 90963, 1 DS, Republic of Congo,  
Mambili River, Odzala National Park; AMNH 235705, 7 ALC, Republic of Congo,  
Downstream from Brazzaville, shallow pool, channel leading to Congo River; MCZ  
50152, 4 C&S, Zaire, Zaire River at Gombe or Ngombe, about 200 km W of Kinsasha.  
*Synodontis acanthoperca*, CU 80105, 1 C&S, 7 ALC, Gabon, Louétsi River just below  
falls at Bongolo Hydroelectric Facility; CU 89005, 1 ALC, Gabon, Ogooué R. at and  
below the Rapids of Masuku (Massoukou); CU 89006, 2 ALC, Gabon, Ogooué R. at and  
below the Rapids of Masuku (Massoukou); CU 91830, 10 ALC, Gabon, Ogooué R. at  
and below the Rapids of Masuku (Massoukou). *Synodontis alberti*, CU 91393, 2 C&S,  
31 ALC, Central African Republic, Oubangui River upriver from Bangui; AMNH  
235718, 1 C&S, 4 ALC, Republic of Congo, West bank of Congo River, ca. 1 kilometer

upstream of Foulakari River, in channel (ca. 70 meters long) between rocks. *Synodontis angelicus*, AMNH 90250, 1 DS, unspecified, unspecified; AMNH 94488, 1 DS, unspecified, unspecified. *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 below bridge. *Synodontis clarias*, AMNH 19678, 1 C&S, Central African Republic, Birao; USNM 229746, 1 C&S, 8 ALC, Nigeria, Nigeria: North-Western, Pumping Station At Bridge Over Rima R., Illela Rd. *Synodontis congicus*, CU 91397, 1 C&S, 18 ALC, Central African Republic, Oubangui River upriver from Bangui; CU 88252, 1 ALC, Republic of Congo, Lékoli River, Odzala National Park; CU 88584, 2 C&S, 39 ALC, Republic of Congo, Lékoli River, Odzala National Park. *Synodontis decorus*, CU 91398, 1 C&S, 10 ALC, Central African Republic, Oubangui River shoreline at uncompleted bridge at Mobaye; AMNH 55626, 1 DS, unspecified, unspecified. *Synodontis eupterus*, 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, Togble-Kope, Togo - Zio R. At Togble-Kope Above and Below Bridge On Main Road; AMNH 90242, 1 DS, unspecified, unspecified. *Synodontis haugi*, CU 80694, 1 DS, Gabon, Ogooué River at rocky point on Lambaréné Island facing Schweitzer Hospital; CU 86528, 1 ALC, Gabon, Just off east side of Lambarene Island in main channel of Ogooué River; CU 86400, 4 ALC, Gabon, Just off east side of Lambarene Island in main channel of Ogooué River. *Synodontis katangae*, CU 91003, 1 C&S, 10 ALC, Zambia, Samfa Rapids at pontoon on Chambeshi River *Synodontis longirostris*, CU 91861, 1 DS, Central African Republic, Fishes purchased in 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 mainstream near Bulu, W of Luozi; SAIAB 74303, 2 ALC, Congo, Lower Congo Rapids at Brazzaville.

*Synodontis macrostigma*, UMMZ 200089, 2 DS, Zambia, Kafue River at Ceres, river km 86 above Kafue dam site, 14 km NNE Mazabuka, Southern Prov; Middle Zambezi drainage; UMMZ 200075, 8 ALC, Zambia, Kafue River at Ceres, River km 86 above Kafue Dam Site, 14 km NNE Mazabuka; Middle Zambesi River dr. *Synodontis nigrita*, USNM 230125, 1 C&S, 23 ALC, Nigeria, Nigeria: Bunza. Lower Reaches of 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, Odzala National Park; AMNH 55166, 1 C&S, unspecified, Congo Basin. *Synodontis njassae*, USNM 266765, 1 C&S, Malawi, Malawi: Lake Malawi: Nkhata Bay North Bay Along Peninsula, ca 15 m From Its Tip; USNM 261879, 1 C&S, 9 ALC, Malawi, Malawi: Lake Malawi: Thumbi I. West, Bay Facing N At W Tip of N Shore. From Offshore Rocks To ca. Midway Along W Shore of Bay.

*Synodontis notatus*, CU 91418, 1 ALC, Central African Republic, Oubangui River upriver from Bangui; CU 91875, 1 DS, Central African Republic, Fishes purchased in fish markets in Bangui. *Synodontis ocellifer*, USNM 230099, 1 C&S, Niger, Niger: Middle/Upper Niger At Niamey (Republic of Niger). *Synodontis ornatipinnis*, ANSP 55983, 1 C&S, Angola, Quanza River, at Chouzo village, 25mi. N of new Benguella Railroad crossing of Quanza River. *Synodontis pleurops*, CU 91415, 1 C&S, 6 ALC, Central African Republic, Oubangui River upriver from Bangui; CU 91876, 1 DS, Central African Republic, Mbourou River at AXMIN Ndassima mine camp; CU 87571, 1

