

# Phylogenetic relationships within the South American fish family Anostomidae (Teleostei, Ostariophysi, Characiformes)

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Analysis of a morphological dataset containing 152 parsimony-informative characters yielded the first phylogenetic reconstruction spanning the South American characiform family Anostomidae. The reconstruction included 46 ingroup species representing all anostomid genera and subgenera. Outgroup comparisons included members of the sister group to the Anostomidae (the Chilodontidae) as well as members of the families Curimatidae, Characidae, Citharinidae, Distichodontidae, Hemiodontidae, Parodontidae and Prochilodontidae. The results supported a clade containing *Anostomus*, *Gnathodolus*, *Pseudanos*, *Sartor* and *Synaptolaemus* (the subfamily Anostominae sensu Winterbottom) albeit with a somewhat different set of relationships among the species within these genera. *Anostomus* as previously recognized was found to be paraphyletic and is split herein into two monophyletic components, a restricted *Anostomus* and the new genus ***Petulanos* gen. nov.**, described herein. *Laemolyta* appeared as sister to the clade containing *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*. *Rhytidodus* and *Schizodon* together formed a well-supported clade that was, in turn, sister to the clade containing *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*. *Anostomoides* was sister to the clade formed by these nine genera. *Leporinus* as currently defined was not found to be monophyletic, although certain clades within that genus were supported, including the species with subterminal mouths in the former subgenus *Hypomasticus* which we recognize herein as a genus. *Abramites* nested in *Leporinus*, and *Leporellus* was found to be the most basal anostomid genus. The presence of cis- and trans-Andean species in *Abramites*, *Leporellus*, *Leporinus* and *Schizodon*, all relatively basal genera, suggests that much of the diversification of anostomid species pre-dates the uplift of the Andean Cordilleras circa 11.8 million years ago. Several important morphological shifts in anostomid evolution are illustrated and discussed, including instances of convergence and reversal. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 70–210.

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## INTRODUCTION

Members of the Anostomidae inhabit myriad fresh-water environments in tropical and subtropical South America that range from the Río Atrato of north-

western Colombia south to the central portions of Argentina. The greatest diversity at both the specific and the generic levels occurs east of the Andes Cordilleras where representatives of the family inhabit all major drainages from the Río Orinoco basin (Lasso *et al.*, 2004b) to the Río de La Plata system (Garavello & Britski, 2003). The vast reaches of the Amazon and

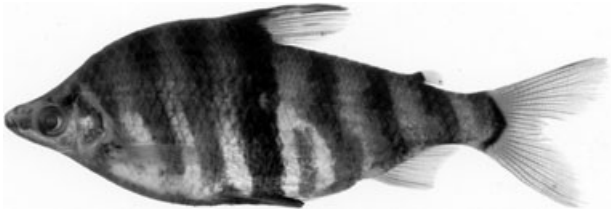
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**Figure 1.** *Rhytiodus microlepis*, USNM 229095, 121.5 mm SL; Brazil, Amazonas, Ilha da Marchantaria; lateral view.



**Figure 3.** *Synaptolaemus cingulatus*, AMNH 91095, 78 mm SL; Venezuela, Bolivar, Río Paraguay, at Carapo Rapids, just upriver of mouth of Río Carapo; lateral view.



**Figure 2.** *Abramites hypselonotus*, MCZ 59240, 98.6 mm SL; Ecuador, Río Punino, above Coca; lateral view.



**Figure 4.** *Leporinus friderici*, FMNH 116829, 180.5 mm SL; Suriname, Rechter Coppename River; lateral view.

the adjoining Río Orinoco basin are inhabited by the largest number of genera and species, including some of the most modified members of the family. The Atlantic versant of the Guayana shield in Guyana, Suriname and French Guiana also harbours many species (Planquette, Keith & Le Bail, 1996), while a less diverse fauna inhabits the hydrographically highly-dissected trans-Andean portions of South America. West of the Andean Cordilleras, anostomids are present in the arch from Lago Maracaibo of the Caribbean Sea versant as far south as the Guayas basin of Ecuador, which drains into the Pacific Ocean. Although few species inhabit the trans-Andean regions, most that do occur there are endemic to very small regions. For example, *Abramites eques* and *Leporinus muyscorum* are known only from trans-Andean Colombia (Steindachner, 1900, 1902; Vari & Williams, 1987) and *Schizodon corti* only from Lago Maracaibo in Venezuela (Vari & Raredon, 1991).

Overall body form in the Anostomidae ranges from the elongate, fusiform species of *Rhytiodus* (Fig. 1; Géry, 1977: 180; Santos, 1980: fig. 12) to the deep-bodied, laterally compressed species of *Abramites* (Fig. 2; Vari & Williams, 1987: fig. 3). Most anostomids, however, are moderately elongate species that are rounded in cross-section. Despite their similarity in overall body form, members of the Anostomidae demonstrate a wide range of jaw, tooth, neurocranium and suspensorium morphologies (Sidlauskas, 2007). Mouth positions range from distinctly subterminal within *Hypomasticus*, particularly in *Hypomasticus mormyrops* (Steindachner, 1875: pl. 6) and *Hypomasticus pachycheilus* (Britski, 1976; Sidlauskas, 2007: fig. 2B) to supraterminal and posteriorly directed in

*Sartor* (Myers & Carvalho, 1959: figs 1–3; Sidlauskas 2007: fig. 2D). Although some of the highly modified genera such as *Sartor* and *Synaptolaemus* (Fig. 3) have limited geographical distributions, small body sizes (c. 0.1 m standard length (SL)) and are apparently rare in nature based on museum holdings, other genera [e.g. *Anostomoides*, *Laemolyta*, *Leporinus* (Fig. 4), *Rhytiodus* and *Schizodon*] are geographically widespread and have large body sizes up to approximately 0.3 m SL. The larger species are commonly exploited in commercial and artisanal food fisheries (Goulding, 1980, 1981). Many anostomids feed largely on aquatic vegetation (Goulding, Leal Carvalho & Ferreira, 1988); other species have more diverse diets including larval and adult insects, nematodes, sponges, larval fishes and detritus (Knöepfel, 1972; Winterbottom, 1974b; Saul, 1975; Taphorn, 1992; Santos & Rosa, 1998; Balassa *et al.*, 2004).

The first anostomids known to western science were described by Linnaeus (1758) who based his species descriptions on specimens previously reported on by Gronovius (1756). Günther (1864) first united various anostomid genera in his 'Anostomina', but the next century brought little agreement about relationships of what is now recognized as the Anostomidae to other taxa. Boulenger's Anostominae (1904) significantly expanded the Anostomina of Günther (1864) to include a number of taxa now assigned to other families (see summary in Vari, 1998), but none of those taxa is currently considered to be closely related to the Anostomidae. Regan (1911) proposed a family Anostomidae that encompassed the Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae of present concepts, an insightful grouping under current hypotheses of relationships (Vari, 1983).

Gregory & Conrad (1938) recognized a broader Anostomidae consisting of Regan's (1911) family of that name plus taxa now included by Langeani (1998) in the Hemiodontidae (*sensu* Greenwood *et al.*, 1966). Géry (1961a: 108), reiterating the concept of Regan (1911), united the present Anostomidae (his Anostominae) with the Chilodontidae, Prochilodontidae and Curimatidae (his Chilodinae, Prochilodontinae and Curimatinae), without providing explicit evidence in support of that grouping. Roberts (1973: 221) hypothesized an explicit relationship between the Anostomidae and Prochilodontidae. Subsequently, Vari (1983: 50) detailed numerous synapomorphies in support of the hypothesis that the Anostomidae was the sister group to the Chilodontidae rather than the Prochilodontidae as proposed by Roberts (1973).

Hypotheses of intrafamilial phylogenetic relationships are less well developed. Winterbottom (1980) addressed the species-level problems and phylogenetic questions within his Anostominae [*Pseudanos*, *Gnathodolus*, *Sartor*, *Synaptolaemus* and *Anostomus* (the last with *Mormyrhynchus*, *Histiiodromus* and *Pithecocharax* as synonyms)]. This group encompasses the most externally distinctive species in the family, with the opening of the oral jaws positioned on the dorsal surface of the head (Fig. 3; Sidlauskas, 2007: fig. 2D). The genera *Abramites*, *Anostomoides*, *Hypomasticus*, *Leporellus*, *Leporinus*, *Rhytiodus* and *Schizodon* have a more generalized external morphology (Figs 1, 2, 4) with the notable exception of some members of the genus *Schizodon* (e.g. *Schizodon nasutus*) and *Hypomasticus* that possess strongly subterminal mouths (Steindachner, 1875: pl. 6; Borodin, 1929; Géry, 1960a; Britski, 1976). The seven genera cited above include the majority of the species of the family and were traditionally delimited by differences in the dentition, degree of caudal-fin squamation and body proportions.

Following Winterbottom's (1980) study of the assemblage that he recognized as the Anostominae, Santos & Jégu (1987) described two new species of *Sartor* and Sidlauskas & Santos (2005) described a new species of *Pseudanos*. *Abramites* (Vari & Williams, 1987) and *Laemolyta* (Mautari & Menezes, 2006) have been revised fully, while partial revisions have been undertaken for *Anostomoides* (Santos & Zuanon, 2006), *Hypomasticus* (Santos, Jégu & Lima, 1996) *Leporinus* (Garavello, 1988; Garavello & Britski, 1988; Géry, Planquette & Le Bail, 1988; Garavello, 1989, 1990; Santos & Jégu, 1996), *Rhytiodus* (Géry, 1987) and *Schizodon* (Bergmann, 1988); Garavello & Britski, 1990; Vari & Raredon, 1991; Sidlauskas, Garavello & Jellen, 2007). Nonetheless, most genera and subgenera outside of Winterbottom's Anostominae, including the most species-rich taxa (e.g. *Leporinus*), have not been revised comprehensively.

The partial revisionary studies cited above have yielded many previously undescribed species, and numerous questions remain as to which of the approximately 140 nominal species should be recognized and how they can be discriminated (Garavello & Britski, 2003). These issues and others preclude an attempt to develop a species-level phylogeny in the Anostomidae at this time.

This study had four goals:

1. to propose a hypothesis of higher level phylogenetic relationships within the Anostomidae;
2. to define the nominal genera in the Anostomidae on the basis of derived features;
3. to determine the number of times that major transitions in jaw orientation have evolved within the Anostomidae; and
4. to evaluate the historical biogeography of the Anostomidae within the context of the reconstructed phylogeny.

## MATERIAL AND METHODS

*Institutional abbreviations:* The following abbreviations for institutions and collections are used: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences, San Francisco; CAS-SU, Former Stanford University collections, now in CAS; FMNH, Field Museum of Natural History, Chicago; INHS, Illinois Natural History Survey, Champaign; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MZUSP, Museu de Zoologia da Universidade de São Paulo; NMW, Naturhistorisches Museum Wien, Vienna; UFSC, Universidade Federal de São Carlos; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

### TAXONOMIC SAMPLING AND NOMENCLATURE

The assemblage herein recognized as the Anostomidae is equivalent to the familial concept of Greenwood *et al.* (1966), Vari (1983) and Nelson (2006) and to the Anostominae of Eschmeyer (1990, 1998). Family-level names for Neotropical outgroups are those utilized in CLOFFSCA (Reis, Kullander & Ferraris, 2003).

We examined the morphology of 46 species representing all recognized genera and subgenera in the Anostomidae (Appendix 1) as well as 14 outgroups. Close outgroups include the Chilodontidae (three species examined), which is the sister group to the



Anostomidae (Vari, 1983: 50), the Curimatidae (three species examined) and the Prochilodontidae (two species examined). These last two families form a clade (Vari, 1983: 46, 1989b: 51; Castro & Vari, 2004: 59) which is the sister group to the Anostomidae plus Chilodontidae (Vari, 1983: 46; Castro & Vari, 2004: 58). Character state distributions in more distant outgroups were drawn from skeletal material and published descriptions of skeletal and external anatomy for *Parodon* (Pavanelli, 1999, one species examined), *Hemiodus* (Vari, 1982a, one species examined), *Brycon* (Weitzman, 1962, one species examined), *Citharinus* (Daget, 1962b, one species examined), *Distichodus* (Daget, 1959, one species examined) and *Xenocharax* (Daget, 1960, one species examined), the last of which was hypothesized by Vari (1979) to be the most basal and generalized member of the family Distichodontidae, which is, in turn, basal within the Characiformes (Fink & Fink, 1981; Orti & Meyer, 1996; Buckup, 1998; Calcagnotto, Schaefer & DeSalle, 2005). A full list of examined outgroup material, including comparative material not formally coded, appears in Appendix 1. Appendix 1 also contains taxonomic authorship for all examined ingroup and outgroup species.

Because diagnoses for anostomid species vary considerably in detail and accuracy, it is necessary to discuss the assignment of some material to terminal taxa (nominally species). The genus *Leporellus* has never been satisfactorily revised, although several of its nominal species have been suggested to be in the synonymy of *Leporellus vittatus* and *Leporellus pictus* (Garavello & Britski, 2003). There is no published diagnosis between *L. pictus* and *L. vittatus*, and we assigned specimens to these two species-groups based on geography and separation among drainages. None of the nominal species of *Leporellus* has type localities in the Río Orinoco, but *Leporellus vittatus* has a type locality of 'Amazon River, Brazil' (Cuvier & Valenciennes, 1850), which is confluent with the Orinoco via Venezuela's Casiquiare canal. Based on the confluence between the Amazon and Orinoco, we assigned the specimens from the Orinoco to *Leporellus vittatus*, albeit provisionally. Because *Leporellus pictus* has a type locality of 'Irisanga' (= Orissanga) in the rivers of São Paulo state, Brazil, which lie outside the Amazon drainage, we assigned the specimens that originated in São Paulo state to *Leporellus pictus*.

The cleared and stained specimens of *Leporinus agassizi* come from the Río Napo of Ecuador and the Río Nanay of Peru, localities distant from the type locality (Amazon River, Tabatinga and Tefé, Brazil). *Leporinus agassizi* has a large purported range for an anostomid, including Ecuador, Guyana, Peru, Venezuela and Amazonian Brazil. The name may refer to a

species complex, and as such, the examined material from the far west of the continent may not be conspecific with the true *Leporinus agassizi*, which has a type locality in the central Amazon.

Fowler (1914) erected the subgenus *Myocharax* of *Leporinus* on the basis of the tusk-like symphyseal dentary teeth possessed by the type species, *L. desmotes*, from Guyana. Ovchynnyk (1971) later described the very similar *L. jatuncochi* from Amazonian Ecuador with no reference to, or comparison with, *L. desmotes*. Based on the two descriptions there is no way to separate the two species other than based on geography, and *L. jatuncochi* may be in the synonymy of *L. desmotes*. We assigned our cleared and stained material of the *L. desmotes/jatuncochi* complex from Amazonian Peru to *L. jatuncochi* based on proximity of the collecting locality to the type localities, recognizing that *L. jatuncochi* may prove to be a junior synonym.

One of the cleared and stained specimens of *Leporinus fasciatus* from the Río Orinoco (FMNH 103450) was taken from a lot of specimens that, in hindsight, appears to contain more than one species. The jar contains several juvenile *Leporinus* specimens of similar standard lengths that, nonetheless, display variable banding patterns. Some of the juvenile specimens in the lot, including the cleared and stained specimen, may belong to one of the other banded species of *Leporinus* that occur in the Río Orinoco system (e.g. *L. falcipinnis* and *L. yophorus*). To reflect the uncertainty in this identification, the cleared and stained specimen from FMNH 103450 appears as *Leporinus* cf. *fasciatus*, while specimens more confidently assignable to *Leporinus fasciatus* (USNM 103847, 225991, 233574) appear without that qualification.

The Río Napo basin of eastern Ecuador is home to a species of *Leporinus* that closely resembles the paratypes of *L. ecuadorensis* housed at FMNH, but *L. ecuadorensis* has a known distribution restricted to the Pacific versant on the western side of the Andes in Ecuador (Eigenmann & Henn, 1916). No other recognized species in the Anostomidae or its proximate outgroups (Chilodontidae, Curimatidae, Prochilodontidae) has a geographical distribution spanning the Andes Cordilleras. The Río Napo species may be undescribed, or it may be synonymous with *L. ecuadorensis* or one of several other similar species such as *L. friderici* from Suriname. We identify the Río Napo material throughout this contribution as *L.* cf. *ecuadorensis*, an assignation which reflects its similarity to and potential synonymy with *L. ecuadorensis*.

*Leporinus friderici* (Fig. 4) has a very wide cited distribution including Brazil, French Guiana, Guyana, Suriname, Trinidad and Tobago (Garavello & Britski,

2003). The cleared and stained specimen that appears herein as *Leporinus friderici* (USNM 225409) comes from the inexact type locality (Suriname). Material from elsewhere in South America (for example, the dry skeleton INPA 21605 from the fish market of Manaus, Brazil) appears as *Leporinus* cf. *friderici*.

The subgenus *Leporinops* of *Leporinus* currently contains two small-bodied, poorly known species, *L. moralesi* (the type species) and *L. jamesi*, both from the Amazon River of Brazil (Géry, 1960b, 1977). The subgenus was distinguished by a notched morphology of the symphyseal teeth of the premaxilla, with the two species diagnosed on minor details of coloration. The holotype of *L. jamesi* was unavailable for examination and searches of major museums failed to reveal any additional specimens of that species. These searches also yielded only very old specimens of *L. moralesi* (MCZ 19409 and 19476, both collected in 1865 as part of the Thayer expedition) that were unsuitable for clearing and staining. The UMMZ collection did yield a probable new species of this subgenus from Bahia, Brazil, in the far east of the continent. The material from Bahia possesses the divided symphyseal premaxillary teeth and small body size that characterize *Leporinops*, but the Bahia specimens differ from the reported colour patterns for *L. jamesi* and *L. moralesi* and were collected far outside the known geographical range of the two described species. More detailed comparison is impossible without access to fresh material of *L. jamesi* and *L. moralesi*. The Bahia material appears in this contribution as *L.* cf. *moralesi*.

The cleared and stained specimen of *Leporinus* cf. *niceforoi*, FMNH 102150, originated in the Río Napo of Ecuador, outside the purported range of *L. niceforoi* in the Río Ortegusa basin of Colombia. The specimens from the Río Tocantins of Brazil cited as *Leporinus pellegrinii* (INPA 15672) may be synonymous with *L. maculatus* (see Géry *et al.*, 1988).

The two described species of small-scaled *Rhytiodus*, *R. microlepis* and *R. lauzannei*, are diagnosed by a difference in body depth, with *R. lauzannei* the deeper-bodied (Géry, 1987). *Rhytiodus microlepis* is cited from the Amazon River basin with a type locality of Manaus, Brazil (Kner, 1858; Garavello & Britski, 2003), while *R. lauzannei* was described as endemic to the Río Mamoré of Bolivia (Géry, 1987). Many specimens from near Manaus have body depths in the cited ranges for *R. lauzannei*, while some from the Río Mamoré have body depths in the cited range for *R. microlepis*. The status of these nominal species must await careful study. For current purposes, material was identified using Géry's (1987) plots of body depth versus standard length.

#### NOMENCLATURAL CHANGES

As a result of the phylogenetic conclusions arrived at in this study, we make three revisions to the genus-level nomenclature within the Anostomidae:

- elevation of *Hypomasticus* from a subgenus of *Leporinus* to a genus containing the following species most recently assigned to *Leporinus*: *L. despaxi*, *L. garmani*, *L. julii*, *L. megalepis*, *L. mormyrops*, *L. pachycheilus* and *L. thayeri*;
- restriction of *Anostomus* to *A. anostomus*, *A. anostomus longus*, *A. brevior* and *A. ternetzi*; and
- erection of a new genus, *Petulanos*, containing the following species most recently assigned to *Anostomus*: *A. intermedius*, *A. plicatus* and *A. spiloclistron*, with *A. plicatus* as the type species.

We do not utilize *Leporinops* and *Myocharax*, both nominal subgenera of *Leporinus*, in light of the lack of resolution for the portion of the phylogeny involving *Leporinus*. The full list of nominal genera and subgenera and their synonyms appears in Table 1. We employ this revised classification throughout the remainder of this paper. For a full discussion of the rationale behind these changes and a formal diagnosis of *Petulanos*, please see the section on 'Changes to classification and comparisons with previous classifications' following the discussion of phylogenetic results and support.

#### OSTEOLOGICAL PREPARATIONS AND TERMINOLOGY

Samples of all species included as terminal taxa were cleared and counterstained (C&S) for cartilage and bone using the method outlined by Taylor & Van Dyke (1985). Whenever possible, two or more specimens of each species were prepared to facilitate checks for anomalous features. One side of each C&S specimen was dissected according to Fink & Weitzman (1974) during character analysis. Data from external morphology including pigmentation patterns and scale counts was based on the examination of alcohol-preserved specimens. Typically these were non-C&S members of the same lots from which the osteological material was prepared. Additional lots examined as alcohol-preserved specimens only are indicated by (A) in Appendix 1. A few specimens were prepared as dry skeletons and are indicated by (DS) in Appendix 1.

Osteological terminology is that of Weitzman (1962) with the following modifications. Vomer is used instead of prevomer and intercalar is used instead of opisthotic following the practice in recent studies of the Characiformes (Langeani, 1998; Zanata & Toledo-Piza, 2004; Zanata & Vari, 2005). The use of epioccipital rather than epiotic follows Patterson (1975). Following Nelson (1969), the ossification traditionally

**Table 1.** Nominal genera and subgenera assigned to the family Anostomidae in this and other publications with citation for original description and recognized equivalent genus

Nominal genus or subgenus	Assignment herein
<i>Abramites</i> Fowler, 1906	<i>Abramites</i>
<i>Anostomoides</i> Pellegrin, 1909	<i>Anostomoides</i>
<i>Anostomus</i> Scopoli, 1777	<i>Anostomus</i>
<i>Anostomus</i> Cuvier, 1816	Same as <i>Anostomus</i> Scopoli, 1777
<i>Garmanina</i> Fowler, 1906	<i>Rhytiodus</i>
<i>Gnathodolus</i> Myers, 1927	<i>Gnathodolus</i>
<i>Histiodromus</i> Gistel, 1848	<i>Anostomus</i>
<i>Hypomasticus</i> Borodin, 1929 (subgenus of <i>Leporinus</i> )	<i>Hypomasticus</i>
<i>Laemolyta</i> Cope, 1872	<i>Laemolyta</i>
<i>Lahilliella</i> Eigenmann & Kennedy, in Eigenmann, 1903	<i>Schizodon</i>
<i>Leporellus</i> Lütken, 1875	<i>Leporellus</i>
<i>Leporinodus</i> Eigenmann, 1922	<i>Leporellus</i>
<i>Leporinops</i> Géry, 1960b (subgenus of <i>Leporinus</i> )	<i>Leporinus</i>
<i>Leporinus</i> Agassiz, in Spix and Agassiz, 1829	<i>Leporinus</i>
<i>Mormyrynchus</i> Swainson, 1839	<i>Anostomus</i>
<i>Myocharax</i> Fowler, 1914 (subgenus of <i>Leporinus</i> )	<i>Leporinus</i>
<i>Petulanos</i> Sidlauskas & Vari, this contribution	<i>Petulanos</i>
<i>Pithecocharax</i> Fowler, 1906	<i>Anostomus</i>
<i>Pseudanos</i> Winterbottom, 1980	<i>Pseudanos</i>
<i>Rhytiodus</i> Kner, 1858	<i>Rhytiodus</i>
<i>Sartor</i> Myers & Carvalho, 1959	<i>Sartor</i>
<i>Schizodon</i> Agassiz, in Spix & Agassiz, 1829	<i>Schizodon</i>
<i>Schizodontopsis</i> Garman, 1890 (subgenus of <i>Anostomus</i> )	<i>Laemolyta</i>
<i>Synaptolaemus</i> Myers & Fernández-Yépez, in Myers, 1950	<i>Synaptolaemus</i>

Genera and subgenera are arranged alphabetically with original generic assignment noted in parentheses in cases of subgenera.

termed the epihyal is referred to as the posterior ceratohyal, and the ceratohyal of many previous authors as the anterior ceratohyal. Use of mesethmoid rather than ethmoid follows Fink & Fink (1981, 1996). Nomenclature for muscles and associated tendons follows Winterbottom (1974a).

Members of the Anostomidae have one or more tubular ossifications that enclose the laterosensory canal system anterior of the main body of the preopercle. These ossifications are hypothesized to be com-

ponents of the preopercle (Winterbottom, 1980; see also comments by Vari, 1983: 31) and are labelled as such because they occupy an area occupied by the anterior portion of the preopercle in most other characiforms, such as *Brycon meeki* (Weitzman, 1962: figs 8, 9).

ILLUSTRATIONS AND MICROGRAPHS

Pen and ink illustrations were prepared from pencil sketches drawn with the use of a camera lucida attached to a Zeiss Stemi dissecting microscope. Some illustrations were prepared from the right (dissected) side of various specimens and have been reversed left-to-right to place the anterior portion of the morphology in the traditional left position. Reversed images are noted in the figure captions.

Micrographs were prepared using the Zeiss LEO scanning electron microscope at the Field Museum. Except where otherwise indicated, micrographs were prepared from dissections of the right side of the cited specimens. All specimens were air dried and mounted on adhesive carbon discs prior to imaging at a working distance of approximately 11 mm.

PHYLOGENETIC METHODS

In total, 123 characters that vary within the Anostomidae or that diagnose that family as monophyletic are based upon examination of the specimens cited in Appendix 1 and are described below under ‘Character description and analysis’. To provide phylogenetic structure to the outgroup comparisons, 35 additional characters that vary among the outgroup families but not within the Anostomidae were drawn from Vari (1979, 1983, 1989a) and Castro & Vari (2004) and coded from the specimens at hand. These appear in summary form in Appendix 2. All characters were divided into two or more discrete character states, with 29 of the 158 characters being multistate.

Ordering of multistate characters is controversial; it has been suggested that ordering characters along morphoclines using a principle of intermediates increases information content and adheres to Hennig’s auxiliary principle because it employs shared apomorphy as evidence of relationships (Wilkinson, 1992). Similarly, Wiens (2001: 693–694) suggested that the assumption that ‘taxa sharing similar but non-identical trait values should be more closely related than taxa sharing more dissimilar trait values’ is a logical extension of parsimony and provides a basis for ordering characters because it assumes the minimum amount of change *a priori*. Counterarguments posit that ordered characters amount to *a priori* hypotheses of gradual evolutionary transition that should be inferred *a posteriori* through



character congruence and parsimony, and that the practice of ordering character states according to a principle of intermediates equates overall similarity with relatedness in a manner dangerously close to phenetics (Hauser, 1992). We tend towards the latter view, particularly when only similarity among character states (as opposed to fossil or developmental evidence) is available to support *a priori* hypotheses of character state trees in the sense of Slowinski (1993), as was the case in this study.

Our final phylogenetic topology represents the results of analysis with all characters unordered. To determine whether ordering the four multistate characters (17, 46, 72 and 77) that include clear intermediate states and deal with size, extent or rotation of skeletal elements would alter the topological conclusions, we repeated the analysis with those four characters ordered and also discuss those results. Conversely, we assumed equal probabilities of change among all observed meristic states and treated multistate meristic characters as unordered in all analyses. We made this assumption because changes in single regulatory genes (Leary, Allendorf & Knudsen, 1984) or small numbers of quantitative trait loci (Peichel *et al.*, 2001) have been known to cause major shifts in meristic counts in fishes, and because the range of heritable meristic variation within populations sometimes approaches the range of meristic variation among closely related species (Ahn & Gibson, 1999). It is therefore highly plausible that shifts from high to low meristic counts and vice versa may proceed without progression through intermediate conditions.

A small number of characters and character states describe distinctive morphologies possessed by only one ingroup species. These autapomorphies are included in the character list and are discussed because future analyses with more comprehensive intrafamilial taxon sampling may reveal them to be synapomorphies of two or more species. Although the six parsimony-uninformative characters were excluded from analysis, the overall consistency index reported herein is slightly inflated by the inclusion of autapomorphic character states within parsimony-informative multistate characters.

The data matrix was assembled in Mesquite v. 1.12 (Maddison & Maddison, 2006) and appears in Appendix 3. Phylogenetic analysis proceeded according to the parsimony optimality criterion in PAUP\* 4.0 Beta 10 (Swofford, 2003). Relationships among the outgroups and ingroups were reconstructed simultaneously from the combined dataset of 152 parsimony-informative characters.

Polymorphisms were handled as follows. Where polymorphisms were apparent among specimens of greatly varying sizes (i.e. distinctive juvenile and adult morphologies), the species was coded as pos-

sessing the condition apparent in the largest specimens. In cases of polymorphism among individuals within a single life-history stage, a frequency coding approach has been found to retain the most phylogenetic signal (Wiens, 1995). That approach was not, however, feasible in this study because of insufficient specimens to determine precise frequencies of alternative observed states. Instead, if a clear majority of examined specimens possessed one of the alternative states, we coded that species as possessing that state; otherwise we coded the species as polymorphic (the `mstaxa = polymorph` option in PAUP\*). That procedure instructs the program to assign a state to the taxon *a posteriori* based on its position in the tree. Wiens (1995) found these two methods (majority-rule coding and polymorphic coding) to give the best performance (after frequency coding) under his phylogenetic signal, bootstrapping and sampling-error criteria. Specific polymorphisms are discussed under individual character descriptions.

One thousand heuristic searches of treespace were undertaken, each with a random sequence of taxon addition, tree bisection–reconnection (TBR), and the program set to collapse branches of zero maximum length. The resulting topologies were rooted at the examined members of the Distichodontidae and Citharinidae (*Xenocharax spilurus*, *Citharinus* sp. and *Distichodus* sp.), a monophyletic unit of two families (Vari, 1979) that is basal within the Characiformes (Fink & Fink, 1981; Orti & Meyer, 1997; Buckup, 1998; Calcagnotto *et al.*, 2005). This rooting constrained *Xenocharax*, *Citharinus* and *Distichodus* to monophyly; all other taxa were unconstrained in phylogenetic position. Strict and 50% majority rule consensus trees were calculated. To determine if collapsing branches with ambiguous support would result in a different consensus topology, the search was repeated with the program set to collapse branches of zero minimum length. Character state distributions were examined using both ACCTRAN and DELTRAN optimization. Bremer support values (also known as decay indices or branch support values, Bremer 1988, 1994) were calculated in PAUP\* via a script generated in DNA Stacks (Eernisse, 1992, 2000) using the strict consensus generated in PAUP\* as the baseline topology.

It is debatable whether it is statistically sound to bootstrap morphological datasets, as the characters underlying analysis cannot be assumed reasonably to be drawn randomly from the distribution of all available characters. Furthermore, the sample size of characters is much too low to meet the statistical assumptions underlying the bootstrap (see discussion in Kitching *et al.*, 1998: 129–131). In the interests of completeness 250 bootstrap replicates were performed in PAUP\*, each comprising ten heuristic

searches with all characters unordered, TBR, random addition sequences and character resampling with replacement across the entire dataset. To restrict the search to a reasonable length of time each individual bootstrap replicate was limited to 1000 000 trees.

### PHYLOGENETIC RESULTS

Analysis of the data matrix (Appendix 3) in PAUP\* with branches of zero maximum length collapsed and multistate characters unordered yielded 1312 most parsimonious trees of length 529 steps in a single tree island, which was discovered in 991 of the 1000 addition sequence replicates. The other nine replicates found shortest trees of 531 steps; results from these runs were not retained. Each most parsimonious tree had a CI = 0.425 and RI = 0.805. The repeated analysis with branches of zero minimum length collapsed yielded 240 most parsimonious trees in a single tree island. Parallel analyses with multistate characters 17, 46, 72 and 77 ordered obtained 1200 most parsimonious trees (collapsing branches with zero maximum length) or 240 most parsimonious trees (collapsing branches with zero minimum length), again in a single tree island discovered in 99% of all heuristic replicates. Each of the most parsimonious trees resulting from analyses with multistate characters ordered had length 531, CI = 0.424 and RI = 0.805.

All four analyses discussed above yielded identical strict consensus topologies (Fig. 5). All four majority rule consensus trees returned fundamentally similar topologies (Fig. 6), although the percentages of trees containing nodes not present in the strict consensus varied slightly among the four treatments. Three nodes that appear in the majority rule consensus under the zero maximum length branch collapsing rule are unresolved in the majority rule consensus based on the zero minimum length branch collapsing rule; these are indicated with asterisks in Figure 6.

In general the relative strengths of Bremer support and bootstrap values, which appear above and below the nodes in the strict consensus (Fig. 5), respectively, were concordant across the phylogeny. For example, all nodes receiving Bremer values of 3 or higher have bootstrap values of 74 or more, while nodes with Bremer values of 1 typically have bootstrap values below 60.

Overall, phylogenetic results were robust to changes in branch collapsing rule and ordering of characters. We consider the strict consensus topology and associated support values returned by the unordered analysis with branches of maximum length zero collapsed (Fig. 5) to be the final hypothesis of relationships arrived at herein. The 32 ingroup clades in the final phylogenetic hypothesis are numbered in Figure 7 and referenced in the character descriptions and analyses

that follow. A complete list of synapomorphies for each numbered clade appears in Appendix 4.

### CHARACTER DESCRIPTION AND ANALYSIS

Each of the 123 morphological characters described below varied within the Anostomidae or was found to be informative about the monophyly of the Anostomidae. Discussions are arranged by discrete body systems in an overall anterior to posterior pattern. Each character description includes the name of the character, descriptions of the character states, the consistency and retention indices on the final phylogenetic hypothesis (Fig. 5), a discussion of the distribution of states among the terminal taxa, and the optimization of the character on the final phylogeny with reference to the numbered nodes in Figure 7. In some instances, citations of figures from the literature involve congeners rather than the exact outgroup species examined as skeletal preparations and coded in the data matrix. For example, we often cite Weitzman's (1962) illustrations of the skeleton of *Brycon meeki* in our discussion of its very similar congener, *B. falcatus*, which we used as an outgroup.

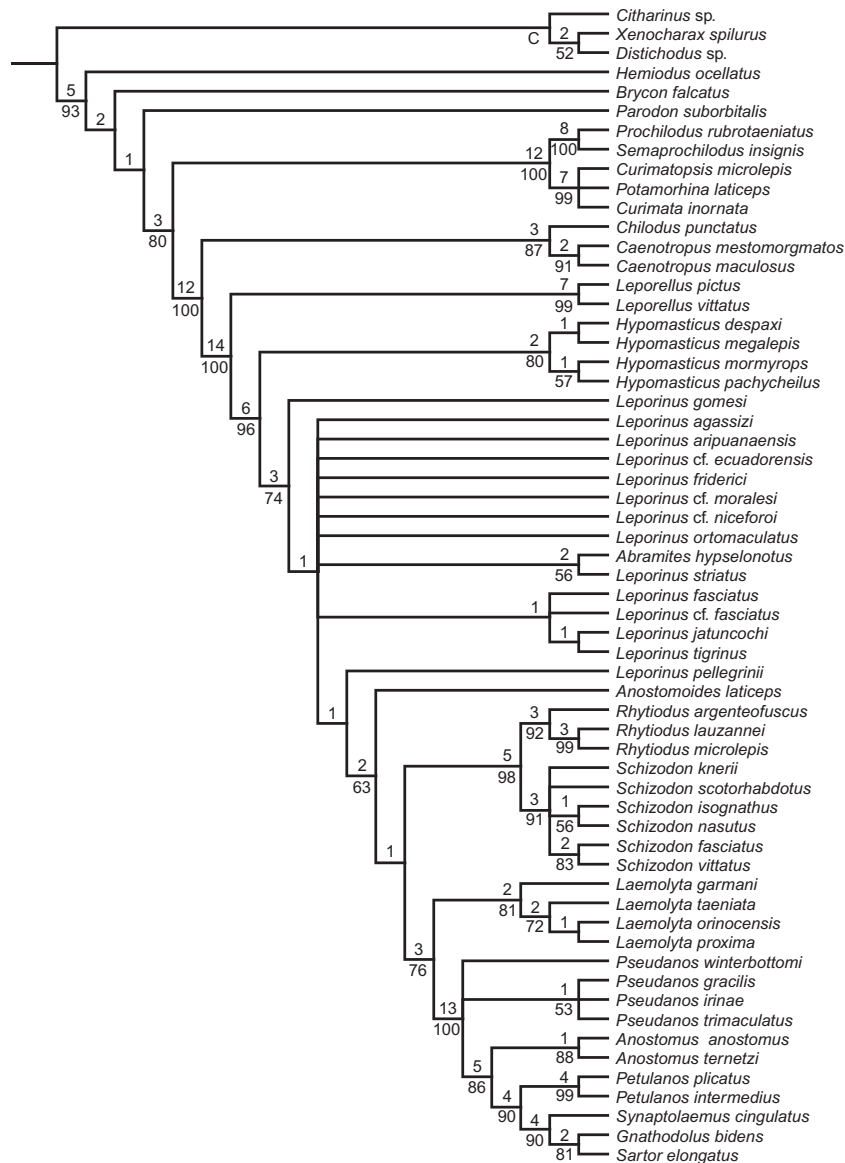
#### ANTORBITAL, SUPRAORBITAL AND INFRAORBITALS

1. *Presence or absence of horizontal flange of antorbital*: (0) antorbital small, vertically orientated and running posterior to nasal cavity with only slight horizontal expansion along ventral margin; (1) antorbital relatively large, with distinct horizontally directed flange running ventral to nasal cavity; flat bony plate may join vertical and horizontal portions of antorbital to varying degrees (CI = 1.000; RI = 1.000).

Within the Anostomidae, *Leporellus pictus* and *L. vittatus* uniquely possess a small antorbital in the shape of a vertically orientated bar which is positioned just posterior of the lateral opening into the nasal cavity (state 0; Fig. 8). All other examined members of the Anostomidae have an antorbital with an additional horizontally directed flange running ventral to the aperture (state 1; Figs 9–13). That flange is absent in the species of *Leporellus*. The morphology of the antorbital varies greatly within the Anostomidae outside of *Leporellus*, ranging from a thin, somewhat L-shaped ossification in some species of *Leporinus* (e.g. *L. fasciatus*, Fig. 9) to a wide, plate-like ossification bordering the entire ventral, lateral and posterior margins of the nasal cavity (e.g. *Petulanos plicatus*, Fig. 12). Other than for the presence or absence of the horizontal flange, much of this variation in antorbital morphology proved impossible to parse discretely.

All examined members of the proximate and second outgroups to the Anostomidae (Chilodontidae, Curimatidae, Prochilodontidae) have the smaller form of



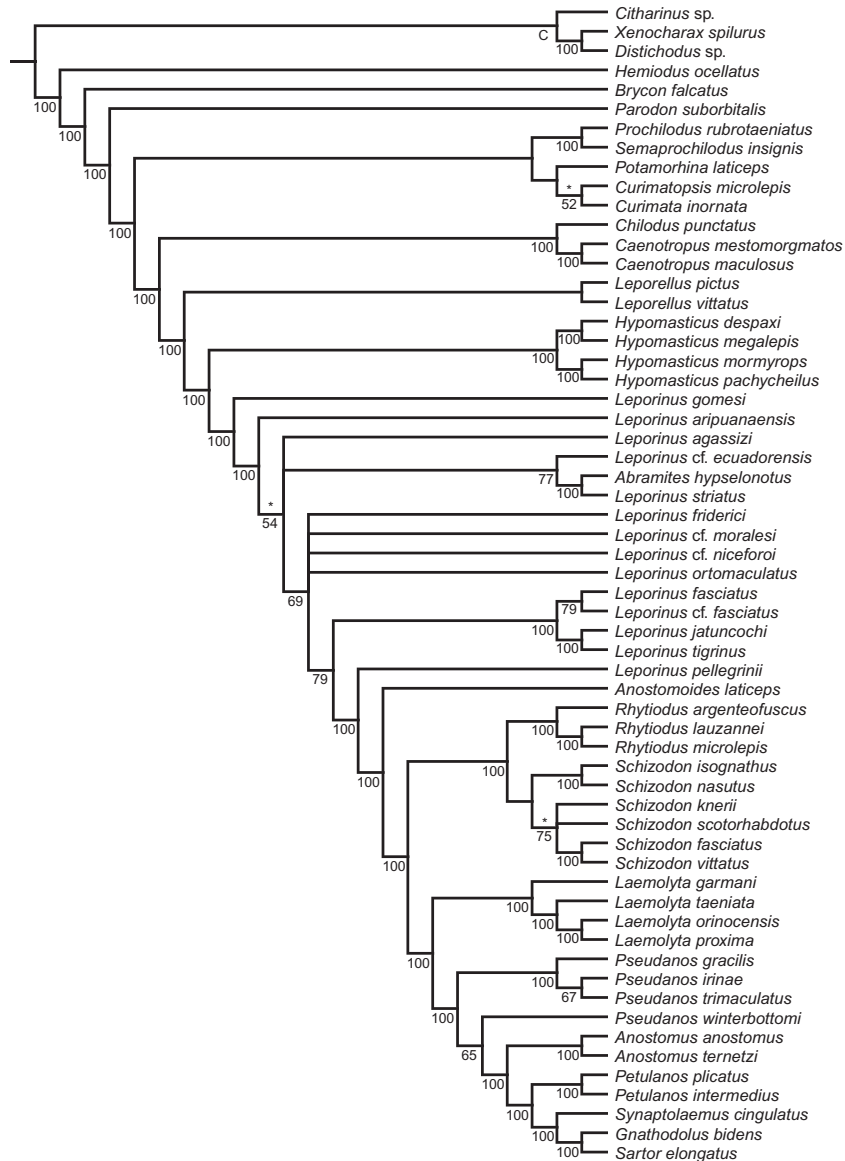


**Figure 5.** Strict consensus of 1312 most parsimonious trees generated in PAUP\* with branches of zero maximum length collapsed and all characters unordered. Repeated analysis with branches of zero minimum branch length collapsed and/or multistate characters ordered yielded the same consensus topology. Each of the most parsimonious trees has length = 529, CI = 0.425 and = 0.805. Numbers above nodes indicate Bremer support values, numbers below nodes indicate bootstrap percentages. The letter C indicates where the Citharinidae and Distichodontidae were constrained to cluster via their joint designation as a monophyletic root.

the antorbital (state 0) lacking the horizontal flange, with the exception of *Curimatopsis microlepis*, which lacks an antorbital entirely. The smaller form of the antorbital (state 0) also occurs in the examined members of the Characidae, Citharinidae, Distichodontidae, Parodontidae and Hemiodontidae. Under the final reconstruction of relationships, the horizontal expansion of the antorbital is a synapomorphy of all examined species in the Anostomidae except for *Leporellus pictus* and *L. vittatus* (clade 3).

2. *Anteroposterior positioning of antorbital*: (0) anterior margin of antorbital positioned just dorsal of, or dorsal and posterior of, anterodorsal opening of sensory canal of first infraorbital; (1) anterior margin of antorbital positioned distinctly anterior of anterodorsal opening of sensory canal of first infraorbital (CI = 0.167; RI = 0.750).

Within the Anostomidae, members of *Anostomus*, *Gnathodolus*, *Leporellus*, *Petulanos*, *Sartor* and *Synaptolaemus*, as well as *Hypomasticus despaxi*,

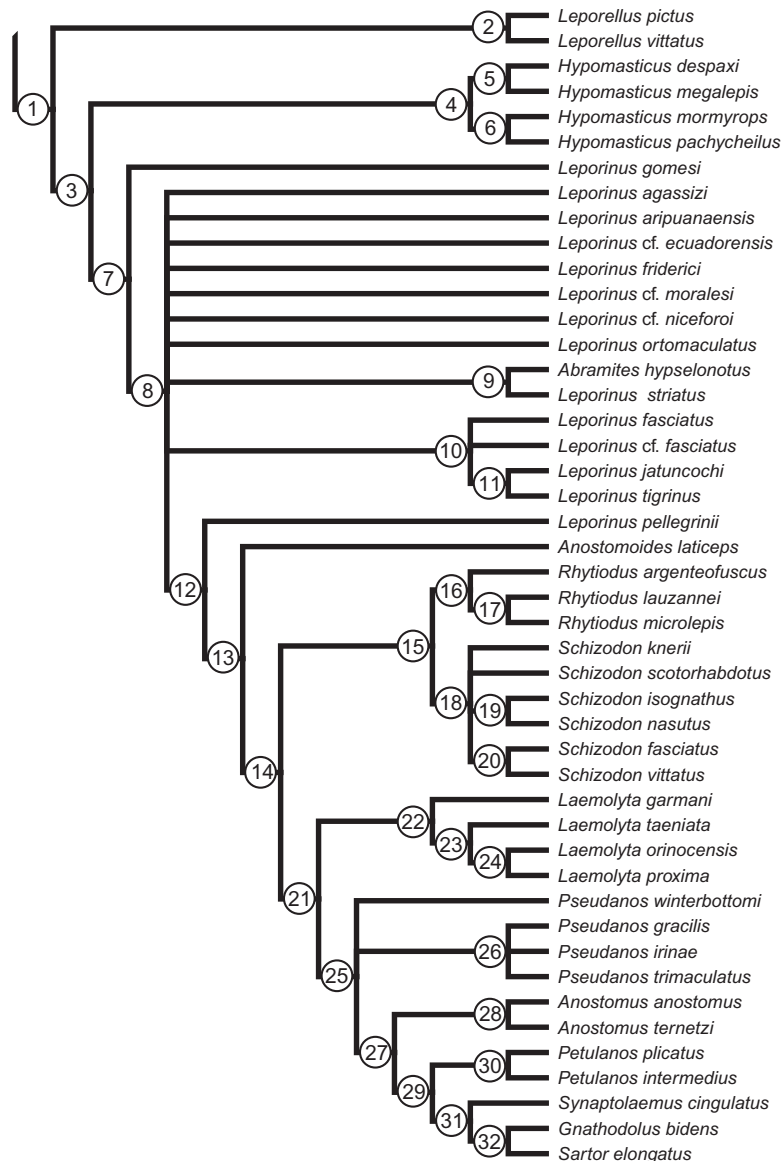


**Figure 6.** Majority rule consensus of 1312 most parsimonious trees generated in PAUP\* with branches of zero maximum length collapsed and all characters unordered. Numbers below branches indicate percentages of trees containing the subtended nodes. The three asterisks indicate nodes that do not appear in the majority rule consensus based on a zero minimum length branch collapsing rule. The letter C indicates where the Citharinidae and Distichodontidae were constrained to cluster via their joint designation as a monophyletic root.

*H. mormyrops*, *H. pachycheilus* and two of the three specimens of *H. megalepis* possess an antorbital with an anterior margin that terminates posterior of, or just dorsal to, the anterodorsal opening of the sensory canal of the first infraorbital (state 0; Figs 8, 12, 13). Species in *Abramites*, *Anostomoides*, *Laemolyta*, *Leporinus*, *Pseudanos*, *Rhytiodus* and *Schizodon* and the smallest of the three specimens of *Hypomasticus megalepis* have an antorbital that terminates distinctly anterior of the anterodorsal opening of the sensory canal of the first infraorbital (state 1; Figs 9–

11). *Hypomasticus megalepis* is coded as possessing state 0, reflecting the presumed adult morphology possessed by the largest available specimens.

All members of the proximate outgroup to the Anostomidae (the Chilodontidae) possess state 0, as do *Curimata inornata* (Curimatidae) and *Prochilodus rubrotaeniatus* (Prochilodontidae). *Curimatopsis macrolepis* in the Curimatidae lacks an antorbital and cannot be scored, while *Potamorhina laticeps*, also in that family, has a very short sensory canal associated with the first infraorbital which consequently



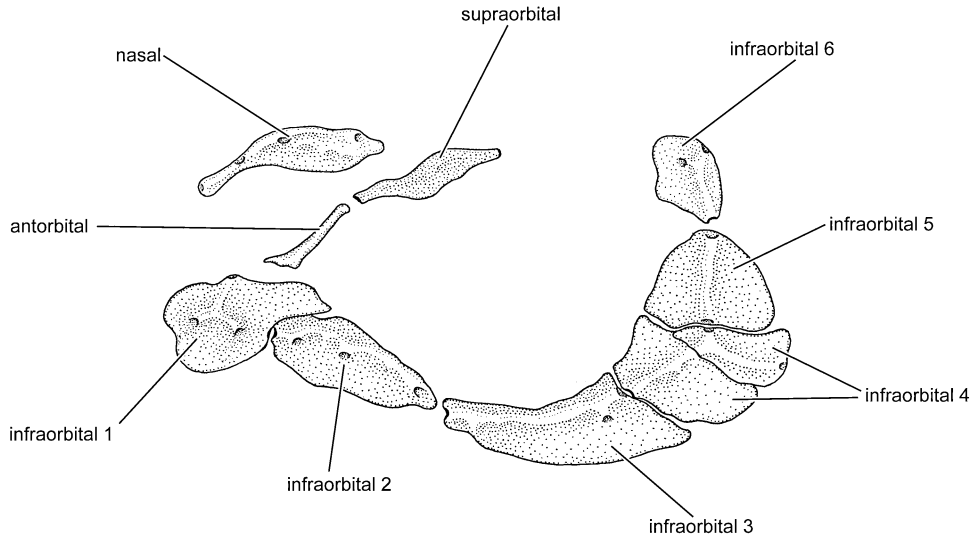
**Figure 7.** Reconstruction of relationships among the 46 examined species of the Anostomidae based on 152 parsimony-informative characters. Numbers correspond to clades discussed in the text and in the synapomorphy list (Appendix 4).

terminates posterior of the anterior margin of the antorbital (state 1). *Semaprochilodus insignis* (Prochilodontidae) also possesses state 1 for this character. Among more distant outgroups, *Brycon falcatus* (Weitzman, 1962: fig. 8), *Citharinus* sp. and *Hemiodus ocellatus* possess state 1 for this character, while *Xenocharax spilurus* (Daget, 1960: fig. 7), *Distichodus* sp. and *Parodon suborbitalis* possess state 0. In the final phylogenetic hypothesis, state 0 is plesiomorphic within the Anostomidae, with state 1 synapomorphic for clade 7. The reversal to state 0 is a clear synapomorphy for clade 27.