ALC, Republic of Congo, Large Rapids on Mambili River, Odzala National Park; CU 90919, 1 DS, unspecified, unspecified. *Synodontis rebeli*, CU 90827, 1 DS, Cameroon, Eololoma Island, Chutes of Nachtigal; CU 89984, 6 ALC, Cameroon, Eololoma Island, Chutes of Nachtigal. *Synodontis schall*, UMMZ 241265, 2 DS, Ethiopia, Omo River, near Kibish (southwestern Ethiopia); USNM 229774, 1 C&S, 13 ALC, Nigeria, Nigeria: Bahindi, ca 15 km From Confluence of Sokoto and Niger; USNM 229806, 1 C&S, Nigeria, Nigeria: North-Western, Pumping Station At Bridge Over Rima R., Illela Rd; 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, At Daboya; USNM 229795, 3 ALC, Nigeria, Nigeria: Argungu. Main Sokoto R. At Festival Site. *Synodontis sp.*, AMNH 236078, 3 C&S, Sierra Leone, Tiwai Island, River Moa, local womens posion station opposite visitors center boat landing, small pool blocked off from main channel by rocks, boulders; 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, Rocks along Lake Mwueru shoreline. *Synodontis victoriae*, CAS 211279, 4 ALC, Kenya, Two localities: 1) Lake Victoria, Winam Gulf; 2) Creeks in Nandi Hills; UMMZ 187335, 1 DS, 6 ALC, Uganda, Lake Victoria, Hannington Bay about 12 mi. easterly from Jinja; Nile River drainage. *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. flood plain, Ngodo Pan.

#### PANGASIIDAE

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

#### PIMELODIDAE

*Calophysus macropterus*, CU 79415, 1 DS, Venezuela, Rio Cunaviche.

#### PSEUDOPIMELODIDAE

*Pseudopimelodus apurensis*, CU 81223, 1 DS, Venezuela, Rio Apure.

#### SCHILBEIDAE

*Schilbe grenfelli*, CU 87558, 1 DS, Republic of Congo, Mambili River, Odzala National Park. *Schilbe intermedius*, CU 88310, 1 DS, Republic of Congo, Mambili River, Odzala National Park. *Schilbe laticeps*, CU 86377, 1 C&S, 16 ALC, Gabon, Lower Balé Creek below bridge.

### APPENDIX 2: DATA MATRIX

#### FIGURE CAPTIONS

Figure 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.

Figure 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.

Figure 3. Ventral view of neurocranium of A) *Ictalurus punctatus*; CU 79403, B) *Synodontis acanthomias*; CU 91613 and C) *Euchilichthys royauxi*; CU 91614. Hashed mark represents the boundary of the gas bladder.

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

Figure 5. Ventral view of neurocranium of *Chiloglanis micropogon*; CU 91434. Hashed mark represents the boundary of the gas bladder.

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

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

Figure 8. Dorsal view of mandible of A) *Ictalurus punctatus*; CU 79403 and B)

*Synodontis acanthomias*; CU 91613.

Figure 9. Anterior view of mandible of A) *Synodontis acanthomias*; CU 91613 and B)

*Euchilichthys royauxi*; CU 91614.

Figure 10. Mochokid auxiliary dentary teeth in lateral view, tips shown in anterior view;

A) *Euchilichthys*, B) *Acanthocleithron*, C) *Atopochilus*, D) *Microsynodontis*, E)

*Chiloglanis* and F) *Synodontis*.

Figure 11. Ventral (A) and medial (B) views of premaxillary tooth plate of *Ictalurus*

*punctatus*; CU 79378, right side.

Figure 12. Ventral (A) and medial (B) views of premaxillary tooth plate of *Synodontis*

*acanthomias*; CU 89763, right side.

Figure 13. Dorsal (A), ventral (B) and medial (C) views of premaxillary tooth plate of

*Euchilichthys royauxi*; CU 91614, right side.

Figure 14. Dorsal (A), ventral (B) and medial (C) views of premaxillary tooth plate of

*Chiloglanis micropogon*; CU 91434, right side.

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

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

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

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

Figure 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.

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

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

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

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

Figure 24. Ventral view of pelvic girdle of A) *Ictalurus punctatus*; CU 81105, B) *Synodontis acanthomias*; AMNH 235705 and C) *Euchilichthys royauxi*; SAIAB 40150.

Figure 25. Lateral view of caudal skeleton of *Ictalurus punctatus*; CU 79403.

Figure 26. Lateral view of caudal skeleton of *Euchilichthys royauxi*; CU 91614.

Figure 27. Lateral view of caudal skeleton of *Synodontis acanthomias*; CU 91613.

Figure 28. Lateral view of caudal skeleton of *Mochokus niloticus*; CU 91386.

Figure 29. Ventral view of compound centrum and elastic spring apparatus of *Synodontis serratus*; UMMZ 241265.

Figure 30. Singly (A) and doubly (B) branched mandibular barbels in the Mochokidae.

Figure 31. Results of Analysis 1: 61 taxa, 92 characters. Strict consensus (406 steps, CI = .3571, RI = .8467) of 6 equally parsimonious trees. Numbers above the branches are decay indices.

Figure 32. Results of Analysis 2: 24 taxa, 92 characters. Strict consensus (270 steps, CI = .4924, RI = .7729) of 2 equally parsimonious trees. Numbers above the branches are bootstrap proportions and numbers below the branches are decay indices. Nodes are labeled with letters for use in discussion. Arrowheads designated the three major shifts in jaw morphology within the Mochokidae. Fish icons from top to bottom: *Mochokus niloticus*, *Mochokiella paynei*, *Acanthocleithron chapini*, *Microsynodontis*, *Synodontis*, *Hemisynodontis membranaceous*, *Chiloglanis macropterus*, *Atopodontis adriaensi*, *Euchilichthys royauxi*, *Atopochilus savorgnani*, *Chiloglanis micropogon*.