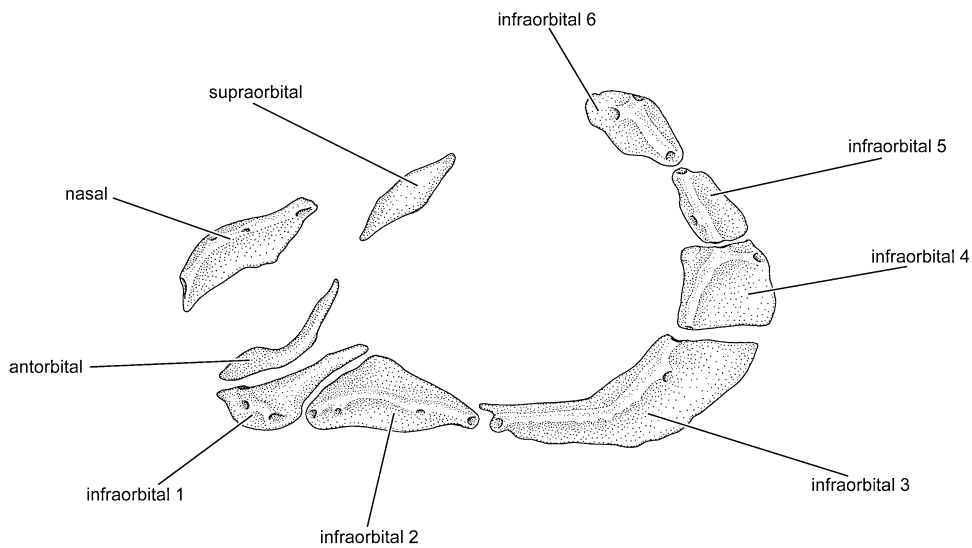
3. *Presence or absence of deep lateral notch on supraorbital:* (0) notch absent or weakly developed; supraorbital with smoothly convex, straight or slightly concave anteroventral margin; (1) notch present; supraorbital with deeply concave, distinctly notched anterior or anterolateral margin (CI = 0.167; RI = 0.167).

Most members of the Anostomidae have a rhomboid supraorbital without distinct notches along the ventral margin of the bone (state 0; Figs 8–12). *Hypomasticus despaxi*, *H. megalepis*, *H. mormyrops*, *Leporinus gomesi*, *Gnathodolus bidens*, *Schizodon*





**Figure 8.** Left infraorbital series of *Leporellus pictus*, USNM 302487, 115 mm SL; lateral view, infraorbital 4, normally a single ossification, is divided into two bones on this side of this specimen.

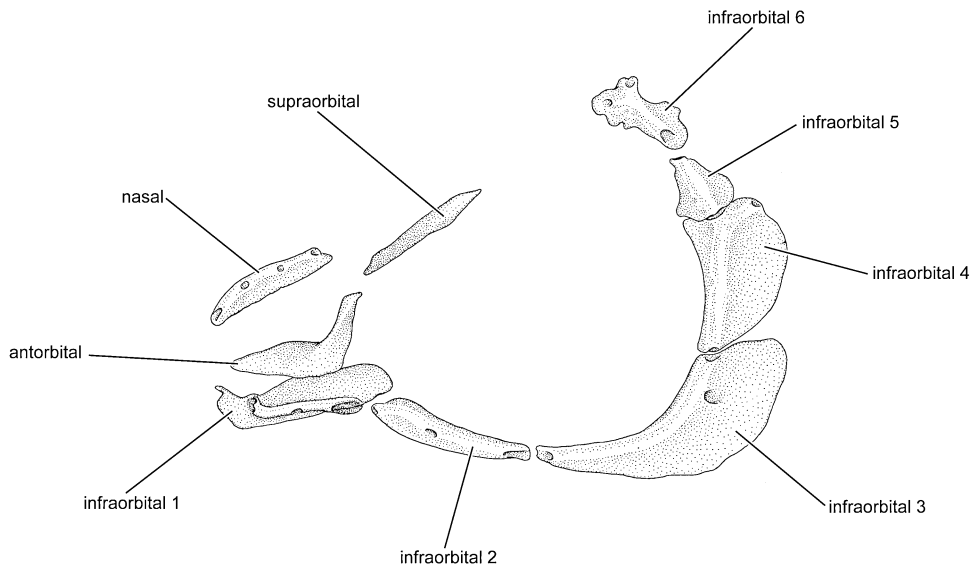


**Figure 9.** Left infraorbital series of *Leporinus fasciatus*, USNM 225991, 87.8 mm SL; lateral view.

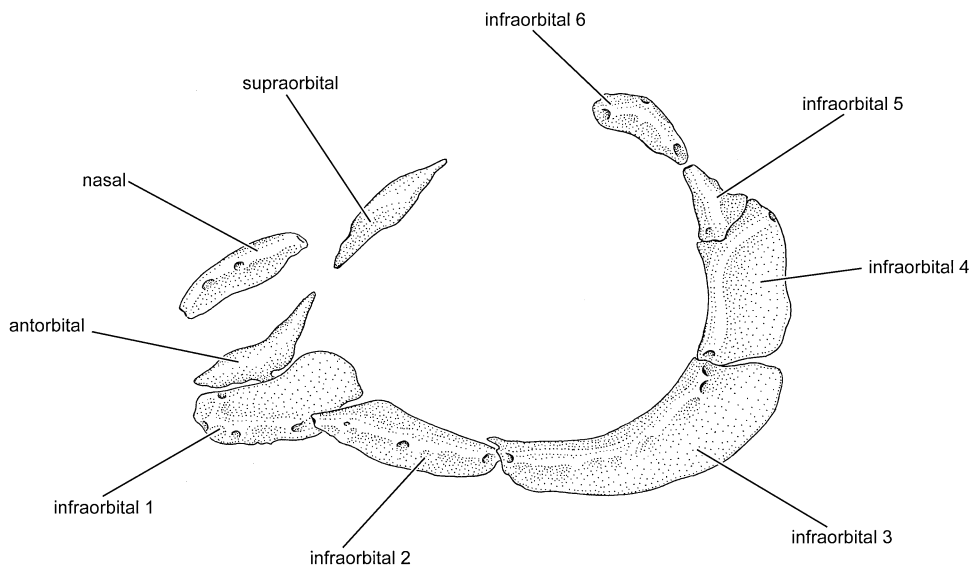
*isognathus* and *S. knerii* have a very deep notch along the anteroventral margin of the supraorbital (state 1, Fig. 13). The notch in the supraorbital of *S. knerii* is more anteriorly positioned than is the notch in the other cited taxa, but is nevertheless deep and thus coded as state 1. Although *Gnathodolus* has a supraorbital with a notch that meets the definition of state 1 (Fig. 13) and is coded accordingly, the whole bone is restructured with an additional ventral process intersecting the flat plate of the supraorbital that is typical of other members of the Anostomidae. The restructuring of the supraorbital in *Gnathodolus* renders the homology of the notch of the supraorbital

in *Gnathodolus* with that present in the various species of *Hypomasticus*, *Leporinus* and *Schizodon* doubtful, a conclusion supported by the phylogenetic results arrived at herein.

*Hypomasticus pachycheilus* has a slightly concave anterolateral margin on the supraorbital, but that incision is shallower than is the notch present in the other species of *Hypomasticus* cited above. *Hypomasticus pachycheilus* is consequently coded as possessing state 0. Adult specimens of *Leporinus* cf. *ecuadorensis* and *L. pellegrinii* as well as *Anostomoides laticeps* also have a weakly concave anteroventral margin of the supraorbital and are



**Figure 10.** Left infraorbital series of *Rhytidodus argenteofuscus*, USNM 229055, 108 mm SL; lateral view, sensory canal of first infraorbital in this species normally with two or three intermediate pores, but only one intermediate pore present in this specimen.



**Figure 11.** Left infraorbital series of *Laemolyta orinocensis*, USNM 270311; 91.6 mm SL; lateral view.

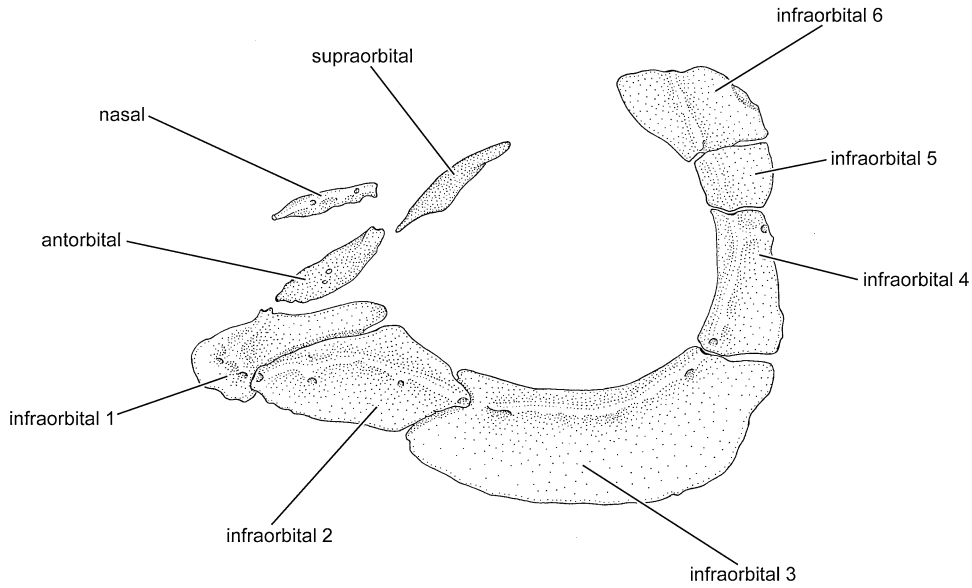
coded as having state 0. All remaining members of the Anostomidae and all examined outgroup taxa lack a notch in the ventral margin of the supraorbital.

Gregory & Conrad (1938: 348) erroneously reported that the supraorbital was lacking in *Leporinus*. This mistaken observation probably resulted from their basing their drawing and observation on a dry skeleton that presumably had lost that ossification during preparation.

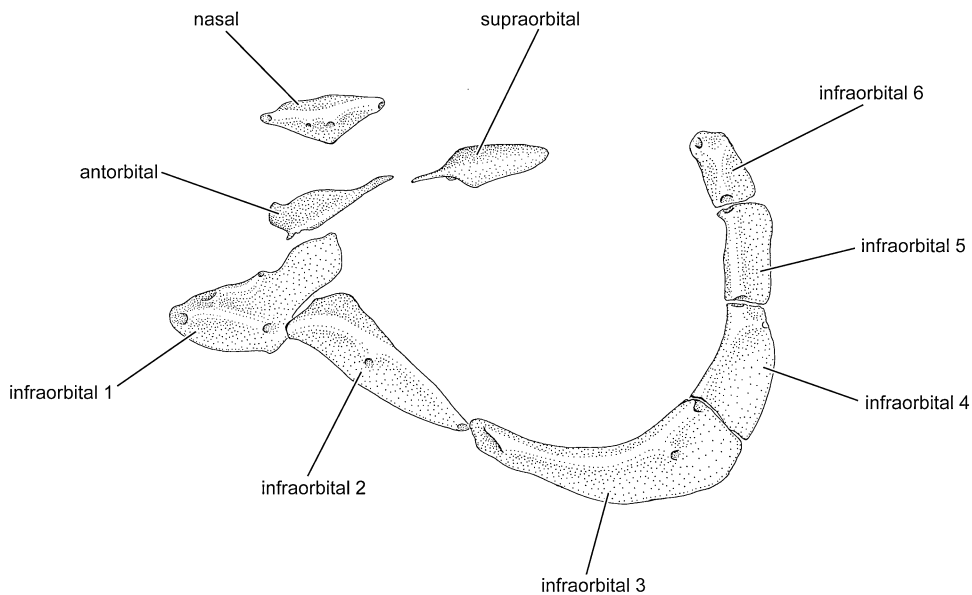
Optimization of this character on the final phylogeny is largely ambiguous. The notched condition

clearly originated once in *Gnathodolus*, and the polytomy in clade 18 makes it impossible to know whether a notched antorbital evolved once or twice in *Schizodon*. Near the base of the phylogeny the notch either evolved in the common ancestor of clade 3 with subsequent loss in *Hypomasticus pachycheilus* and clade 8, or originated independently in *Hypomasticus mormyrops*, *Leporinus gomesi* and clade 5.

4. Orientation of sensory canal of first infraorbital: (0) origin of sensory canal of first infraorbital in region



**Figure 12.** Left infraorbital series of *Petulanos plicatus*, USNM 225396, 75.8 mm SL; lateral view.



**Figure 13.** Right infraorbital series of *Gnathodolus bidens*, USNM 389623, 71 mm SL; lateral view, drawing reversed to place anterior at left.

proximate to antorbital positioned anterior of distal terminus of sensory canal where that canal contacts sensory canal of second infraorbital; (1) origin of sensory canal of first infraorbital situated directly dorsal to, or posterodorsal to, distal terminus of canal of first infraorbital where that canal contacts canal of second infraorbital (CI = 1.000; RI = 1.000).

In *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytidodus* and *Schizodon*, the primary laterosensory canal segment

of the first infraorbital canal has a horizontal orientation, with the canal beginning near the antorbital, running ventrally for a short distance through the anterior portion of the first infraorbital and then continuing posteriorly to contact the anterior opening of the canal of the second infraorbital (Figs 8–11). In *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* the canal runs from the pore proximate to the antorbital anteroventrally towards the snout for at least a short distance before



first turning ventrally and then again posteriorly to contact the canal segment in the second infraorbital (Figs 12, 13). This additional torsion of the sensory canal segment in the first infraorbital results in the opening of the canal closest to the antorbital being positioned dorsal to the area of contact of the canal of the first infraorbital with the second infraorbital (or in the case of *Petulanos intermedius* and *P. plicatus*, being located posterodorsal to the connection of the canal in the first infraorbital with that of the second infraorbital, Fig. 12).

All examined outgroups possess state 0 for this character except for *Curimatopsis microlepis*, which lacks a sensory canal on the first infraorbital and cannot be coded for this character. In the Chilodontidae and *Leporinus gomesi*, the usually horizontal posterior segment of the canal is angled ventrally to contact a more ventrally positioned canal on the anterior portion of the second infraorbital. This results in the posterior terminus of the canal of the first infraorbital being situated far ventral of, and only slightly posterior to, the origin of the canal system near the antorbital. The condition in the Chilodontidae and *L. gomesi* is superficially similar to the form of the canal in some of the taxa possessing state 1 for this character (notably *Anostomus anostomus*), but the Chilodontidae and *L. gomesi* meet the definition of state 0 and are coded accordingly.

The reconfiguration of the laterosensory canal of the first infraorbital represents an unambiguous synapomorphy for *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25).

5. *Number of intermediate pores along ossified portion of sensory canal of first infraorbital between area of contact of first and second infraorbitals and anterior terminus of sensory canal proximate to antorbital*: (0) no pores; (1) one pore; (2) two pores; (3) three or more pores (CI = 0.333; RI = 0.565).

As noted by Winterbottom (1980: 49), the number of pores along the length of the laterosensory canal (herein termed the intermediate pores) of the first infraorbital varies considerably within the Anostomidae and the immediate outgroups. Although there is clearly considerable homoplasy in this character, it is included in the analysis because it encompasses phylogenetic information.

All examined members of the Anostomidae have at least one intermediate pore along the length of the laterosensory canal segment on the first infraorbital. A single pore on that canal segment (state 1) is found in *Leporellus* (Fig. 8), *Petulanos* (Fig. 12), all species of *Hypomasticus* except *H. pachycheilus*, all species of *Leporinus* (Fig. 9) except *L. cf. ecuadorensis* and *L. striatus*, all species of *Schizodon* with the exception of *S. nasutus*, and most specimens of *Pseudanos gracilis*

(coded as 1). The single examined specimen of *Leporinus cf. moralesi* has two intermediate pores on one side and one pore on the other; it is coded as polymorphic for states 1 and 2. One side of one specimen of *Leporinus fasciatus* has two intermediate pores but the typical condition in this species is a single pore; *L. fasciatus* is coded as possessing state 1. Two intermediate pores (state 2) are found in *Abramites*, *Anostomoides*, *Anostomus*, *Gnathodolus* (Fig. 13), *Laemolyta* (Fig. 11), *Sartor*, *Synaptolaemus*, *Hypomasticus pachycheilus*, large specimens of *Leporinus cf. ecuadorensis* (this is assumed to represent the adult condition for the species), *L. striatus*, *Schizodon nasutus* and all members of *Pseudanos* except for most specimens of *P. gracilis*. *Rhytiodus argenteofuscus* is polymorphic with one (rarely, Fig. 10), two or three intermediate pores present on the first infraorbital (coded as a polymorphism for states 2 and 3). The small-scaled species of *Rhytiodus* (*R. microlepis* and *R. lauzannei*) have three or four intermediate pores on the first infraorbital (state 3).

*Caenotropus* and *Chilodus* typically have a single pore on the first infraorbital, albeit with a range of 0–2 pores (coded as state 1). Examined members of the Curimatidae lack intermediate pores on the sensory canal of the first infraorbital (state 0), while in the Prochilodontidae, *Prochilodus rubrotaeniatus* possesses two intermediate pores on the first infraorbital and *Semaprochilodus insignis* possesses one (see also Castro & Vari, 2004: fig. 18A, B). A single intermediate pore on the first infraorbital also occurs in *Parodon suborbitalis*, *Hemiodus ocellatus*, *Citharinus* sp. and *Xenocharax spilurus*, while two intermediate pores on that bone appear in *Brycon falcatus* and *Distichodus* sp.

Optimization of the character in our phylogeny is largely ambiguous, but character state 3 is a synapomorphy for *Rhytiodus lauzannei* and *R. microlepis* (clade 17), character state 2 is a synapomorphy for *Abramites* and *Leporinus striatus* (clade 9), and character state 1 is a synapomorphy for *Petulanos intermedius* and *P. plicatus* (clade 30). The plesiomorphic condition within the Anostomidae appears to be a single pore, and a transition to two pores is synapomorphic for either clade 13 or clade 14 (optimization ambiguous).

6. *Thickness and position of canals of first infraorbital*: (0) walls of sensory canal of first infraorbital thin and laterosensory canal mostly incorporated within main lamina of bone proper; (1) walls of sensory canal of first infraorbital thickened and laterosensory canal located lateral to main lamina of bone; canal fused only weakly along its medial surface to main lamina of first infraorbital (CI = 1.000; RI = 1.000).

The three examined species of *Rhytiodus* possess an unusual morphology of the sensory canal of the first infraorbital unique among the examined species inside and outside the Anostomidae. In *Rhytiodus* the walls of this canal are thickened and overall the canal has the appearance of a tube located lateral to, albeit fused medially to, the main lamina of the bone along the medial one-third of the canal (state 1; Fig. 10).

Members of several other anostomid genera (notably the species of *Schizodon*, many species of *Leporinus*, and *Laemolyta garmani*) also have somewhat thickened or raised sensory canals of the first infraorbital, but in none of these taxa are the conditions nearly as pronounced as the thickening and lateral displacement found in *Rhytiodus*. No examined members of the outgroups possess a comparable raised and thickened condition of the canal. In the final hypothesis of relationships, this character optimizes as a synapomorphy for the species of *Rhytiodus* (clade 16).

7. *Extent of development of dorsal lamina of second infraorbital*: (0) lamina located dorsal to sensory canal absent or poorly developed with maximum height less than diameter of sensory canal; (1) lamina located dorsal to sensory canal well developed with maximum height of dorsal lamina greater than diameter of sensory canal along at least part of length of canal (CI = 0.200; RI = 0.500).

Most members of the Anostomidae have a highly developed triangular or rounded lamina of bone extending dorsal of the ossified sensory canal of the second infraorbital (state 1, Figs 8, 9, 11–13). In *Rhytiodus*, *Schizodon nasutus*, *S. fasciatus*, *S. scotorhabdotus* and *S. vittatus*, this lamina is alternatively either very narrow or entirely absent (state 0, Fig. 10). In *Laemolyta taeniata* and *L. proxima*, the dorsal lamina is poorly developed but still present, with the width of the lamina greater than the diameter of the sensory canal for at least part of the length of the canal (coded as state 1). In *Anostomoides laticeps*, *Laemolyta garmani*, *L. orinocensis*, *Schizodon isognathus* and *S. knerii*, the dorsal lamina is present and wider than the canal, with the bulk of this process anteriorly positioned and the lamina effectively absent along the posterior portion of the bone (coded as state 1). The various species of *Leporinus* and *Hypomasticus* possess a well-developed dorsal lamina on the second infraorbital but vary considerably in the form of that lamina. In some cases (e.g. *L. striatus*) the greatest width of the lamina is anteriorly positioned while other species of *Leporinus* have the lamina widest above the midpoint of the horizontal length of that bone. Despite the variation in the form of the dorsal lamina on the second infraorbital, we found it impossible to parse unambiguously that variation into discrete character

states and elected to code only the presence or absence of a dorsal lamina greater in width than the width of the associated sensory canal.

The form of the second infraorbital varies widely among the proximate outgroups to the Anostomidae. The dorsal flange is well developed in most members of the Chilodontidae, e.g. *Chilodus punctatus* (Vari, Castro & Raredon, 1995: fig. 1B) albeit narrower in *Caenotropus mestomorgmatos* (Vari *et al.*, 1995: fig. 1A), and narrow and anteriorly positioned but still present in the examined members of the Prochilodontidae (Castro & Vari, 2004: fig. 18A–C) and Curimatidae (Vari, 1991: fig. 9A, B). The lamina is also present in the distant outgroups *Brycon* (Weitzman, 1962: fig. 9), *Hemiodus*, *Parodon* and *Distichodus*, but absent in *Citharinus* sp. and *Xenocharax spilurus*.

The plesiomorphic condition of the character in the Anostomidae appears to be state 1 (lamina well developed). The reduction of the dorsal lamina of the second infraorbital is a synapomorphy for *Rhytiodus* plus *Schizodon* (clade 15), with a subsequent reversal to a well-developed lamina in *Schizodon knerii* and *S. isognathus*.

8. *Number of intermediate pores along ossified portion of sensory canal of second infraorbital*: (0) no pores; (1) one pore; (2) two pores; (3) three pores (CI = 0.333; RI = 0.630).

Anostomids have 1–3 intermediate pores present along the body of the sensory canal of the second infraorbital. All examined species of *Abramites*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Pseudanos*, *Sartor* and *Synaptolaemus*, along with *Hypomasticus pachycheilus*, *Rhytiodus argenteofuscus*, *Leporinus striatus* and *Schizodon nasutus* have only a single intermediate pore present along the length of the body of the sensory canal of the second infraorbital (state 1; Figs 10, 11, 13). *Leporinus tigrinus* has three intermediate pores on the canal of the second infraorbital (state 3). The remaining species of *Hypomasticus* and *Leporinus* (Fig. 9) as well as *Anostomoides*, *Leporellus* (Fig. 8), *Petulanos* (Fig. 12), *Schizodon knerii*, *S. fasciatus*, *S. scotorhabdotus* and *S. vittatus* have two intermediate pores along the length of the sensory canal (state 2). Although some specimens of *Rhytiodus microlepis* have one intermediate pore on the second infraorbital, the majority have two pores and this species is coded as state 2. *Rhytiodus lauzannei* and *Schizodon isognathus* are polymorphic for states 2 and 3.

The examined proximate outgroups vary in the number of intermediate pores along the sensory canal of the second infraorbital. The first outgroup (Chilodontidae) is variable for the feature with one intermediate pore present in *Chilodus punctatus* (Vari *et al.*, 1995: fig. 1B) and two intermediate pores occurring in the species of *Caenotropus* (Vari *et al.*, 1995:

fig. 1A). Members of the Curimatidae usually have a single intermediate pore, although some species in the family have a second pore (Vari, 1991: fig. 9) and with the examined specimens of the basal *Curimatopsis macrolepis* lacking an intermediate pore on this bone. *Semaprochilodus insignis* in the Prochilodontidae has three intermediate pores, with two or occasionally three pores present in other species of that genus along with *Prochilodus* and *Ichthyoelephas* (see Castro & Vari, 2004: fig. 18). Among more distant outgroups, *Parodon suborbitalis*, *Hemiodus ocellatus*, *Citharinus* sp. and *Xenocharax spilurus* possess a single intermediate pore on the second infraorbital, *Distichodus* sp. possesses two pores, and *Brycon falcatus* lacks an intermediate pore on that bone.

In the final reconstruction character state 2 is plesiomorphic within the Anostomidae. State 1 is a synapomorphy for clades 9 and 21 with a reversal to state 2 synapomorphic for clade 30 (*Petulanos*).

9. *Fusion of fourth and fifth infraorbitals*: (0) unfused; (1) fused (CI = 0.333; RI = 0.200).

The typical condition of the fourth and fifth infraorbitals in the Characiformes, including most members of the Anostomidae, is for these elements to be present as separate ossifications (state 0). These two bones occasionally fuse in anomalous individuals of species that otherwise have the ossifications separate (see condition in *Pseudanos gracilis*; Sidlauskas & Santos, 2005: fig. 2A). In light of such intraspecific variation, we scored the fused condition as being present only for those specimens in which the conjoined fourth and fifth infraorbitals were observed on both sides of that individual. *Hypomasticus despaxi*, *H. megalepis*, *Leporinus aripuanaensis*, *L. ortomaculatus*, *L. pellegrinii* and *L. tigrinus* exhibit invariant fusion of the fourth and fifth infraorbitals (state 1). *Laemolyta orinocensis* is polymorphic for this character. One of the two examined cleared and stained specimens of *L. orinocensis* has a fusion of the fourth and fifth infraorbitals on both sides of the head, whereas the other specimen retains unfused infraorbitals on both sides. The remaining examined species in the Anostomidae have separate fourth and fifth infraorbitals.

The fourth and fifth infraorbitals are separate in proximate outgroups to the Anostomidae (Curimatidae, see Vari, 1991: fig. 9; Chilodontidae, see Vari *et al.*, 1995: fig. 1; Prochilodontidae, see Castro & Vari, 2004: fig. 18). Autogenous fourth and fifth infraorbitals are also present in the Parodontidae (Roberts, 1974: 61–62), Hemiodontidae [e.g. *Hemiodus ocellatus* (Vari, 1982a)], the Citharinidae [e.g. *Citharidium* (Daget, 1962a: fig. 10) and *Citharinus* (Daget (1962b: fig. 7)] and the Distichodontidae [e.g. *Paradistichodus* (Daget, 1958: fig. 9) and *Xenocharax* (Daget, 1960: fig. 7)].

Under the final hypothesis of relationships, the fusion of the fourth and fifth infraorbitals is a synapomorphy for *Hypomasticus despaxi* and *H. megalepis* (clade 5). The relationship of *Leporinus aripuanaensis* to *L. ortomaculatus* is unresolved due to the polytomy in clade 8, but the fusion of the fourth and fifth infraorbitals is potentially synapomorphic for those two species. The independent fusions of the fourth and fifth infraorbitals in *Leporinus tigrinus* and *L. pellegrinii* are homoplasies with respect to the fusions in *Hypomasticus* and in the other cited species of *Leporinus*.

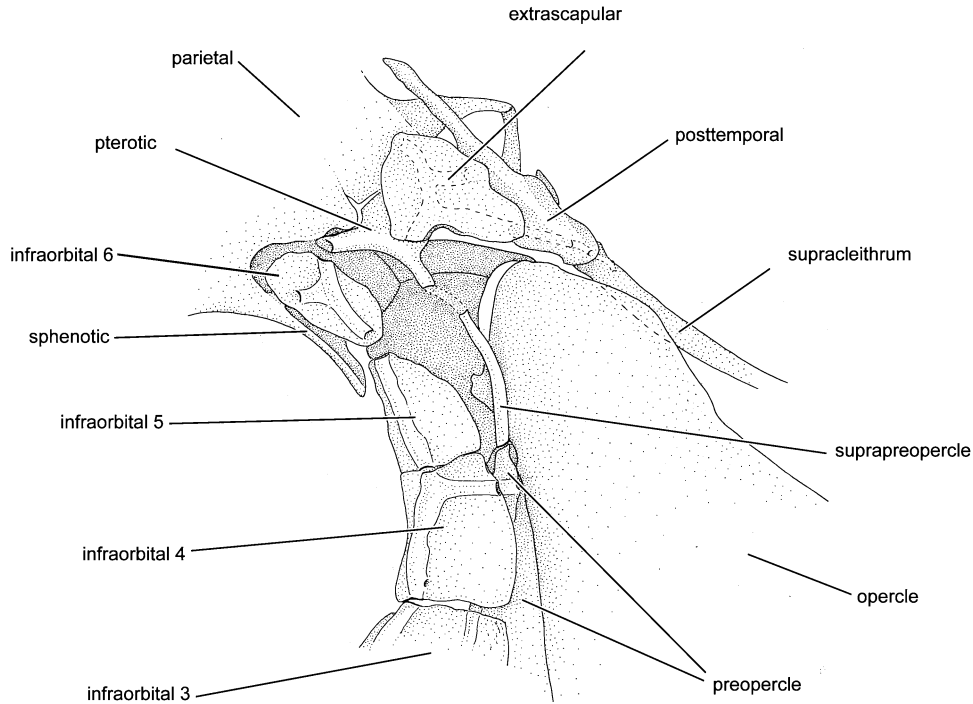
10. *Relative height of fourth and fifth infraorbitals*: (0) vertical extent of fourth and fifth infraorbitals approximately equal or fifth infraorbital longer along vertical axis than fourth; (1) fourth infraorbital much longer along vertical axis than fifth infraorbital (CI = 0.333; RI = 0.917).

In the typical characiform condition the vertical extents of the fourth and fifth infraorbitals are approximately equal and both contribute to the posterior margin of the orbit to the same approximate degree (state 0). This condition, or a condition in which the fifth infraorbital is longer along the vertical axis than is the fourth, occurs in all examined outgroups (e.g. Chilodontidae, Vari *et al.*, 1995: fig. 1).

Like the outgroups, members of *Hypomasticus*, *Leporellus* and *Leporinus* possess a large fifth infraorbital. *Leporellus* has an abbreviated fourth infraorbital that is slightly shorter in vertical extent than the fifth infraorbital (state 0; Fig. 8, noting that the fourth infraorbital is anomalously separated into two ossifications in the illustrated specimen). Many species of *Leporinus* possess fourth and fifth infraorbitals of roughly equivalent vertical extents (state 0, Figs 9, 14). Several species in *Hypomasticus* and *Leporinus* cannot be coded for this character because of the fusion of the fourth and fifth infraorbitals (see character 9). In *Abramites*, *Anostomoides*, *Anostomus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytidodus*, *Sartor*, *Schizodon* and *Synaptolaemus*, the fourth infraorbital is vertically distinctly more developed than the fifth and forms a much greater portion of the posterior margin of the orbit (state 1, Figs 10–12). In *Gnathodolus* the fourth and fifth infraorbitals are very narrow relative to the condition in other anostomids, but of about equivalent heights (Fig. 13). *Gnathodolus* is thus coded as state 0 for this character.

State 1 for this character (fourth infraorbital much longer along vertical axis than fifth) is a synapomorphy for either clade 12 or 13 in the final reconstruction. The ambiguity is due to *Leporinus pellegrinii* (a component of clade 12 but not clade 13), which has fused fourth and fifth infraorbitals and cannot be coded for this character. The occurrence of state 1 (fourth infraorbital





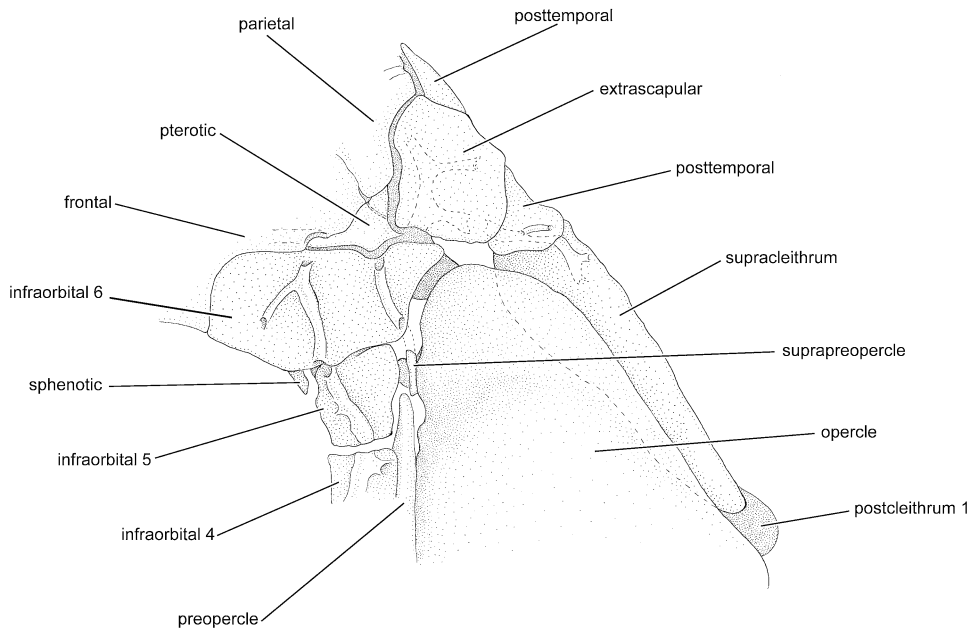
**Figure 14.** Dorsal portions of left infraorbital series, opercular series and pectoral girdle of *Leporinus agassizi*, FMNH 102219, 98.6 mm SL; lateral view.

longer along vertical axis than is the fifth infraorbital) in *Abramites* is a homoplasy relative to its occurrence in either clade 12 or 13 and is possibly correlated with the great increase in body depth in that taxon. The deeply nested *Gnathodolus bidens* has reverted to the plesiomorphic condition of fourth and fifth infraorbitals of approximately equivalent heights.

11. *Degree of development of flange of fifth infraorbital posterior of sensory canal:* (0) flange present along entire margin of bone; (1) flange less extensive or entirely absent, with at least dorsal section of flange missing (CI = 0.143; RI = 0.538).

The fifth infraorbital in the Anostomidae commonly has the form of a flat plate with a dorsoventrally aligned sensory canal running through the anterior portion of the bone and with a wide ossified lamina extending posterior of the posterior margin of the sensory canal (Figs 8, 9, 12, 13; Winterbottom, 1980: figs 30, 32; Sidlauskas & Santos, 2005: fig. 2). *Rhytiodus argenteofuscus* and the species of *Laemolyta* lack the dorsal portion of this posterior lamina. The posterodorsal limit of the sensory canal consequently forms the posterodorsal margin of the fifth infraorbital (state 1; Figs 10, 11). In *Rhytiodus lauzannei* and *R. microlepis* the entire posterior lamina of the fifth infraorbital is missing, with the posterior margin of that ossification completely delimited by the posterior wall of the sensory canal (also coded as state 1).

Among the proximate outgroups to the Anostomidae, the posterior lamina on the fifth infraorbital is absent in the Chilodontidae in which that ossification is reduced to a tubular ossification (Vari *et al.*, 1995: fig. 1), but present and fully developed in the Prochilodontidae (Castro & Vari, 2004: fig. 18). Within the Curimatidae a well-developed posterior lamina is absent in *Curimatopsis microlepis*, present in *Potamorhina* (Vari, 1989a: fig. 35B) and greatly reduced or absent in more derived components of that family including *Curimata inornata*, *Steindachnerina* (Vari, 1991: fig. 9), *Psectrogaster* (Vari, 1989a: fig. 34A) and *Curimatella* (Vari, 1989a: fig. 34C). Among more distant outgroups, the lamina is present in the Parodontidae (Roberts, 1974: figs 61, 62), *Hemiodus ocellatus*, *Xenocharax spilurus* (Daget, 1960: fig. 7) and *Brycon* (Weitzman, 1962: fig. 8). In light of that information and that fact that both *Laemolyta* and *Rhytiodus* appear in a relatively derived position in the final hypothesis of relationships for the Anostomidae, the presence of a complete posterior lamina on the fifth infraorbital is most parsimoniously hypothesized to be the plesiomorphic condition for the clade consisting of the Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae, with a reduction of the lamina having arisen independently in the Chilodontidae, and some components of the Curimatidae and Anostomidae.



**Figure 15.** Dorsal portions of left infraorbital series, opercular series and pectoral girdle of *Abramites hypselonotus*, FMNH 97711, 76.0 mm SL; lateral view, fusion of infraorbital 6 and dorsal supraopercle in this specimen not typical of the species.

The final phylogenetic hypothesis suggests that the reduction or elimination of the posterior lamina of the fifth infraorbital arose separately in *Laemolyta* (clade 22) and *Rhytiodus* (clade 16). Despite the global homoplasy, character state 1 is synapomorphic for each of these clades considered individually.

12. *Branching and poring pattern of sensory canals in sixth infraorbital*: (0) canal tripartite or with form of angled tube with medial pore situated at angle of tube; (1) canal straight and lacking medial pore; (2) canal with five or more components (CI = 0.364; RI = 0.462).

The typical characiform condition for the sixth infraorbital is a flat plate bearing a tripartite sensory canal (state 0), as in *Xenocharax* (Daget, 1960: fig. 7) and other members of the Distichodontidae (Vari, 1979: 296–301). Most anostomids share this tripartite condition of the canal [*Abramites* (Fig. 15), *Anostomoides*, *Gnathodolus* (Fig. 13), *Leporellus* (Fig. 8), *Rhytiodus* (Fig. 10), *Schizodon*, *Synaptolaemus*, *Laemolyta garmani*, one of two specimens of *L. taeniata*, and most species of *Hypomasticus* and *Leporinus* (Figs 9, 14)] or a slightly modified condition in which the posterodorsal branch of the canal is significantly truncated and represented only by the pore situated at the angle along the primary canal [*Laemolyta proxima*, *L. orinocensis* (Fig. 11) and the other specimen of *L. taeniata*, also coded as state 0]. In *Anostomus*, *Petulanos*, *Pseudanos*, *Sartor*, *Hypomasti-*

*cus despaxi* and most specimens of *H. mormyrops* one of the dorsal branches of the sensory canal and the associated pore are absent and the laterosensory canal in the sixth infraorbital has the form of a simple, dorsoventrally inclined, unbranched tube (Fig. 12; see discussion in Winterbottom, 1980: 49). Although most specimens of *H. mormyrops* have this unbranched morphology, one has tripartite canals on both sixth infraorbitals. One specimen of *L. fasciatus* and the sole examined specimens of *L. gomesi* and *L. striatus* differ between contralateral sides in the presence of the third branch of the canal in question, indicating apparent latent intraspecific developmental variability.

A reduction to an effectively single tube with a medial pore within the sixth infraorbital is common to both *Caenotropus* and *Chilodus* of the Chilodontidae (state 0, Vari *et al.*, 1995: fig. 1) as well as *Curimatopsis microlepis* within the Curimatidae, whereas a tripartite canal (state 0) or an elaboration of that system to five or more branches (state 2) is common to *Potamorhina*, *Curimata* and *Psectrogaster* within the Curimatidae (Vari, 1989a: 39, fig. 36A–C). The remaining genera in that family have the laterosensory system in the sixth infraorbital reduced to a single canal (Vari, 1989a: fig. 36D). Similarly, *Prochilodus* and *Semaprochilodus* in the Prochilodontidae have a canal with three or more branches in the sixth infraorbital (Castro & Vari, 2004: fig. 18A, B). Among the more distant outgroups, *Parodon suborbitalis* has an unbranched

canal of the sixth infraorbital while *Hemiodus ocellatus*, *Brycon falcatus*, *Citharinus* sp., *Xenocharax spilurus* and *Distichodus* sp. possess the tripartite condition.

In the final phylogenetic reconstruction, the tripartite condition of the canal of the sixth infraorbital is plesiomorphic with respect to the Anostomidae and the unbranched condition is a synapomorphy for clade 25. Reversion to the tripartite condition occurs in *Synaptolaemus* and *Gnathodolus* within clade 25. The occurrence of the unbranched condition of the sixth infraorbital canal in *Hypomasticus despaxi*, *H. mormyrops*, *Leporinus gomesi* and *L. striatus* are homoplasies under this reconstruction.

13. *Overlap of anteroventral process of sphenotic by sixth infraorbital*: (0) anteroventral portion of sixth infraorbital expanded and overlapping anteroventral process of sphenotic, with anterior margin of sixth infraorbital reaching or surpassing anterior border of ventral process of sphenotic that forms posterodorsal portion of the bony orbit; (1) anteroventral portion of sixth infraorbital not greatly expanded and overlapping anteroventral process of sphenotic (CI = 0.333; RI = 0.538).

In most members of the Anostomidae the sixth infraorbital covers the dilatator fossa, a dorsally concave, posteroventrally aligned indentation situated on the dorsolateral portion of the neurocranium and formed by adjoining sections of the sphenotic, frontal and pterotic bones. In general, the sixth infraorbital in members of the Anostomidae is circumscribed by the sphenotic, frontal and pterotic bones and fails to overlap significantly any of these ossifications (state 1, e.g. *Leporinus agassizi*, Fig. 14). In *Abramites* (Fig. 15), *Anostomus anostomus*, *Leporellus*, some specimens of *Hypomasticus mormyrops* and one side of the specimen of *Leporinus striatus*, the sixth infraorbital overlaps the sphenotic and contributes to the rim of the orbit (state 0). The overall frequency of such overlap is impossible to determine in *H. mormyrops* and *L. striatus*; those two species are coded as polymorphic for this character.

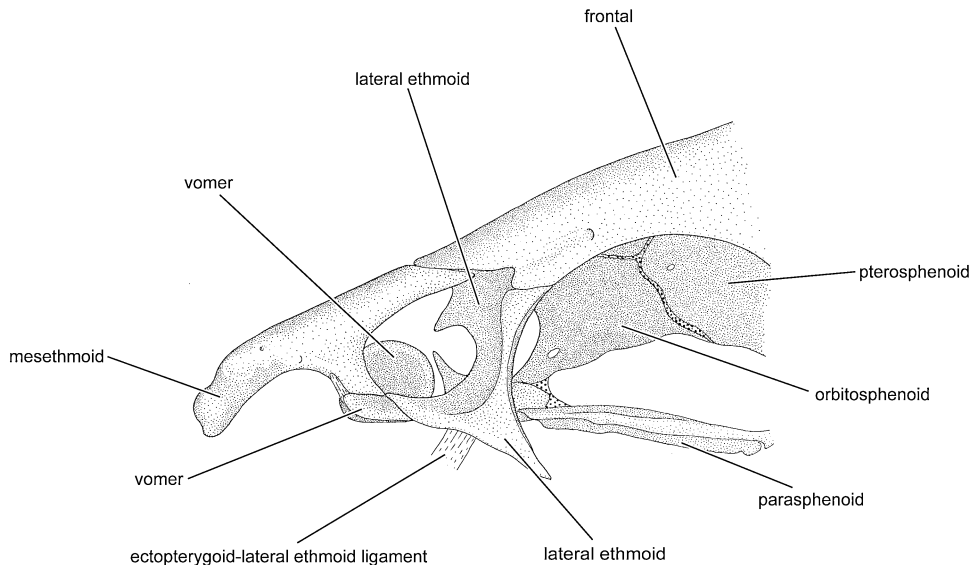
Within the Chilodontidae, the first outgroup to the Anostomidae, the sixth infraorbital demonstrates two different conditions, being either a flat plate-like bone with an enclosed sensory canal (*Chilodus*) or limited to an ossified tube surrounding the segment of the canal (*Caenotropus*). In *Chilodus* the plate-like sixth infraorbital extends further anteriorly and passes lateral to the ventral process of the sphenotic. As a consequence the anteroventral margin of the sixth infraorbital in that genus forms a portion of the posterodorsal margin of the bony orbit (state 0). The overlap of the sphenotic by the sixth infraorbital is also observed in *Curimata inornata*, *Prochilodus*

*rubrotaeniatus*, *Parodon suborbitalis*, *Hemiodus ocellatus*, *Brycon falcatus*, *Xenocharax spilurus* and *Distichodus* sp. The overlap is absent in *Curimatopsis microlepis*, *Potamorhina laticeps*, *Semaprochilodus insignis* and *Citharinus* sp.

Within the Anostomidae, the occurrence of the overlap of the sphenotic by the sixth infraorbital in *Leporellus* reflects the retention of the plesiomorphic morphology of the ossification under the arrived-at phylogenetic hypothesis. The loss of that overlap (state 1) is a synapomorphy for clade 3, containing the remainder of the Anostomidae. Although *Abramites*, *Leporinus striatus* and *Hypomasticus mormyrops* are relatively basal components of the Anostomidae, their possession of state 0 for this character is homoplastic with respect to the similar condition in *Leporellus* and the outgroups. If an examination of a larger series of *L. striatus* reveals that state 0 is typical for that species (currently coded as polymorphic), then reversal to state 0 would then optimize as a synapomorphy of clade 9, linking *L. striatus* to *Abramites*. *Anostomus anostomus*, which shares a sixth infraorbital that overlaps the sphenotic, possesses many other derived features that nest it within the clade consisting of *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25). Due to the phylogenetic separation between *Anostomus anostomus*, on the one hand, and the basal genera in the Anostomidae and *Chilodus* in the Chilodontidae, on the other, the overlap of the ventral process of the sphenotic by the sixth infraorbital in *Anostomus anostomus* is clearly homoplastic with respect to the similar condition in those taxa.

14. *Posterior extent of sixth infraorbital and fusion with suprapreopercle*: (0) sixth infraorbital not posteriorly expanded and entirely separate from suprapreopercle; (1) sixth infraorbital posteriorly expanded and fused with suprapreopercle (CI = 0.500; RI = 0.857).

In the species of *Anostomus*, *Petulanos* and *Pseudanos* the sixth infraorbital is expanded posteriorly along the ventral margin of the pterotic to extend over a portion of the dilatator fossa that is plesiomorphically covered solely by soft tissue in most characiforms. In the three taxa cited above, the sixth infraorbital encloses a portion of the sensory canal leading from the preopercle into the posterior pore of the pterotic [state 1, for condition in *Pseudanos* see Sidlauskas & Santos (2005: fig. 2)] and is apparently fused with the upper of the two components of the suprapreopercle that are present in many anostomids. *Leporinus striatus* has a posteriorly expanded sixth infraorbital that contacts the fleshy sensory canal leading into the posterior pore on the pterotic but does not fuse with a suprapreopercle; *L. striatus*



**Figure 16.** Right anterior portion of neurocranium of *Leporellus vittatus*, INHS 56128, 78.2 mm SL; lateral view, drawing reversed to place anterior at left.

is coded as possessing state 0. *Abramites hypselonotus* also has a posteriorly expanded sixth infraorbital which contacts a separate plate-like suprapreopercle (five specimens) or fuses with it (one specimen, FMNH 97711, Fig. 15). Because the clear majority of specimens of *Abramites hypselonotus* possess unfused suprapreopercles and sixth infraorbitals, that species is coded as possessing state 0. The remaining species within the Anostomidae possess relatively compact sixth infraorbitals (Fig. 14) that are not expanded posteriorly along the ventral margin of the pterotic (state 0) and which do not fuse with a suprapreopercle (two suprapreopercles in *Sartor* and *Gnathodolus*, one in all other examined taxa). *Sartor elongatus* is notable in possessing a plate-like morphology of the upper suprapreopercle, which extends anteriorly toward the sixth infraorbital, but these bones remain separate and *Sartor* is coded as possessing state 0.

An incorporation of the dorsal component of the suprapreopercular laterosensory canal into a posteriorly expanded sixth infraorbital also occurs in a derived clade within the basal characiform family Distichodontidae (Daget, 1958: fig. 9, 1961: fig. 7; Vari, 1979: figs 22, 24, 26). This clearly represents a homoplastic occurrence of the feature within the context of the understanding of the relationships of the Distichodontidae and Anostomidae within the Characiformes (Vari, 1979; Fink & Fink, 1981; Vari, 1983; Buckup, 1998).

Under the final phylogenetic hypothesis, the posterior expansion of the sixth infraorbital and its fusion with the suprapreopercle is a synapomorphy for clade 25 that is reversed in clade 31. Although not explicitly

coded, the posterior expansion of the sixth infraorbital without fusion with the suprapreopercle seen in *Leporinus striatus* and most specimens of *Abramites hypselonotus* may represent a synapomorphy linking those two species, as they cluster together in clade 9 in the final phylogenetic hypothesis.

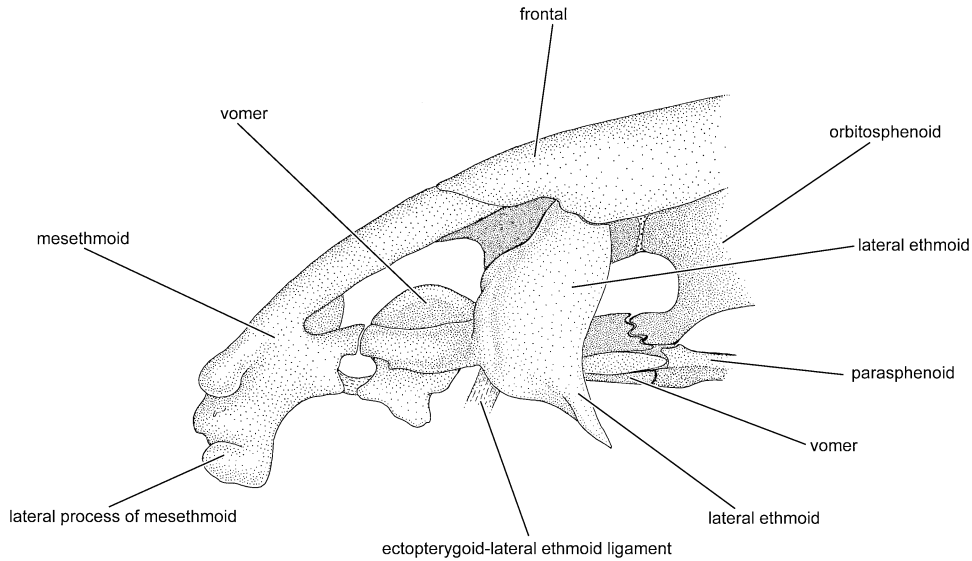
#### NEUROCRANIUM

15. *Form and orientation of anterior portion of mesethmoid*: (0) anterior portion of mesethmoid ventrally directed and with strong hook; (1) anterior portion of mesethmoid anteriorly or anteroventrally aligned and without strong hook (CI = 0.200; RI = 0.556).

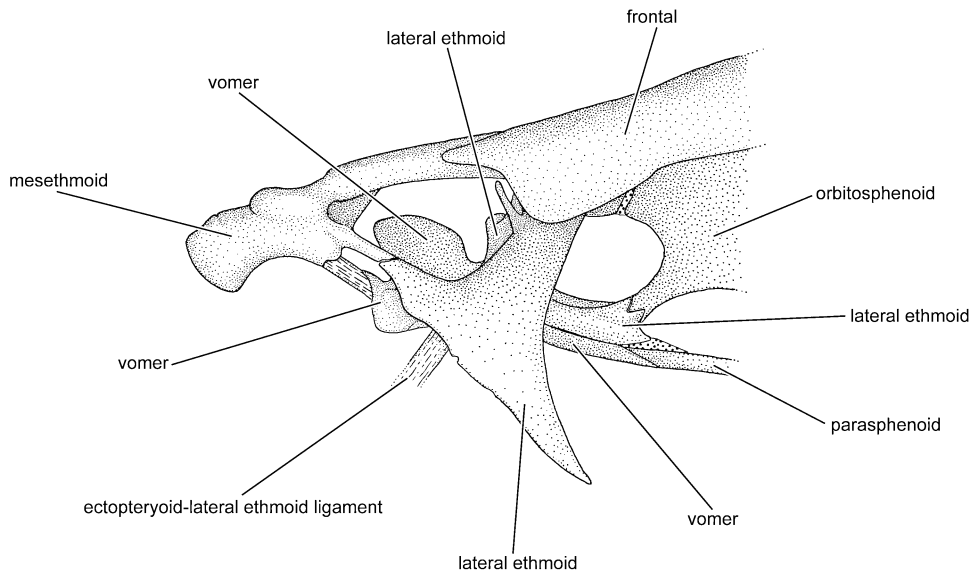
In *Hypomasticus*, *Leporellus*, *Leporinus jatuncochi* and *Schizodon nasutus*, the mesethmoid has a pronounced ventral curvature along its anterior portion in lateral view (state 1; Figs 16, 17). Most of the species with this anteriorly hooked form of the mesethmoid also have ventrally positioned mouths (*Hypomasticus*, *Leporellus* and *Schizodon nasutus*). Despite possessing the hooked mesethmoid, *Leporinus jatuncochi* has a terminal mouth, suggesting that the hook-shaped anterior portion of the mesethmoid and the ventrally positioned mouth are not always functionally correlated. In the remaining species in the Anostomidae, the anterior portion of the mesethmoid runs parallel, or nearly parallel, to the longitudinal axis of the body and lacks a ventrally directed hook (state 0; e.g. *Leporinus fasciatus*, Fig. 18).

Members of *Caenotropus* in the Chilodontidae possess a hooked anterior portion of the mesethmoid





**Figure 17.** Left anterior portion of neurocranium of *Hypomasticus mormyrops*, USNM 318140, 104 mm SL; lateral view.



**Figure 18.** Left anterior portion of neurocranium of *Leporinus fasciatus*, USNM 225991, 87.8 mm SL; lateral view.

(Vari, 1983: fig. 32A). Conversely, *Chilodus* in the Chilodontidae as well as all other examined out-groups possess a straight anterior portion of the mesethmoid. Optimization of this character near the base of the Anostomidae is ambiguous. Under ACCTRAN optimization, the hooked mesethmoid is a synapomorphy for the Chilodontidae + Anostomidae that is reversed in *Chilodus* and clade 7 within the Anostomidae, with *Leporinus jatuncochi* and *Schizodon nasutus* switching back to the hooked form within clade 7. Under DELTRAN, a straight mesethmoid is plesiomorphic for the Anostomidae and Chilodontidae with the hooked form arising independently

in *Caenotropus*, *Leporellus*, *Hypomasticus*, *Leporinus jatuncochi* and *Schizodon nasutus*.

16. Presence or absence of lateral process of anterior portion of mesethmoid: (0) mesethmoid without distinct lateral processes that fit into concavities on medial surface of premaxilla; (1) mesethmoid with two distinct lateral processes that fit into concavities on medial surface of premaxilla (CI = 0.500; RI = 0.800).

In all species of the Anostomidae the articulation of the premaxilla with the mesethmoid occurs along a concavity on the medial surface of the premaxilla. The

lateral surfaces of the mesethmoid contacting the premaxilla are typically flat or slightly curved (Figs 16, 18). In the four examined species of *Hypomasticus* (*H. despaxi*, *H. megalepis*, *H. mormyrops* and *H. pachycheilus*) the anterior margin of the hooked process of the mesethmoid (see character 15) instead has two prominent lateral processes that fit into the concavity on the medial surface of the premaxilla (Fig. 17). These processes are most highly developed in *Hypomasticus mormyrops* and *H. pachycheilus* and less prominent in *H. despaxi* and *H. megalepis*. Some other species in the Anostomidae have indistinct convexities or knob-like processes on the lateral surfaces of the mesethmoid (e.g. *Leporinus pellegrinii*), but in none of those species is the degree of development of the lateral processes of the mesethmoid as pronounced as that present in the species of *Hypomasticus*.

With the exception of the species of *Caenotropus*, examined members of the outgroups lack lateral processes on the mesethmoid that serve as areas of articulation of that ossification with the premaxilla. In *Caenotropus* there is a lateral process of the hooked portion of the mesethmoid (coded as state 1), but this process arises from the posterior margin of the hooked portion of the mesethmoid rather than the anterior margin of that bone as in the four cited species of *Hypomasticus*. This positional difference suggests that the lateral process of the anterior mesethmoid is non-homologous in *Caenotropus* with respect to the process present in the four *Hypomasticus* species, a hypothesis congruent with the phylogenetic reconstruction in which the lateral process of the mesethmoid is a synapomorphy for clade 4 (*Hypomasticus*).

17. *Orientation of ventral process of mesethmoid contacting anterior limit of vomer*: (0) ventral process of mesethmoid runs vertically or nearly so, anterior portion of vomer positioned directly ventral to ventral process of mesethmoid; (1) ventral process of mesethmoid posteroventrally aligned; (2) ventral process of mesethmoid horizontally or slightly posterodorsally aligned, vomer directly posterior of ventral portion of mesethmoid (CI = 0.333; RI = 0.765).

In many members of the Anostomidae, the mesethmoid connects to the vomer along the ventral portion of the anterior region of the neurocranium by way of a distinct process that has a posteroventral orientation (*Anostomoides*, *Laemolyta*, *Leporinus*, *Hypomasticus megalepis*, *Rhytidodus*, *Schizodon fasciatus*, *S. knerii*, *S. scotorhabdotus*, *S. vittatus*) (Fig. 18). In another set of taxa (*Abramites*, *Anostomus*, *Gnathodolus*, *Leporellus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*) the anterior margin of the vomer is positioned directly ventral to or nearly ventral to

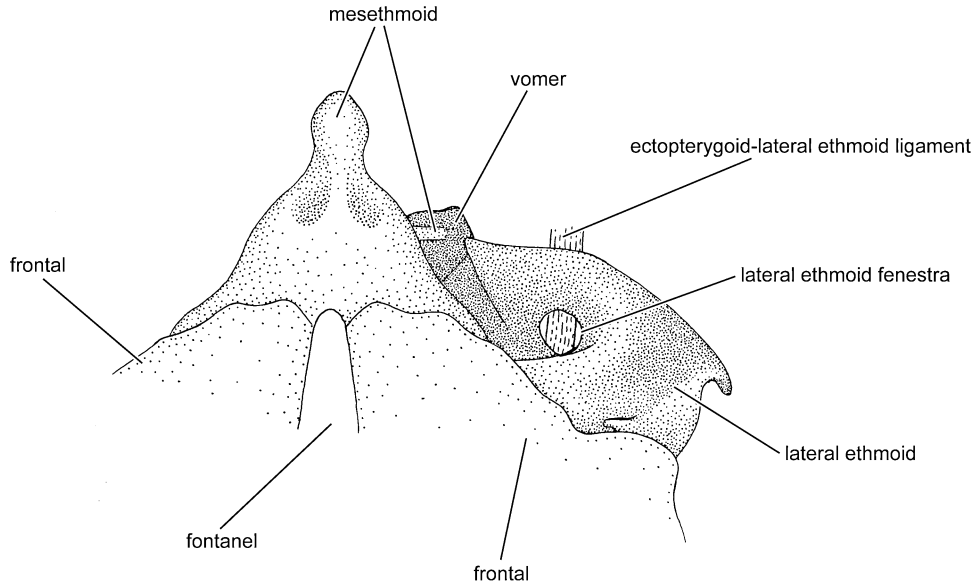
the connecting process of the mesethmoid, which has a distinctly vertical orientation (Fig. 16; see also Winterbottom, 1980: fig. 51). A third set of species (*Hypomasticus despaxi*, *H. mormyrops*, *H. pachycheilus*, *Schizodon isognathus* and *S. nasutus*) has the vomer located directly posterior of the connecting process of the mesethmoid and the process has either a primarily horizontal or a slightly posterodorsally inclined orientation (Fig. 17). All five members of this last group of species possess slightly to strongly subterminal mouths.

Most of the outgroups to the Anostomidae lack a clear homologue of the process of the mesethmoid that connects to the vomer, although *Chilodus punctatus* and *Distichodus* sp. do have such processes orientated posteroventrally (state 1). In light of the homology problem, we refrained from coding the remaining outgroups for this character.

Under the final phylogenetic hypothesis in this study, state 1 (posteroventral process) is the plesiomorphic condition, with state 0 (vertical process) arising separately in *Leporellus*, *Abramites* and clade 25. State 2 (posterodorsal or horizontal process) optimizes as a synapomorphy for *Schizodon isognathus* and *S. nasutus* (clade 19). State 2 is ambiguously optimized within *Hypomasticus*; it either evolved in clade 4 with a reversal to state 1 in *H. megalepis*, or evolved independently in *H. despaxi* and clade 6.

18. *Presence or absence of ventromedial plate-like process of mesethmoid*: (0) ventromedial process on mesethmoid absent or very small; (1) distinct ventromedial plate-like process of mesethmoid extends ventrally and posteriorly towards vomer (CI = 0.500; RI = 0.938).

The anterior region of the neurocranium in members of the Anostomidae has a concavity bordered by the mesethmoid anteriorly and dorsally, the vomer ventrally, and the lateral ethmoid posteriorly. A bony and/or cartilaginous medial plate separates the left and right halves of this cavity, and in all examined species within the Anostomidae except the species of *Leporellus*, one specimen of *Leporinus ortomaculatus* and possibly *Laemolyta proxima*, a distinct ventromedial process of the mesethmoid contributes to the medial plate in the anterior portion of the neurocranium (Figs 17, 18). Conversely, *Leporellus pictus*, *L. vittatus*, *Laemolyta proxima* and the smaller of two specimens of *Leporinus ortomaculatus* have the contribution of the mesethmoid to the medial plate either much less extensive or absent (Fig. 16). The absence of the plate in the small specimen of *Leporinus ortomaculatus* appears to represent the juvenile condition, as the plate is fully ossified in the larger examined specimen of the species. *Leporinus ortomaculatus* is therefore coded as state 1 (the



**Figure 19.** Anterior portion of neurocranium of *Anostomoides laticeps*, INHS 53677, 106.6 mm SL; dorsal view.

adult condition). Part of the medial portion of the mesethmoid blocks a view of the anteromedial section of that bone in *Leporellus* (Fig. 16). The portion that is blocked from view potentially harbours a small medial process of the mesethmoid which, if present, would be much less extensive than the condition typical for the other genera cited above. No ventromedial process of the mesethmoid is visible in the specimen of *Laemolyta proxima*, but the specimen is small and failed to stain well for cartilage, and the plate may be present as an unossified unstained process. *Laemolyta proxima* is coded as having the process absent in keeping with the morphology apparent in the specimen.

The medial plate-like extension of the mesethmoid is absent in all examined outgroups. Under the final hypothesis of relationships, a small or absent medial plate of the mesethmoid is a plesiomorphic condition shared between *Leporellus* and the members of the proximate outgroups, and the fully developed medial plate is a synapomorphy for clade 3, with a potential reversal in *Laemolyta proxima*.

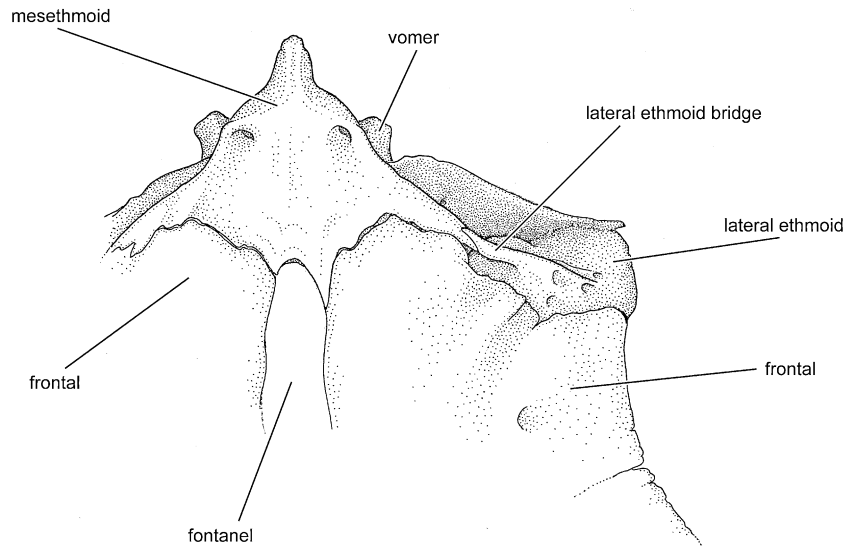
19. *Width of mesethmoid*: (0) mesethmoid wide, with maximum width along transverse axis greater than maximum length along longitudinal axis; (1) mesethmoid narrow, with maximum width along transverse axis much less than maximum length along longitudinal axis (CI = 0.167; RI = 0.688).

The mesethmoid in most members of the Anostomidae is maximally as wide as, or wider, along the transverse axis as it is long along the longitudinal axis. The overall shape of this wide form of the mesethmoid approximates an equilateral triangle

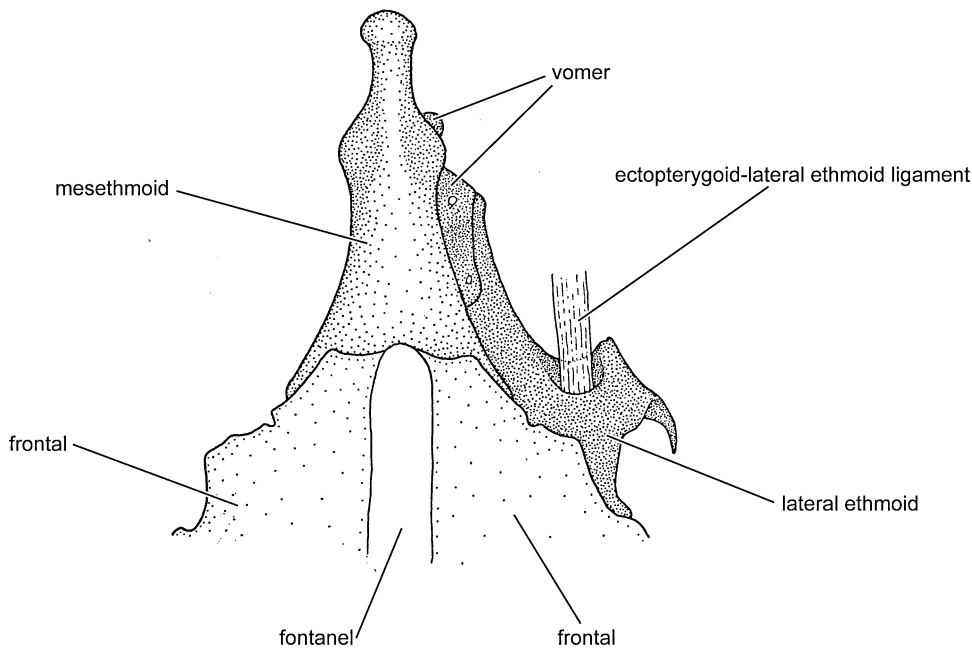
(Figs 19, 20; see also Winterbottom, 1980: fig. 53, the ethmoid of that author). Species of *Anostomus*, *Petulanos*, *Gnathodolus*, *Leporellus*, *Sartor* and *Synaptolaemus*, as well as *Hypomasticus despaxi*, *H. mormyrops* and *H. pachycheilus* have narrow mesethmoids that are longer along the longitudinal axis than they are wide along their transverse axis (Fig. 21). Winterbottom (1980: 51) cited the narrow form of the mesethmoid in *Anostomus* (encompassing *Petulanos*), *Gnathodolus*, *Sartor* and *Synaptolaemus* as a synapomorphy for those genera.

Both conditions of the mesethmoid are observed among the outgroups. *Caenotropus* and *Chilodus* in the Chilodontidae, the immediate outgroup to the Anostomidae, possess a narrow mesethmoid, as do the more distantly related *Parodon suborbitalis* and *Hemiodus ocellatus*. The mesethmoids of examined members of the Curimatidae, Prochilodontidae, Distichodontidae and *Brycon meeki* are, by contrast quite wide. *Citharinus* possesses a mesethmoid with an intermediate width that is nevertheless closer to the wide form of the bone than to the narrow morphology (see Daget, 1962b: fig. 7). *Citharinus* is coded as state 0.

Under the final hypothesis of relationships arrived at in this study, the narrow form of the mesethmoid optimizes as plesiomorphic for the Anostomidae. Variation in mesethmoid shape within the family represents at least two evolutionary transitions: the widening of the mesethmoid in *Hypomasticus megalepis* and clade 7 and a subsequent reversion to the narrow morphology of that bone in the lineage leading to *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus* (clade 27).



**Figure 20.** Anterior portion of neurocranium of *Schizodon fasciatus*, INPA 21606, 283 mm SL; dorsal view.



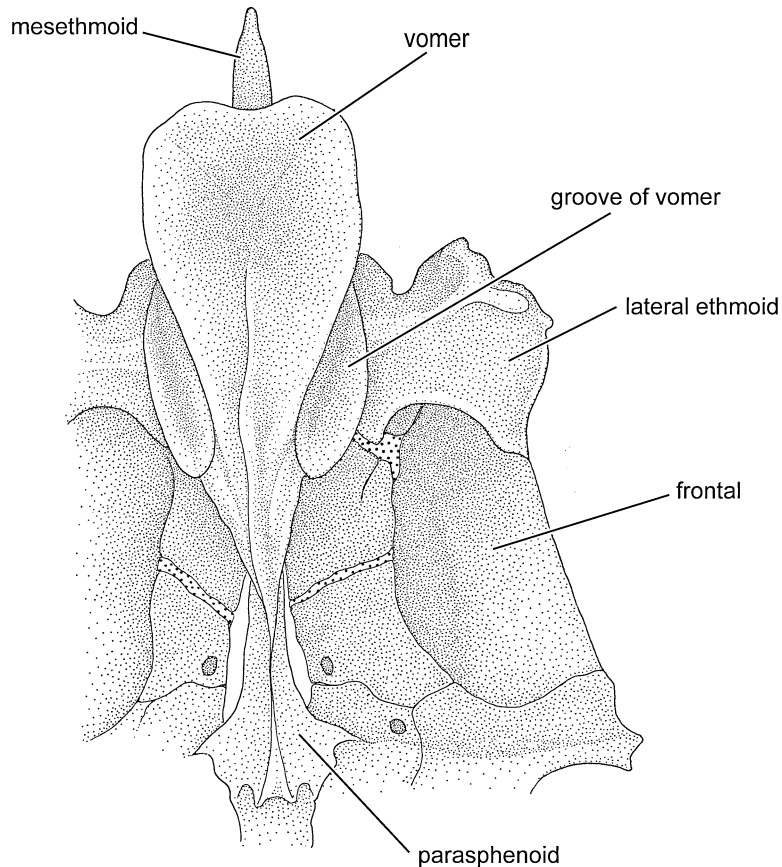
**Figure 21.** Anterior portion of neurocranium of *Synaptaemus cingulatus*, USNM 389693, 99 mm SL; dorsal view.

20. Presence or absence of deep grooves on each side of vomer that receive dorsal portion of mesopterygoid and metapterygoid: (0) vomer without two deep grooves on ventral surface that receive dorsal margins of mesopterygoid, metapterygoid and palatine; (1) vomer with two deep grooves on ventral surface that receive dorsal margins of mesopterygoid, metapterygoid and palatine (autapomorphy).

Uniquely among the examined members of the Anostomidae and outgroups, *Gnathodolus bidens* possesses a greatly expanded vomer with two deep,

ventral, longitudinal grooves (Fig. 22; see also Winterbottom, 1980: fig. 58) that receive the dorsal portions of the also restructured metapterygoid, mesopterygoid and quadrate (see characters 70, 81). There is no apparent ligamentous or muscular connection between the dorsal portions of the suspensorium and the vomer, and we infer from the motion of the suspensorium in cleared and stained specimens that the suspensorium slides along the groove in the vomer during jaw opening and closing in this species. We are unaware of any other characiform with a





**Figure 22.** Anterior portion of neurocranium of *Gnathodolus bidens*, USNM 389623, 71 mm SL; ventral view.

similar modification to the vomer and at present this character is an autapomorphy for *Gnathodolus bidens*. Should *Gnathodolus* contain one or more undescribed species as suggested by Winterbottom (1980: 23–24), it is likely that the unusual form of the vomer will represent a synapomorphy for the genus.

21. *Presence or absence of pentagonal ventral extension of vomer*: (0) ventral surface of main body of vomer flat; (1) ventral surface of main body of vomer with pentagonal raised area medial to articulations with left and right palatines in ventral view (CI = 1.000; RI = 1.000).

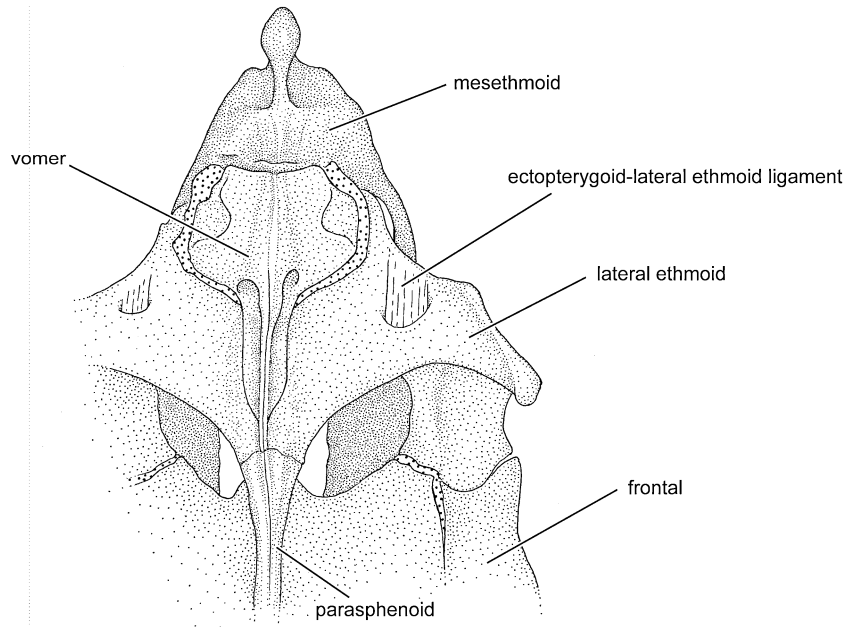
Most members of the Anostomidae (*Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytiodus* and *Schizodon*) possess a vomer with a flat ventral surface other than for a thin medial ridge that is continuous posteriorly with the ventral flange of the parasphenoid (state 0; Figs 23–25). In members of *Anostomus*, *Petulanos* (Fig. 26), *Pseudanos* (Winterbottom, 1980: fig. 52), *Sartor* and *Synaptolaemus*, there is a five-sided raised area on the vomer medial to the articulations of that bone with the left and right palatines in ventral view (state 1). The

condition in *Gnathodolus* (Fig. 22) is difficult to evaluate due to extensive modifications of the region that result in deep longitudinal grooves running along the length of the bone (see character 20). Nonetheless, the medial margins of the grooves in that genus appear to be homologous with the raised area present in *Anostomus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*. *Gnathodolus* is coded accordingly as possessing state 1 for this character.

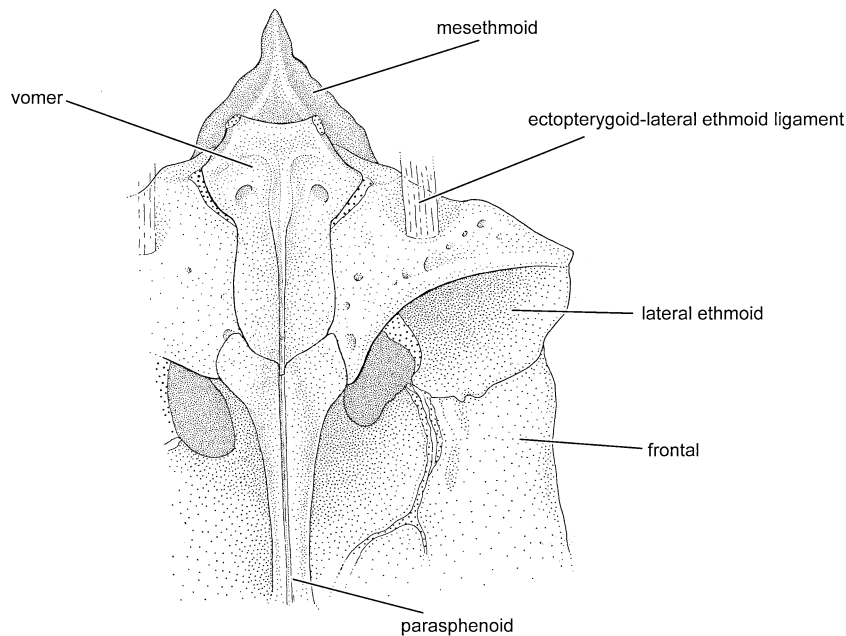
All examined outgroups lack a raised pentagonal region on the vomer in ventral view (state 0). Under the final hypothesis of relationships possession of such a raised area (state 1) is an unambiguous synapomorphy for clade 25.

22. *Form of articulation of vomer with palatine*: (0) articular facets of vomer with palatines angled toward each other anteriorly; (1) articular facets of vomer with palatines parallel and widely separated; (2) articular facets of vomer with palatines parallel and narrowly separated. (CI = 0.200; RI = 0.733).

Species of *Anostomoides*, *Hypomasticus* (Fig. 23), *Rhytiodus* and *Schizodon* (Fig. 25) have the articular facets of the vomer with the palatine running in



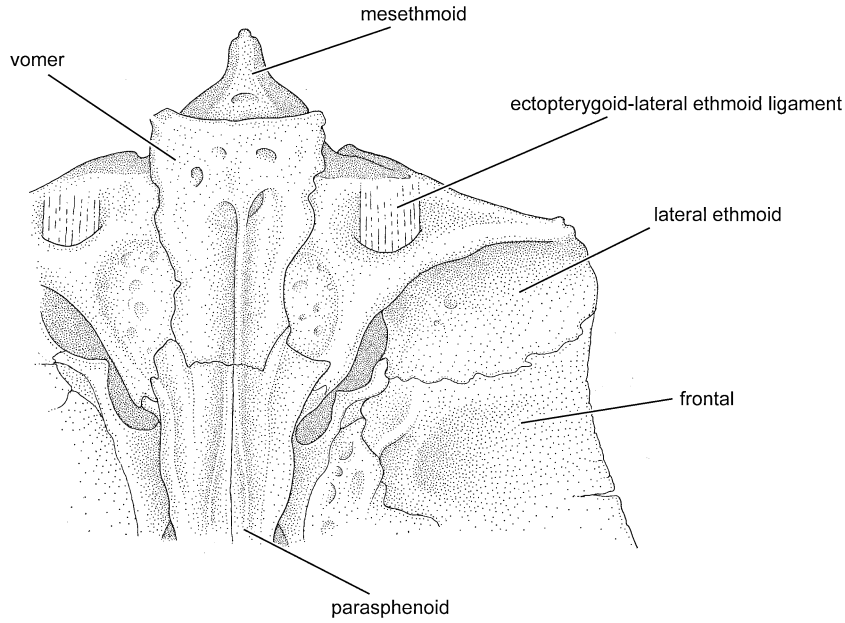
**Figure 23.** Anterior portion of neurocranium of *Hypomasticus megalepis*, INHS 49387, 68.4 mm SL; ventral view.



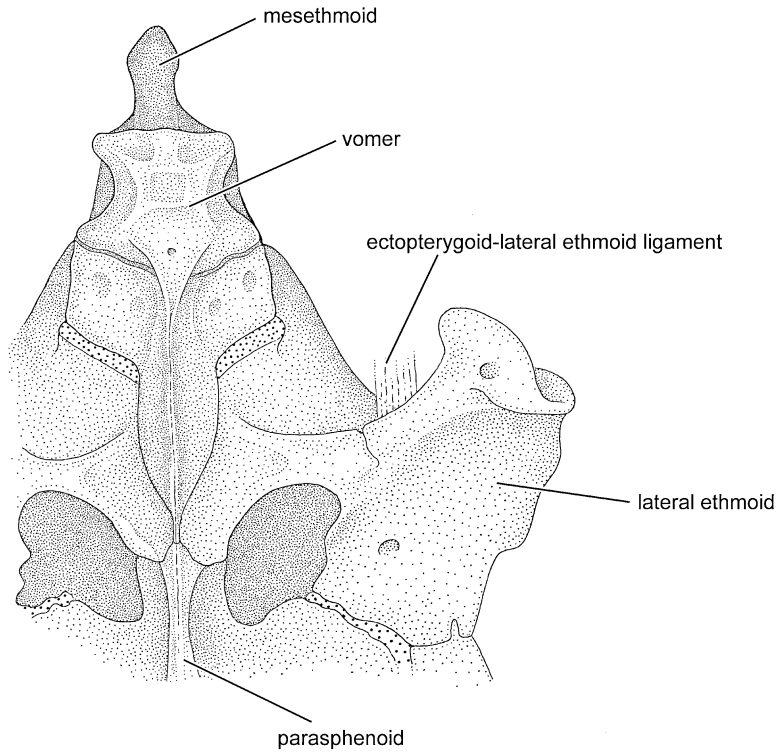
**Figure 24.** Anterior portion of neurocranium of *Leporinus agassizi*, FMNH 102219; 98.6 mm SL, mm SL; ventral view.

parallel and widely separated from each other across the comparatively broad vomer (state 1). Members of *Anostomus*, *Petulanos* and *Synaptolaemus* also have parallel areas for articulation of the vomer with the palatines, but in these taxa the vomer is very narrow and the overall morphology of the vomer (coded as state 2) is very distinct from state 1. In other examined members of the Anostomidae with the exception

of *Gnathodolus* [*Abramites*, *Laemolyta*, *Leporellus* (Fig. 24), *Leporinus*, *Pseudanos* and *Sartor*], the facets of the vomer that articulate with the palatine are angled towards each other anteriorly, resulting in a narrow anterior margin to the vomer (state 0). In *Gnathodolus* both the vomer and the palatine are highly restructured and there is pronounced mobility of the palatine with respect to the vomer (see char-



**Figure 25.** Anterior portion of neurocranium of *Schizodon fasciatus*, INPA 21606, 283 mm SL; ventral view.



**Figure 26.** Anterior portion of neurocranium of *Petulanos plicatus*, USNM 225396, 95.3 mm SL; ventral view.

acters 20 and 70); coding this character is consequently impossible for that taxon.

Among the outgroups, examined members of the Chilodontidae and Curimatidae as well as *Brycon falcatus*, *Citharinus* sp. and *Xenocharax spilurus*

have the articular facets of the vomer with the palatine parallel and widely separated (state 1). The members of the Prochilodontidae as well as *Parodon suborbitalis* and *Hemiodus ocellatus* have the articular facets of the vomer parallel and narrowly sepa-

rated (state 2) while *Distichodus* sp. has the facets of the vomer angled towards each other anteriorly (state 0).

In the final phylogenetic hypothesis arrived at herein, state 1 optimizes as the immediate outgroup condition with respect to the Anostomidae. Within the Anostomidae optimization is ambiguous. Under ACCTRAN, a switch to state 0 is a synapomorphy for the whole Anostomidae (clade 1) that is reversed to state 1 in *Hypomasticus* and clade 13, with reoccurrence of state 0 in clade 21. Under DELTRAN, state 0 evolves independently in *Leporellus* and clade 7, with independent reversion to state 1 in *Anostomoides* and clade 15. Under either reconstruction, state 2 is a synapomorphy for clade 27 that is reversed to state 0 in *Sartor*.

Comparison of Figure 23 with Figure 25 reveals that while the conditions in *Hypomasticus* and *Schizodon* both meet the criteria for state 1 (facets parallel and widely separated), the shape of the facets themselves differs in these taxa. The facets in *Hypomasticus* have a somewhat sinusoidal medial margin, while the medial margin of the facets in *Schizodon* (also *Anostomoides* and *Rhytiodus*) are very straight. This morphological difference, although not formally coded, lends further support to an independent origin of state 1 in *Hypomasticus*, on the one hand, and *Anostomoides*, *Rhytiodus* and *Schizodon*, on the other, as suggested by the final phylogeny arrived at herein.

23. *Presence or absence of lateral ethmoid–ectopterygoid ligament*: (0) ligament absent; (1) ligament present (CI = 0.500; RI = 0.909).

Vari (1983) noted the presence of a novel ligament connecting the lateral surface of the ectopterygoid to the ventral surface of the lateral ethmoid as an unambiguous synapomorphy for the clade consisting of the Anostomidae and Chilodontidae, with the exception of *Gnathodolus bidens*, which has a dramatically restructured anterior portion of the suspensorium and lacks the ligament. He also noted the possible absence of the ligament in *Sartor* and *Synaptolaemus*, genera for which he lacked adequate study material. This study confirms the absence of the ligament in *Gnathodolus* (Fig. 22) and demonstrates the presence of the ligament in *Sartor* and *Synaptolaemus* (Fig. 21). Possession of the ligament clearly optimizes as a synapomorphy for the Anostomidae plus Chilodontidae. Because *Gnathodolus* is deeply nested in the final topology, the absence of the ligament in that taxon appears to be a secondary, autapomorphic loss and not a symplesiomorphy shared with the Curimatidae, Prochilodontidae and more distant outgroups in the Characiformes, all of which lack the ectopterygoid–lateral ethmoid ligament.

24. *Insertion of lateral ethmoid–ectopterygoid ligament on lateral ethmoid*: (0) insertion on ventral surface of anterior wing of lateral ethmoid; (1) insertion on dorsal surface of anterior wing of lateral ethmoid; (2) insertion on lateral margin of lateral ethmoid (CI = 1.000; RI = 1.000).

Vari (1983) noted that the method of attachment of the lateral ethmoid–ectopterygoid ligament differs between the Anostomidae and Chilodontidae. In the Chilodontidae, the ligament is weakly developed and attaches to the lateral margin of the lateral wing of the lateral ethmoid (state 2). In all examined members of the Anostomidae except for *Gnathodolus bidens*, which lacks the ligament (character 23), and *Synaptolaemus cingulatus*, the ligament instead attaches to a cavity on the ventral surface of the lateral wing of the lateral ethmoid (state 0, Figs 16–18, 23–26). In *Synaptolaemus*, the ligament is repositioned dorsally to attach to the dorsal surface of the lateral wing of the lateral ethmoid (state 2, Fig. 21). Under the final hypothesis of relationships arrived at herein, the connection of the ligament in question on the ventral surface of the lateral wing of the lateral ethmoid is an unambiguous synapomorphy for the Anostomidae (clade 1), with the subsequent modification of the attachment in *Synaptolaemus* leading to the unusual dorsal area of insertion on the lateral ethmoid. The mechanism by which the ligament migrated to the dorsal surface of the lateral ethmoid in *Synaptolaemus* is unclear, but it may have involved an intermediate stage with the ligament running through a fenestra in the lateral ethmoid such as the opening present in *Anostomoides laticeps* (Fig. 19, see character 26).

25. *Presence or absence of distinct notch in wing of lateral ethmoid*: (0) wing of lateral ethmoid without distinct notch along anterior margin; (1) wing of lateral ethmoid with distinct notch along anterior margin that accommodates passage of ligament running between wing of lateral ethmoid and ectopterygoid (CI = 0.250; RI = 0.700).

A well-developed ligament runs between the ectopterygoid and the anteroventral surface of the ventral wing of the lateral ethmoid in anostomids (see Vari, 1983; fig. 26). In the species of *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Rhytiodus*, *Schizodon*, *Pseudanos trimaculatus*, *P. irinae* and all examined species of *Leporinus* except *L. striatus*, the concavity of the lateral ethmoid in which the ectopterygoid–lateral ethmoid ligament attaches is located posteriorly on the anteroventral surface of the ventral wing of the lateral ethmoid (Figs 23–25). In the species of *Abramites*, *Anostomus*, *Petulanos*, *Sartor*, *Gnathodolus* and *Synaptolaemus*, as well as *Leporinus striatus*, *Pseudanos gracilis* and *P. winter-*



*bottomi* (Fig. 26), the ligament alternatively attaches on a more anteriorly positioned concavity on the lateral ethmoid. Passage of the ligament to the more anteriorly situated site of attachment on the wing of the lateral ethmoid in these species is accommodated by a distinct notch along the anterior margin of that bone. This notch was noted by Winterbottom (1980: 51–52) in his discussion of the reduction of the size of the wing of the lateral ethmoid in *Anostomus* (encompassing *Petulanos* of this study), *Sartor*, *Synaptolaemus* and *Gnathodolus*.

The notch in the wing of the lateral ethmoid is deep in *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*, and less developed in *Abramites*, *Leporinus striatus*, *Pseudanos gracilis* and *P. winterbottomi*. Winterbottom (1980: 51–52) indicated that the notch is absent in *Abramites* and *Pseudanos gracilis*, indicating either a difference in character state delineation between our analysis and his, or a possible intrageneric polymorphism not indicated in the material examined in this study. Many other examined taxa possess irregular margins or slight concavities along the anterior margin of the wing of the lateral ethmoid, but in no other examined member of the Anostomidae or outgroups is there a well-developed notch for the passage of the ectopterygoid–lateral ethmoid ligament. Under the final phylogeny arrived at in this study, the notched condition of the lateral ethmoid is hypothesized to be derived two to four times within the Anostomidae: once in clade 9 containing *Abramites* and *Leporinus striatus* and between one and three times in the clade formed by *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25). The uncertainty involves the polytomy within clade 26. If the topology suggested by the majority rule consensus (Fig. 6) is correct, then the notched condition of the lateral ethmoid is a synapomorphy for clade 25 that is reversed in the lineage leading to *Pseudanos irinae* and *P. trimaculatus*.

26. Presence or absence of fenestra on portion of lateral wing of lateral ethmoid situated dorsal to lateral ethmoid–ectopterygoid ligament: (0) fenestra absent; (1) fenestra present (CI = 0.500; RI = 0.500).

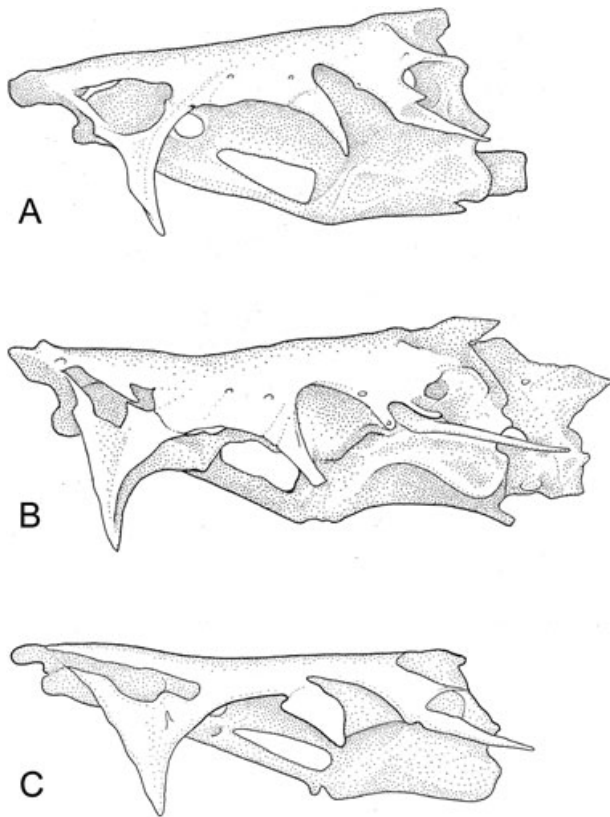
The lateral wing of the lateral ethmoid in *Anostomoides laticeps* and both examined species of *Leporellus* has a fenestra situated dorsal and anterior to the insertion of the ectopterygoid–lateral ethmoid ligament on the lateral ethmoid. The fenestra is much larger in *Anostomoides* than in *Leporellus*, but in dorsal view the ligament can be seen through the fenestra in both genera (Fig. 19). No other examined species in the Anostomidae (e.g. *Schizodon*, Fig. 20) or outgroups possesses such an opening.

In our phylogeny, *Anostomoides* and *Leporellus* are not sister taxa, nor are they in close proximity. The fenestra in *Anostomoides* therefore appears to have been derived independently of the opening that is present in *Leporellus*.

27. Presence or absence of process of lateral ethmoid directed towards posterolateral corner of mesethmoid: (0) process of lateral ethmoid absent; (1) process of lateral ethmoid present (although sometimes incomplete) (CI = 0.167; RI = 0.783).

Species in *Abramites*, *Anostomoides* (Fig. 19), *Laemolyta* and *Rhytiodus* as well as *Schizodon nasutus*, *S. fasciatus* (Fig. 20), *S. scotorhabdotus*, *S. vittatus*, *Leporinus aripuanaensis*, *L. cf. ecuadorensis*, *L. fasciatus* (Fig. 18), *L. cf. fasciatus*, *L. friderici*, *L. jatuncochi*, *L. cf. niceforoi*, *L. pellegrinii*, *L. striatus*, *L. tigrinus* and the larger of the two examined specimens of *L. ortomaculatus* possess a process on the dorsal portion of the lateral ethmoid that is directed towards the posterolateral corner of the mesethmoid. The process usually connects fully to the mesethmoid and bridges the space immediately anterior of the anterior opening of the sensory canal of the frontal where that canal contacts that in the nasal (e.g. *Schizodon fasciatus*, Fig. 20). In some taxa (*Anostomoides laticeps*, *Laemolyta garmani*, *L. fasciatus*, *L. cf. fasciatus*, *L. friderici*, *Leporinus striatus* and all examined species of *Rhytiodus*) the process of the lateral ethmoid falls slightly short anteriorly of the mesethmoid (for condition in *Anostomoides laticeps* see Fig. 19; for condition in *Leporinus fasciatus* see Fig. 18). It is possible that the process develops later in ontogeny, as it is shortest in the cleared and stained specimens that are much smaller than examined full-size adults (*L. cf. fasciatus*, *L. friderici*, *L. striatus*). Among some other examined taxa, one side of a specimen will demonstrate a complete connection between the lateral ethmoid and mesethmoid while the other side has a process on the lateral ethmoid that falls short of the mesethmoid. Given the variation in the degree of connection of the process with the mesethmoid within individuals, we elected to code only the presence or absence of the process rather than its degree of development.

All three species of *Rhytiodus* have a gap between the definite process on the lateral ethmoid and a corresponding process of the mesethmoid. This is the case even in the dry skeleton of a large specimen of *Rhytiodus lauzannei* (INPA 21604, 260 mm SL; Figs 27C, 28C). The cranium is very wide in *Rhytiodus* (see character 30) and the space situated anterior of the opening of the sensory canal of the frontal has a correlated lateral expansion, thereby increasing the distance that would have to be bridged by the processes between the lateral ethmoid and the meseth-



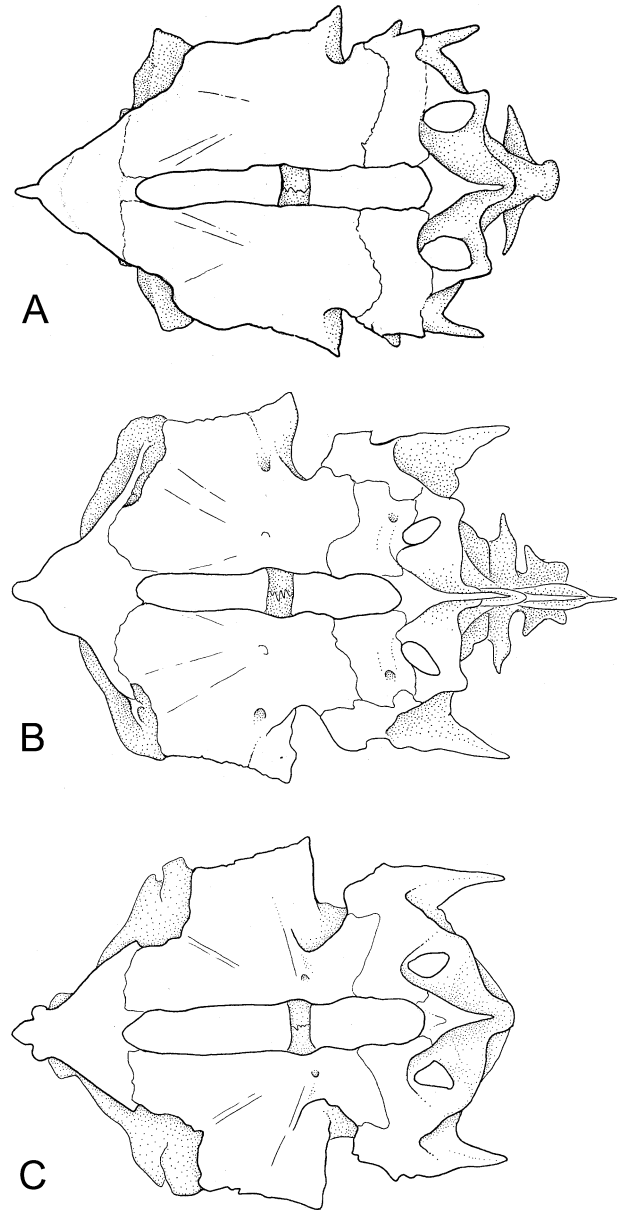
**Figure 27.** Schematic drawings showing variation in relative depth of neurocrania in (A) *Leporinus* cf. *friderici*, INPA 21605, 167.3 mm SL; (B) *Schizodon fasciatus*, INPA 21606, 283 mm SL; (C) *Rhytiodus lauzannei*, INPA 21604, 260 mm SL; lateral views, drawings scaled to same length for ease of comparison.

moid. It may be that the extreme widening of the cranium in the species of *Rhytiodus* led to an interruption of the plesiomorphic connection between the process of the lateral ethmoid and the mesethmoid.

The members of the Anostomidae not cited above and all examined outgroups lack the process of the lateral ethmoid in question. In the final hypothesis of relationships, the presence of the process optimizes as a synapomorphy for clade 8, albeit with subsequent reversals in *Leporinus agassizi*, *L.* cf. *moralesi*, *Schizodon knerii*, *S. nasutus* and clade 25.

28. Degree of development of frontal–parietal fontanel: (0) fontanel open along entire length; (1) fontanel partially or completely closed (CI = 0.167; RI = 0.167).

*Anostomoides*, *Gnathodolus*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Petulanos*, *Pseudanos gracilis*, *P. winterbottomi*, *Rhytiodus*, *Sartor*, *Schizodon* and *Synaptolaemus* have a large fontanel separating the contralateral frontals and parietals along the middorsal surface of the cranium (Figs 19–21). Con-



**Figure 28.** Schematic drawings showing variation in relative width of neurocrania in (A) *Leporinus* cf. *friderici*, INPA 21605, 167.3 mm SL; (B) *Schizodon fasciatus*, INPA 21606, 283 mm SL; (C) *Rhytiodus lauzannei*, INPA 21604, 260 mm SL; lateral views, drawings scaled to same length for ease of comparison.

versely, in *Abramites*, *Anostomus*, *Pseudanos irinae* and *P. trimaculatus*, both the frontals and the parietals are fully in contact middorsally (for condition in *P. trimaculatus*, see Winterbottom, 1980: fig. 53). The character is ontogenetically variable in *Pseudanos* with closure occurring relatively late in ontogeny (Winterbottom, 1980: 41). The closure is complete in the smallest examined specimen of *Abramites*

*hypselonotus*, suggesting that the elimination of the fontanel has an early onset in that species.

Most of the examined outgroups also possess completely open frontal–parietal fontanels but *Distichodus* sp. possesses frontals in contact along their entire medial borders and *Parodon suborbitalis* has complete closure of the fontanel. Both of these species were coded as possessing state 1. Among outgroups that were not formally coded, *Ichthyoelephas humeralis* in the Prochilodontidae and a subset of *Steindachnerina* in the Curimatidae (Vari, 1991: fig. 10) have parietals in partial contact and *Paradistichodus dimidiatus* in the Distichodontidae possesses frontals in full contact medially (Daget, 1958: fig. 9).

In light of the final phylogeny, the plesiomorphic condition in the Anostomidae is clearly an open fontanel, with the complete closure of the fontanel by medial expansions of the frontals and parietals originating independently in *Abramites*, *Anostomus* (clade 26) and once or twice in *Pseudanos*. If the majority rule consensus (Fig. 6) is true, then the partial closure of the fontanel is a synapomorphy for a clade formed by *Pseudanos irinae* and *P. trimaculatus*.

29. *Dorsoventral depression of neurocranium*: (0) neurocranium moderately depressed, depth of neurocranium at angle in parasphenoid about 36–40% of length of neurocranium from anterior tip of mesethmoid to tip of supraoccipital spine; mesethmoid and horizontally orientated portion of vomer separated by wide cavity in lateral view; (1) neurocranium distinctly depressed; depth of neurocranium at angle in parasphenoid about 30–32% of length of neurocranium from anterior tip of mesethmoid to tip of supraoccipital spine; mesethmoid and horizontal portions of vomer separated by narrow gap in lateral view (CI = 1.000; RI = 1.000).

The three examined species of *Rhytiodus* (Fig. 27C) possess a greatly dorsoventrally depressed neurocranium with respect to the condition in all other examined members of the Anostomidae (e.g. *Leporinus* cf. *friderici*, Fig. 27A; *Schizodon fasciatus*, Fig. 27B). In *Rhytiodus* the entire dorsal profile of the neurocranium is wide and distinctly depressed (state 1) as opposed to distinctly transversely convex (state 0). In *Rhytiodus* the horizontal portion of the vomer is furthermore positioned closer to the mesethmoid and with the bones separated by only a small gap that appears as a longitudinal slit from a lateral view. The dorsal margin of the parasphenoid in this condition consequently runs much closer to the orbitosphenoid and pterosphenoid in *Rhytiodus* than is the case in other species in the Anostomidae. Those taxa possess more dorsoventrally spacious openings between the mesethmoid and vomer anteriorly and between the orbitosphenoid/pterosphenoid and parasphenoid in

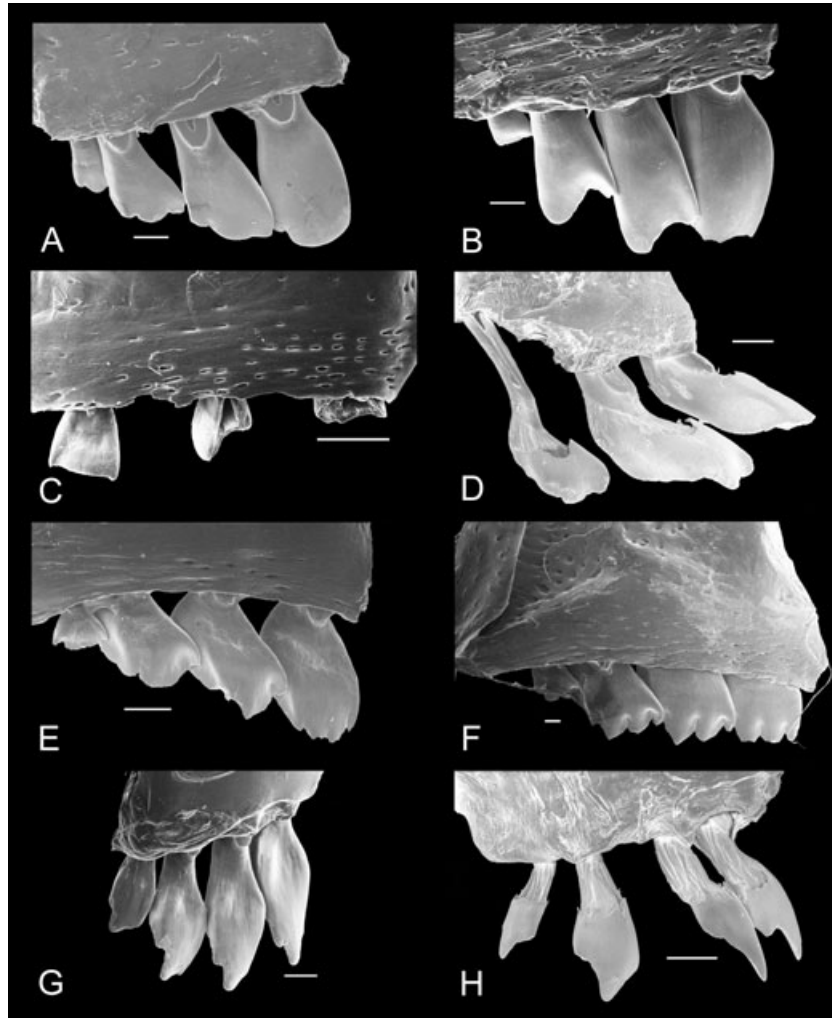
the midlength of the neurocranium. Although some outgroup species also possess somewhat depressed neurocrania (e.g. *Caenotropus* within the Chilodontidae, *Potamorhina* within the Curimatidae), the nested position of *Rhytiodus* within the phylogeny of the Anostomidae and the lack of depression in other anostomid species indicates unambiguously that the depression of the cranium is a synapomorphy for the species of *Rhytiodus* (clade 16).

30. *Width of bony shelf above orbit formed by lateral ethmoid, frontal and sphenotic bones*: (0) shelf not greatly widened; distance between lateral tips of contralateral sphenotics ~75% or less of length of neurocranium from anterior tip of mesethmoid to tip of supraoccipital spine; (1) shelf very greatly widened, distance between lateral tips of contralateral sphenotics 80% or greater of length of neurocranium from anterior tip of mesethmoid to tip of supraoccipital spine (CI = 1.000; RI = 1.000).

The three species of *Rhytiodus* have neurocrania that are both dorsoventrally depressed (character 29) and very wide. The apparently correlated lateral expansion is most obvious in the extreme widening of the bony shelf formed by the portions of the frontal, lateral ethmoid and sphenotic bones that contribute to the dorsal margin of the orbit (width of neurocranium at sphenotics in *Rhytiodus lauzannei* = 82% of length of neurocranium, Fig. 28C). The species of *Schizodon* similarly possess a widened shelf above the orbit relative to the condition present in other genera within the Anostomidae (width of neurocranium at sphenotics in *Schizodon fasciatus* = 84% of length of neurocranium, Fig. 28B) and both *Schizodon* and *Rhytiodus* are coded as state 1. The width of the shelf above the orbit varies across the remainder of the Anostomidae, with the greatest development of the shelf outside of *Rhytiodus* and *Schizodon* occurring in *Anostomoides laticeps*, *Leporinus* cf. *ecuadorensis*, *L. friderici* and *L. jatuncochi*. The development of the shelf in these four species is less pronounced than that present in *Rhytiodus* and *Schizodon* (width of neurocranium at tips of sphenotics in dry skeleton of *Leporinus* cf. *friderici* = 75% of length of neurocranium, Fig. 28A) and these four species are coded as possessing state 0 (shelf not greatly widened).

Among the outgroup characiforms, only the members of the distantly related Citharinidae appear to have shelves above the orbit approaching the width of those present in *Rhytiodus* and *Schizodon* (Daget, 1962b: fig. 7, 1962a: fig. 10). The greatly lengthened supraoccipital spine in the Citharinidae makes comparisons to the Anostomidae difficult. If we exclude the supraoccipital spine, which is effectively absent in the Anostomidae, from the length of





**Figure 29.** Dentition of right premaxilla in (A) *Leporellus vittatus*, INHS 56128; (B) *Hypomasticus mormyrops*, FMNH 112963, margin of symphyseal tooth slightly damaged; (C) *Hypomasticus despaxi*, MCZ 56552; (D) *Leporinus jatuncochi*; INHS 38940, posterior portion of premaxilla damaged and missing; (E) *Rhytiodus argenteofuscus*, INHS 66082; (F) *Schizodon fasciatus*, FMNH 111351; (G) *Sartor elongatus* (paratype), INPA 1168; (H) *Gnathodolus bidens*, ANSP 159389; lateral view, scale bar = 200  $\mu$ m, images rotated to standardize orientation of premaxilla, anterior to right of image in A–C, to bottom-right in D–F and to bottom in G and H.

the neurocranium, the width of the neurocranium in the Citharinidae appears to be approximately 75% of the length of the neurocranium. The Citharinidae is thus coded as possessing state 0. The transverse development of the shelf in *Prochilodus* and *Potamorhina* in the Prochilodontidae and Curimatidae, respectively, is comparable with that in *Anostomoides laticeps*, *Leporinus* cf. *ecuadorensis*, *L. friderici* and *L. jatuncochi* but less than that present in *Rhytiodus* and *Schizodon*. Under the final reconstruction of relationships arrived at in this study, the widened shelf of the frontal, lateral ethmoid and sphenotic is a synapomorphy for the clade formed by *Rhytiodus* and *Schizodon* (clade 15).

#### DENTITION

31. *Number of teeth on premaxilla*: (0) no teeth on premaxilla; (3) three teeth on premaxilla; (4) four teeth on premaxilla; (5) five or more teeth on premaxilla (CI = 0.429 RI = 0.765).

Species in the Anostomidae typically have either three (Fig. 29C, D) or four (Fig. 29A, B, E–H) teeth on the premaxilla, with four being the most common count. Three teeth on the premaxilla are found in *Abramites*, *Hypomasticus despaxi*, *H. megalepis*, *Leporinus* cf. *moralesi*, *L. jatuncochi*, *L. tigrinus* and most specimens of *L. striatus*. Our cleared and stained specimen of *L. striatus* has only two teeth on the right



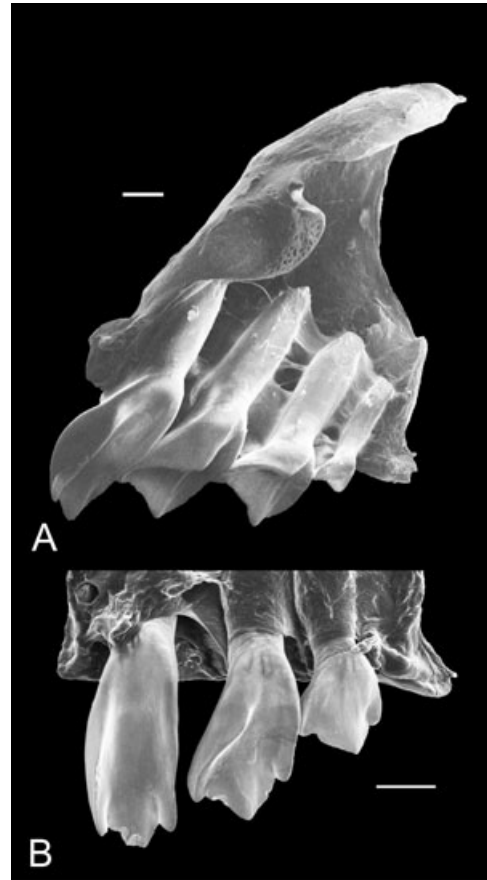
side of the upper jaw and only two incoming replacement teeth on that side, but the left side of that specimen has three teeth, as do all other whole individuals from the same lot. We code *L. striatus* as having three premaxillary teeth, which appears to be the typical count.

The number of teeth on the premaxilla among the close outgroups to the Anostomidae ranges in the Chilodontidae from five in *Caenotropus labyrinthicus* and *Chilodus punctatus* to seven or eight in *Caenotropus mestomorgmatos*. Species in the Prochilodontidae can possess up to several hundred tiny teeth in multiple tooth rows, with Roberts (1973: 217) reporting 600 teeth across the entire 'oral disk' in a 97.2-mm SL specimen of *Ichthyoelephas humeralis*. There are 27–47 teeth present in the inner row of the upper jaw and 20–29 teeth present in the lower jaw of that species with its sister species, *I. longirostris*, having, respectively, 50–76 and 35–70 teeth in those series (Castro & Vari, 2004: 73). The species of the Curimatidae only have teeth as larvae and very small juveniles and information on the number of teeth at such early life stages is available for only few species of that family. Géry (1977: 231) illustrated approximately 12 teeth on the premaxilla in an unidentified species of curimatid and we have also observed about that number of teeth in larval curimatids. Members of the Curimatidae are coded as state 0 for this character, reflecting their edentulous adult condition. Among more distant outgroups, *Parodon suborbitalis* possesses four teeth on each premaxilla, while *Brycon*, *Hemiodus*, *Citharinus*, *Distichodus* and *Xenocharax* possess seven or more (all coded as state 5).

A reduction to fewer than five teeth on the premaxilla optimizes as a synapomorphy for the Anostomidae (clade 1). Based on the final reconstruction of relationships arrived at herein, a subsequent reduction to three teeth on the premaxilla appears to have evolved three or four times in the Anostomidae, once in clade 5 (*Hypomasticus despaxi* and *H. megalepis*), once in clade 11 (*Leporinus jatuncochi* and *L. tigrinus*) and either once or twice within clade 8. A polytomy within that clade makes it impossible to determine whether the loss of the fourth tooth in *Leporinus cf. moralesi* and in clade 9 (*Abramites* + *Leporinus striatus*) represents one or two evolutionary events.

32. *Number of cusps on symphyseal tooth of premaxilla*: (1) tooth with only single cusp; (2) tooth with two cusps; (3) tooth with three cusps; (4) tooth with four cusps; (5) tooth with five cusps (CI = 0.222; RI = 0.588).

Homologies among the tooth cusps are not readily apparent as a consequence of the considerable variation among the species in the Anostomidae in the



**Figure 30.** Right premaxilla and associated dentition in (A) *Leporinus cf. ecuadorensis*, FMNH 102198; (B) *Leporinus cf. moralesi*, UMMZ 216435; medial view, scale bar = 200  $\mu$ m.

number and degree of development of the tooth cusps on the premaxillary teeth (Figs 29, 30). We elected to code only the number of cusps present on the symphyseal tooth without attempting to determine *a priori* a more detailed pattern of cusp gain and/or loss. Cusps on the premaxillary teeth are defined broadly as being portions of the cutting or biting surface of the tooth with either pointed or rounded margins. By this definition, a continuously rounded tooth with no distinct point of inflection was considered to have a single cusp. Where multiple cusps were considered to be present, the cusps were distinguished from each other by a separation via a distinct incision or notch in the margin of the tooth and/or by a distinct thickening of the medial surface of the tooth at the point of greatest development of each cusp (Fig. 30). Because cusps vary in their degree of development even within a species and because tooth wear can obscure cusps, we coded even small or faint cusps as being present for purposes of consistency. Some small cusps near the anterior or posterior margin of

teeth are visible only in medial view, particularly in the various species of *Leporinus*; as a consequence, some species are coded as possessing tooth cusps that are not apparent in the accompanying SEM images of the lateral tooth surfaces.

By the definition utilized above, all species in the Anostomidae possess at least one cusp on the symphyseal tooth of the premaxilla, with most species possessing at least two and some species bearing as many as four cusps on this tooth. Species possessing a unicuspid symphyseal tooth of the premaxilla are *Hypomasticus megalepis*, *H. mormyrops* (Fig. 29B, note that the edge of the tooth is slightly chipped), *H. pachycheilus*, *Leporinus aripuanaensis* and *L. gomesi*. Taxa possessing two cusps on the symphyseal tooth of the premaxilla include *Abramites hypselonotus*, *Anostomoides laticeps*, *Hypomasticus despaxi* (Fig. 29C, unequivocal determination difficult due to damage to teeth), *Gnathodolus* (Fig. 29H), *Leporellus* (Fig. 29A), *Leporinus agassizi*, *L. cf. ecuadorensis* (Fig. 30A), *L. fasciatus*, *L. cf. fasciatus*, *L. striatus* and *Petulanos*. Some of the species cited above possess only weak second cusps (*Leporinus fasciatus*, *L. cf. fasciatus*, *L. striatus*) whereas *Abramites*, *Anostomoides*, *Gnathodolus*, *Leporinus cf. ecuadorensis* and *Petulanos* possess very clearly bicuspid dentition. Species possessing three cusps on the symphyseal tooth of the premaxilla are *Anostomus anostomus*, *A. ternetzi*, *Laemolyta garmani*, *Leporinus friderici*, *L. jatuncochi* (Fig. 29D), *L. cf. moralesi* (Fig. 30B), *L. cf. niceforoi*, *L. ortomaculatus*, *L. pellegrinii*, *L. tigrinus*, *Rhytiodus lauzannei*, *R. microlepis*, *Sartor* (Fig. 29G), *Synaptolaemus* and all four species of *Pseudanos*. Species with four cusps on the symphyseal premaxillary tooth include *Laemolyta orinocensis*, *L. proxima*, *L. taeniata*, *Rhytiodus argenteofuscus* (Fig. 29E, cusps rather poorly developed in this species) and all examined species of *Schizodon* (Fig. 29F).

Proximate outgroups to the Anostomidae possess unicuspid teeth without a definite cutting edge. *Caeotropus* and *Chilodus* in the Chilodontidae possess small rod-like teeth (coded as having one cusp) while species in the Curimatidae possess unicuspid, cone-shaped teeth as larvae and are edentulous as adults (coded herein as missing data). Members of the Prochilodontidae possess distally rounded, spatulate teeth (Castro & Vari, 2004: fig. 7) that are coded as unicuspid in light of the overall form of the distal margin. Among more distant outgroups, members of the Citharinidae and Distichodontidae possess bicuspid dentition at least at some point in their ontogeny (Vari, 1979: 275), while the premaxillary teeth of *Brycon* are tricuspid (Weitzman, 1962: 32, fig. 34). *Hemiodus ocellatus* and *Parodon suborbitalis* have five cusps on each symphyseal premaxillary tooth (coded as state 5). Based on the unicuspid condition in

the proximate outgroups, the various multicuspid forms of dentition observed in the Anostomidae are judged to be apomorphic.

Several genera in the Anostomidae have unusual cusping patterns that may represent synapomorphies for small groups of species but that are not coded explicitly herein. For example, in *Leporellus* (Fig. 29A) the premaxillary teeth have an unusual quasi-multicuspid morphology wherein the cusps form a single unbroken distal edge with a wavy margin as opposed to the more discretely pointed cusps that occur elsewhere in the family. The cusping of the premaxillary teeth is particularly well developed in all examined species of *Schizodon* (Fig. 29F), whereas *Gnathodolus* possesses a markedly forked bicuspid or tricuspid morphology to the upper teeth (Fig. 29H). *Hypomasticus despaxi* possesses small, broad and widely spaced premaxillary teeth unlike those in any other species in the dataset (Fig. 29C). The cusping of the premaxillary dentition of various other anostomid species also appears to be distinctive at the alpha taxonomic level, but coding that extensive series of autapomorphies would be uninformative as to supraspecific relationships.

Perhaps unsurprisingly, the final hypothesis of relationships indicates a high level of lability in the evolution of this character, with 18 state transitions implied on the strict consensus (14 on the majority rule consensus). The presence of two cusps on the symphyseal tooth of the premaxilla optimizes as a synapomorphy for *Leporellus*, clade 9 containing *Abramites* and *Leporinus striatus*, and *Petulanos*. State 2 also occurs homoplastically in *Anostomoides*, *Hypomasticus despaxi*, *Gnathodolus*, *Leporinus agassizi* and *Leporinus cf. ecuadorensis*, although the majority rule consensus (Fig. 6) suggests that the possession of two cusps on this tooth may be a synapomorphy for a clade containing *Abramites*, *Leporinus cf. ecuadorensis* and *L. striatus* and also for a clade containing *Leporinus fasciatus* and *L. cf. fasciatus*. The presence of three cusps is a synapomorphy for clade 8 (albeit with significant degrees of reversal and/or modification at less inclusive levels). Possession of four cusps is a synapomorphy for clade 23 (*Laemolyta orinocensis*, *L. proxima* and *L. taeniata*). State 4 (four cusps) is also either a synapomorphy for clade 15 (*Rhytiodus* + *Schizodon*) that was reversed in clade 17 (*Rhytiodus microlepis* and *R. lauzannei*) or arose independently in *R. argenteofuscus* and *Schizodon* (clade 18).

33. Number of cusps on second and third teeth of premaxilla: (1) each tooth with single cusp; (2) each tooth with two cusps; (3) each tooth with three cusps; (4) each tooth with four cusps; (5) each tooth with five cusps (CI = 0.429; RI = 0.692).

Not only does the pattern of cusping on the premaxillary teeth vary among species in the Anostomidae, but the cusping of the second and third tooth on the premaxilla of some species often differs from the cusping of the symphyseal tooth of the premaxilla. Only *Leporellus pictus* and *Gnathodolus bidens* differ in the cusping of the second versus the third teeth of the premaxilla, with these indicated as polymorphisms and discussed below. The alternative of coding the number of cusps on the second and third teeth separately in order to avoid such polymorphism would give excess weight to what appear to be overall correlated shifts in cusp numbers involving those two teeth. The fourth tooth of the premaxilla is often much reduced compared with the preceding three teeth, being absent entirely in several species (see character 31), and has very faint cusping in most species when present. Given those complications we did not code the cusping of the fourth tooth of the premaxilla.

Anostomids possessing two cusps on the second and third teeth of the premaxilla include *Abramites hypselonotus*, *Hypomasticus* (Fig. 29B, C), *Leporinus agassizi*, *L. aripuanaensis*, *L. cf. ecuadorensis* (Fig. 30A), *L. gomesi* and *L. striatus*. Species possessing three cusps on the second and third teeth of the premaxilla include all examined species in *Anostomoides*, *Anostomus*, *Petulanos*, *Pseudanos*, *Rhytiodes* (Fig. 29E), *Sartor* (Fig. 29G) and *Synaptolaemus*, as well as *Laemolyta garmani*, *Leporellus vittatus* (Fig. 29A), *Leporinus fasciatus*, *L. cf. fasciatus*, *L. friderici*, *L. jatuncochi* (Fig. 29D), *L. cf. moralesi* (Fig. 30B), *L. cf. niceforoi*, *L. ortomaculatus*, *L. pellegrinii* and *L. tigrinus*. *Laemolyta orinocensis*, *L. taeniata*, *L. proxima* and all examined species of *Schizodon* (Fig. 29F) possess four cusps on the second and third teeth of the premaxilla. *Gnathodolus bidens* possesses two cusps on the second tooth and three on the third tooth (Fig. 29H, more obvious in medial view, not shown), while *Leporellus pictus* possesses two cusps on the second tooth and only one on the third tooth.

The coding of the outgroup species is identical to that given for character 32. An increase to at least two cusps on the second and third teeth of the premaxilla appears to be a synapomorphy for either the whole Anostomidae or for clade 3 (the uncertainty relates to the polymorphic condition of *Leporellus pictus*), with a subsequent increase to three cusps a synapomorphy for clade 8 (albeit with as many as four subsequent reversals to two cusps within *Leporinus* and *Abramites*, the number depending on how the polytomy in clade 8 is resolved). The presence of four cusps on the second and third teeth of the premaxilla is an independent synapomorphy of clades 15 (*Schizodon*) and 19 (*Laemolyta taeniata*, *L. orinocensis* and *L. proxima*).

34. *Structure of medial surface of second and third teeth of premaxilla*: (0) medial surface of second and third teeth of premaxilla either flat plane or curved hollow, without raised ridge originating at anterior edge of tooth and extending across medial surface of tooth; (1) medial surface of tooth elaborated, with raised ridge originating at anterior edge of tooth and extending across medial surface of tooth (CI = 0.250; RI = 0.750).

*Anostomoides*, *Leporinus agassizi*, *L. aripuanaensis*, *L. cf. ecuadorensis*, *L. fasciatus*, *L. cf. fasciatus*, *L. friderici*, *L. gomesi*, *L. jatuncochi*, *L. cf. moralesi*, *L. cf. niceforoi*, *L. ortomaculatus* and *L. tigrinus* have a raised ridge on the medial surface of the second tooth or second and third premaxillary teeth, with the ridge beginning at the anterior margin of the tooth and continuing across its medial surface (Fig. 30). In many species in these genera, including but not limited to, *Anostomoides laticeps*, *Leporinus cf. agassizi* and *L. cf. ecuadorensis* (Fig. 30A), this ridge curls over, and overlaps a space on the medial surface of the tooth and thereby forms an additional cutting edge and a distinct cusp (Fig. 30A). In other species such as *L. fasciatus*, *L. cf. fasciatus*, *L. cf. moralesi* (Fig. 30B), *L. tigrinus*, *L. gomesi* and the larger examined specimen of *L. ortomaculatus*, the ridge, although present, is less extensively developed and consequently does not circumscribe a distinct hollow. The smaller examined specimen of *L. ortomaculatus* lacks almost all trace of the ridge, which is best developed in the some of the largest *Leporinus* specimens examined (*L. agassizi* and *L. cf. ecuadorensis*). This may indicate that the presence and degree of development of the ridge is ontogenetically variable, with that structure present only in adults of some species. In most of the species cited above, the medial ridge and cusp on the third tooth is less well developed than that on the second tooth. No trace of the ridge can be found on the third tooth of the premaxilla in *L. jatuncochi* and *L. cf. moralesi*, although the ridge is clearly present on the second tooth (Fig. 30B).

The remaining species in the Anostomidae have fairly compressed second and third teeth on the premaxilla without any hint of a medial ridge. The conical, needle-like or spatulate teeth found in close outgroups are not readily comparable with either of the character states found within the Anostomidae and are thus largely uninformative as to the polarity of this character. None of the species in the proximate outgroups has any indication of a medial ridge on their tooth, so they are coded as possessing state 0.

Acquisition of the medial ridge of the second and third teeth of the premaxilla optimizes as a synapomorphy for clade 7 in the final reconstruction, with subsequent loss of the ridge occurring in clade 9 (*Abramites* + *Leporinus striatus*). There is an ambigu-



ous optimization concerning the loss of the ridge in more derived groups. Under ACCTTRAN, the loss of the ridge is a synapomorphy for clade 12 with *Anostomoides* regaining the ridge. Under DELTRAN, a loss of the ridge occurs independently in *Leporinus pellegrinii* and clade 14.

35. *Curvature of dentition on premaxilla*: (0) teeth on premaxilla essentially straight, without significant dorsal or ventral curvature; (1) at least two of teeth on premaxilla with distinct dorsal curvature distally; teeth appearing strongly ventrally bowed in lateral profile with distal tips of teeth positioned more dorsally than base of teeth; (2) at least two teeth on premaxilla with strong ventral bend followed by anterior-facing alignment, resulting in zigzag shape to tooth in lateral profile (CI = 1.000; RI = 1.000).

Most species of the Anostomidae have teeth on the premaxilla that extend along a straight line from the base of the tooth to its tip without any significant change in direction along the long axis of the tooth. Two small groups within the Anostomidae have modifications of this generalized condition. The first of these restructurings of the teeth on the premaxilla occurs in *Gnathodolus* and *Sartor*, both of which have teeth with a distinct dorsal curvature of the tooth distal to its base (Fig. 29G, H, respectively; curvature much more obvious in the image of *Gnathodolus* than that of *Sartor*). This curvature in the tooth, in conjunction with the restructurings of the premaxilla, results in the crowns of the teeth fanning out to a degree within a plane located somewhat dorsal to the dorsally repositioned premaxilla that is characteristic of those two genera. This unusual morphology of the premaxillary teeth forms a dorsally positioned, curved biting surface that meets the teeth of the elongate or extremely elongate dentary possessed by *Sartor* and *Gnathodolus*.

The second modification in the overall form of the premaxillary teeth within the Anostomidae occurs in *Leporinus jatuncochi*. All three premaxillary teeth in *L. jatuncochi* have a double curvature (first ventrally and then anteriorly) along the length of the tooth (Fig. 29D). The curvature of the teeth displaces their crowns ventrally relative to the dorsal margin of the bases of the teeth. The ventral displacement of the teeth of the premaxilla in *L. jatuncochi* may be necessary to maintain a functional bite with the long horizontal tusk-like symphyseal and second teeth of the dentary. Should *L. jatuncochi* and the very similar *L. desmotes* (not examined) both prove to be valid species following a detailed analysis (see comments under 'Material and methods'), it is likely that this double curvature of the premaxillary dentition, along with the tusk-like dentary teeth, will diagnose a clade containing those two species.

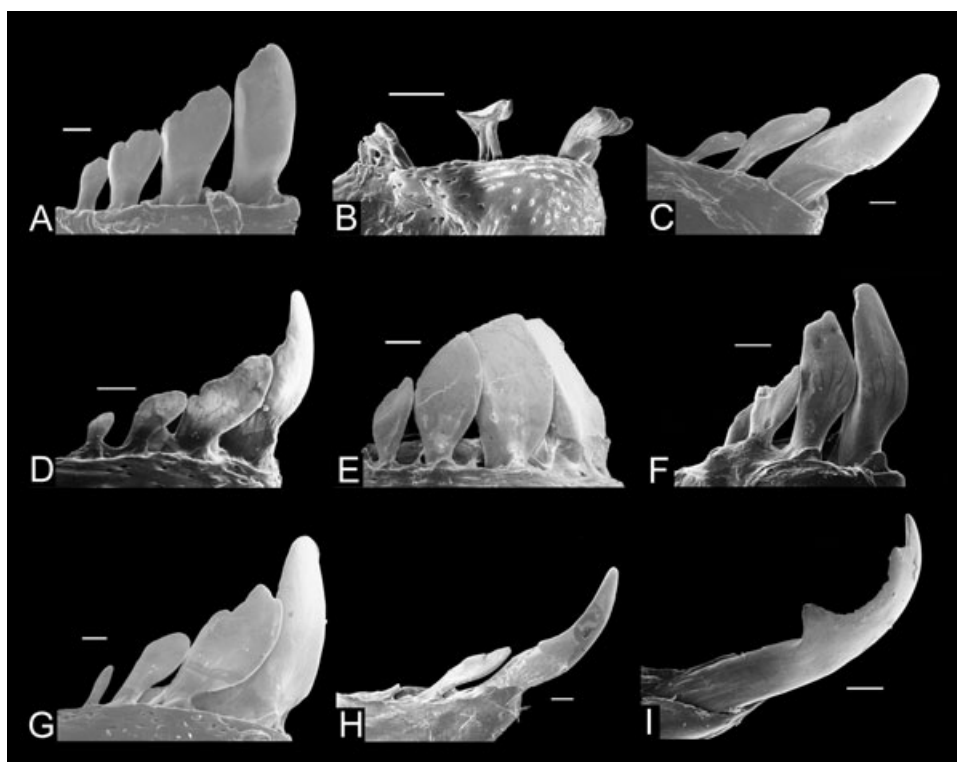
The teeth in the Chilodontidae, the first outgroup, lack any noticeable curvature and species of the Curimatidae of the second outgroup are edentulous as adults, but have straight conical teeth as larvae. Dentition in the Prochilodontidae is of two major forms, both with some curvature, but only in *Ichthyoelephas* (not formally coded as an outgroup) is there a distinct change in angle along the length of the tooth (Castro & Vari, 2004: fig. 7B). The tooth form in that genus differs significantly from that in the species of the Anostomidae that have curvature in their teeth. Tooth form varies widely in the more distant outgroups but none of those morphologies incorporates a distinct curvature, and all outgroups are included in state 0. Within the Anostomidae, state 1 optimizes as a synapomorphy for clade 32 (*Gnathodolus* and *Sartor*). State 2 is an autapomorphy in the current dataset.

36. *Number of teeth on dentary*: (0) no teeth on dentary; (1–6) one to six teeth on dentary, respectively; (7) ten or more teeth on dentary (CI = 0.643; RI = 0.583).

Most anostomids possess four teeth on each dentary (e.g. *Leporellus vittatus*, Fig. 31A), with occasional examined specimens in the family possessing a small fifth tooth posteriorly (one specimen of *Pseudanos gracilis*, one specimen of *Hypomasticus mormyrops* and the right dentary of the single specimen of *H. pachycheilus*). Mautari (2002) also reported that a fifth dentary tooth was rarely present in the species of *Laemolyta*. Within the Anostomidae, a few species have fewer than the four teeth on the dentary typical for most members of the family. *Hypomasticus despaxi* (Fig. 31B), *Leporinus jatuncochi* (Fig. 31C) and *Sartor elongatus* (Fig. 31H) have three teeth on the dentary, while *Gnathodolus bidens* possesses only a single, highly modified dentary tooth (Fig. 31I).

In the Chilodontidae, which is the sister group to the Anostomidae, the species of *Chilodus* have 4–6 needle-like teeth loosely attached to the variably fleshy lower lip. Species of *Caenotropus* vary in the number of dentary teeth both intra- and interspecifically. Dentary dentition is absent in *C. labyrinthicus* (Vari *et al.*, 1995: 22), but 4–6 teeth are present in most individuals of *C. mestomorgmatos*, albeit with some specimens retaining only a few teeth and others lacking dentary dentition (Vari *et al.*, 1995: 14). *Caenotropus maculosus* always has teeth associated with the lower jaw, although the series frequently contains just one or two teeth (Vari *et al.*, 1995: 18). All species of the Curimatidae lack oral dentition as adults but have a dozen or more small, conical dentary teeth as larvae (Géry, 1977: 231). Members of the Prochilodontidae have highly modified, tiny, spatulate teeth attached to the fleshy lips in extensive series, with as





**Figure 31.** Dentition of right dentary in (A) *Leporellus vittatus*, INHS 56128; (B) *Hypomasticus despaxi*, MCZ 56552; (C) *Leporinus jatuncochi*, INHS 38940; (D) *Leporinus cf. fasciatus*, FMNH 103450; (E) *Laemolyta taeniata*, INHS 61513; (F) *Petulanos intermedius*, INPA 15184; (G) *Synaptolaemus cingulatus*, FMNH 103455; (H) *Sartor elongatus*, INPA 1168; (I) *Gnathodolus bidens*, ANSP 159389; lateral view, scale bar = 200  $\mu$ m, images rotated to standardize orientation of dentary, anterior to top of image in A and B, to right in C and D, to bottom right in E–G, and to bottom in H and I.

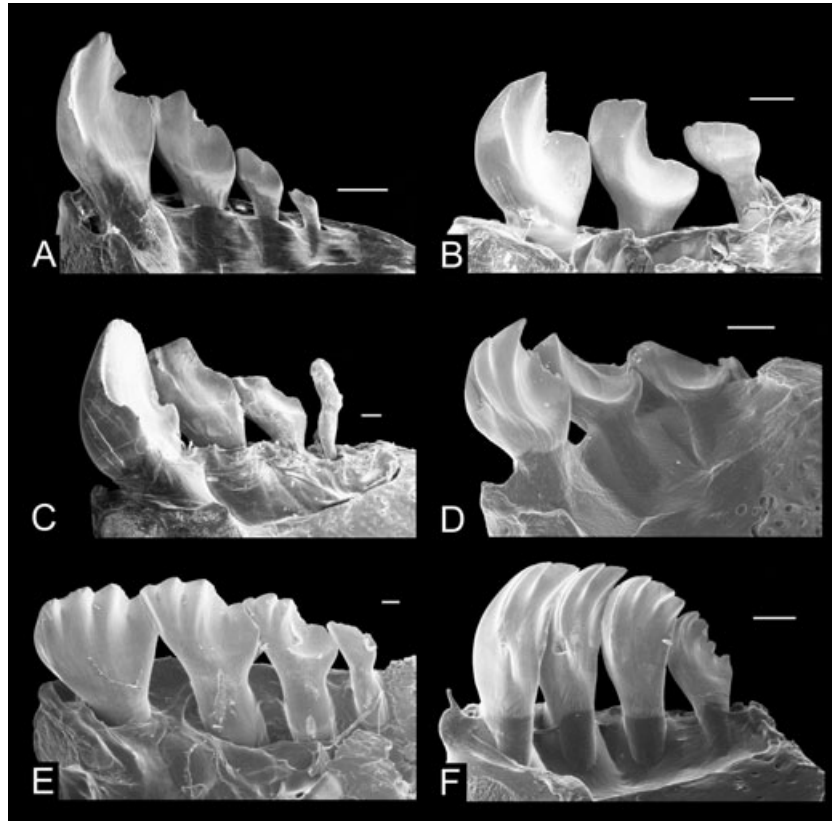
many as 76 teeth present on the inner row alone (Roberts, 1973: fig. 7; Castro & Vari, 2004: 22). The plesiomorphic condition for the Anostomidae appears to have been the possession of four teeth on the dentary, with the reduced numbers of such dentition in a few members of the family considered to be derived.

37. *Overall shape of dentary teeth*: (0) dentary teeth spade- or chisel-shaped, tapering to pointed or blunt distal margin with or without additional cusping; teeth not extremely elongate and resembling awl; (1) dentary teeth elongate with symphyseal tooth extremely elongate and recurved, overall shape reminiscent of awl or very narrow chisel, distal tips may be elaborated with cusps; (2) dentary teeth squat, much wider than high with distinct lateral bend; (3) dentary teeth small, spatulate and affixed to lips; (4) dentary teeth tiny, conical or rod-like in shape; (5) dentary teeth crown-like with 3–5 jagged cusps; (6) dentary teeth in form of large hooks (CI = 0.857; RI = 0.875).

Anostomids possess a greater array of dentary tooth forms relative to the intrafamilial variation

typical within other families in the Characiformes, with the symphyseal tooth demonstrating the greatest range of morphologies of all the teeth on the dentary. The dentary teeth typically have spade- or chisel-shaped morphologies, with variations on this basic form ranging from fairly elongate and pointed (e.g. the symphyseal teeth of *Leporinus cf. fasciatus*, Fig. 31D; *Synaptolaemus*, Fig. 31G), to squat and blunt (e.g. *Anostomoides laticeps*, Fig. 32C), to narrow and distinctly chisel-like (e.g. *Pseudanos trimaculatus*, Fig. 32F), to thin and incisiform (e.g. *Laemolyta taeniata*, Fig. 31E). Exclusive of the cusping and the form of the posterior lamina (see characters 38–44) the variation among the general tooth forms discussed above is continuous. Two additional dentary tooth morphologies seen within the Anostomidae are alternatively so distinctive that they merit recognition with distinct character states.

*Leporinus jatuncochi*, *Gnathodolus bidens* and *Sartor elongatus* possess very elongate, recurved tusk- or awl-like teeth (state 1; Fig. 31C, H, I). Four other examined species also possess elongate morphologies of the symphyseal tooth of the dentary [*Synaptolaemus cingulatus* (Fig. 31G), *L. fasciatus*,



**Figure 32.** Dentition of right dentary in (A) *Leporinus* cf. *moralesi*, UMMZ 216435; (B) *Abramites hypselonotus*, FMNH 106574; (C) *Anostomoides laticeps*, INHS53677, posterior (fourth) tooth dislodged from socket; (D) *Rhytiodus argenteofuscus*, INHS 66082; (E) *Schizodon fasciatus*, FMNH 11135; (F) *Pseudanos trimaculatus*, FMNH 102122; medial view, scale bar = 200  $\mu$ m, images rotated to standardize orientation of dentary, anterior to left in A, B, D and E, to bottom left in C and to bottom in F.

*Leporinus* cf. *fasciatus* (Fig. 32D), and *L. tigrinus*]. The elongation of the teeth in those four taxa is, however, less pronounced than that present in *Sartor*, *Gnathodolus* and *Leporinus jatuncochi*. The variation in symphyseal tooth size is continuous between *L. fasciatus*, *L. cf. fasciatus*, *L. tigrinus*, *Synaptolaemus* and the other species of *Leporinus*. As a consequence all of these species are coded as possessing state 0.

*Hypomasticus despaxi* possesses a squat, widened tooth form in which the distal portion of each tooth displays a pronounced anterolateral curvature (state 2; Fig. 31B). As far as we are aware this tooth form is unique to this species among characiforms, although when more species are examined this tooth morphology may be found to be diagnostic of a small clade within *Hypomasticus*. The function of this unusual tooth form is unknown.

Looking to the conditions in the proximate outgroups, the species of the Prochilodontidae possess variably bowed, spatulate teeth (Castro & Vari, 2004: fig. 7). The Curimatidae lack teeth as adults (coded as missing data) but members of that family have

conical teeth as larvae (Géry, 1977: 231; Vari, 1983: fig. 8) while the species of the Chilodontidae that possess lower-jaw dentition have small rod-like, unicuspid teeth (state 4). All of these conditions are absent within the Anostomidae. Likewise, the numerous small rod-like bicuspid teeth of various morphologies found in basal members of the Citharinidae and Distichodontidae (state 4; see Vari, 1979: figs 2–5), and the strongly pointed and crown-like tri- to pentacuspoid tooth morphology found in *Brycon* (state 5; Weitzman, 1962: figs 4, 8) and the hooked teeth of *Parodon* (state 6) lack direct homologues with the spade- or chisel-shaped morphologies of the dentary teeth seen in the Anostomidae. *Hemiodus ocellatus* also lacks teeth on the dentary (coded as missing data). Possession of spade- or chisel-shaped dentary teeth optimizes as a synapomorphy for the Anostomidae in the final reconstruction, with subsequent modifications of the dentition into distinctive tooth forms occurring in *Hypomasticus despaxi*, *Leporinus jatuncochi*, *Sartor* and *Gnathodolus*. The elongate tooth morphology appears to have evolved twice in the

Anostomidae, once in the lineage leading to *Leporinus jatuncochi*, and a second time in the common ancestor of *Gnathodolus* and *Sartor* (clade 32). It is notable that the species of *Leporinus* with elongate symphyseal dentary teeth cited above form a clade with *L. jatuncochi* in the final reconstruction of relationships. Likewise, *Synaptolaemus* is supported as the sister group to *Gnathodolus* and *Sartor* (clade 31) based on several other characters.

38. *Form of posterior lamina of dentary teeth*: (0) dentary teeth with large, well-developed posterior lamina; (1) dentary teeth either with small, poorly developed posterior lamina or posterior lamina entirely absent (CI = 0.667; RI = 0.958).

Examination of the dentary dentition of members of the Anostomidae reveals that each tooth has two distinct portions. The main body of the tooth is fairly thick, is situated immediately distal to the root of the tooth, and frequently includes one or more distinct cusps marked by additional thickening of the medial surface of the tooth. In addition, a much thinner lamina extends posterolaterally away from the main bulk of the tooth. The image of *Leporinus cf. moralesi* in Figure 32A illustrates these two tooth components, with the main body of the symphyseal tooth marked by a single major cusp and the main body of the second tooth of the dentary with two distinct cusps. The posterior lamina of the symphyseal tooth in this specimen is damaged and contains a small notch which highlights the thinness of that portion of the tooth.

The posterior lamina is well developed on the first three dentary teeth (state 0) in the majority of examined species within the Anostomidae [*Abramites* (Fig. 32B), *Leporellus*, *Leporinus* (Fig. 32C), *Rhytiodus* (Fig. 32D), *Schizodon* (Fig. 32E), and all examined species of *Hypomasticus* with the possible exception of *H. despaxi*]. Conversely, in *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*, the posterior lamina is much reduced or absent and is apparent only under high magnification (state 1). This condition is apparent in the image of *Pseudanos trimaculatus* (Fig. 32F), where the lamina is visible as a thin vertical strip along the extreme right portion of each tooth in the area where that tooth abuts its neighbour. The lamina is present, albeit poorly developed, in *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos* and *Synaptolaemus*. There is no trace of the lamina in *Sartor*. The lamina appears to have been further modified into the lateral process of the claw-like tooth tip in *Gnathodolus* (Fig. 31I).

*Anostomoides laticeps* presents an unusual case in which the posterior lamina is very small on the symphyseal tooth of the dentary, but well developed on

the second and third teeth of that bone (Fig. 32C). We elected to code *Anostomoides* as possessing a polymorphism for this character (analytically equivalent to leaving that species uncoded for this binary character) rather than splitting the character into two features, which would effectively double its weight in the final analysis.

The dentary tooth morphology in *Hypomasticus despaxi* (Fig. 31B) is so distinctive relative to the condition in other anostomids that the homologies of the various margins of the teeth in *H. despaxi* with the tooth margins present in the other members of the Anostomidae is unclear. We refrained from assigning that species a character state for this and several of the characters that follow.

The morphology of the dentary teeth in the examined outgroups to the Anostomidae differs so greatly from the dentition in that family that it makes it difficult to homologize components of the dentary teeth across these groups. The outgroups that possess dentary teeth apparently lack a homologue of the posterior lamina that is found in the Anostomidae and are consequently coded as possessing state 1 (lamina poorly developed or absent).

Under the final hypothesis of relationships within the Anostomidae, the fully developed posterior lamina (state 0) appears as the more plesiomorphic of the two character states and is a synapomorphy for the family. Given the polymorphic coding of *Anostomoides*, the reduction or loss of the lamina optimizes as a further synapomorphy for clade 21 in the final phylogeny but the homology of the reduction of the lamina of the symphyseal dentary tooth in *Anostomoides* is uncertain. If the reduction of the lamina in *Anostomoides* is homologous with the condition in clade 21, then the species in clade 15 (*Rhytiodus* and *Schizodon*) reacquired a well-developed lamina after its loss in the common ancestor of clade 13. Equally parsimoniously, *Anostomoides* could have experienced reduction of the lamina of the symphyseal dentary tooth independently of the reduction in clade 21.

39. *Presence or absence of distinct notch in posterior lamina of symphyseal tooth of dentary*: (0) notch in symphyseal tooth of dentary absent; (1) distinct notch divides symphyseal tooth of dentary into anterior and posterior lobes (CI = 0.250; RI = 0.667).

*Abramites* (Fig. 32B), *Gnathodolus* (Fig. 31I), *Rhytiodus* (Fig. 32D) and to a less pronounced degree the species of *Schizodon* (Fig. 32E) have a large notch along the distal margin of the posterior lamina of the symphyseal tooth of the dentary. The notch divides the tooth into large anterior and smaller posterior lobes. In *Abramites* this division gives the impression of a bicuspid tooth, while in *Rhytiodus* and *Schizodon* the presence of additional cusps within the anterior

lobe (main body) of the tooth results in multiple distal cusps along that portion of the tooth margin. Among the examined species of *Schizodon*, the notch is least apparent in *S. fasciatus* (Fig. 32E), but even in that species it is present in the separation of the tricuspid anterior lobe from the smaller single cusp of the posterior lobe. A large notch in the symphyseal dentary tooth was absent in all other examined species of the Anostomidae and also in proximate outgroups.

Under the final hypothesis of relationships, the notch in the posterior lamina of the symphyseal tooth of the dentary in *Rhytiodus* and *Schizodon* is clearly homologous, as those two genera form the well-supported clade 13. *Abramites* and *Gnathodolus* are not closely related to clade 13 or to each other in the final phylogenetic hypothesis and the notched morphology of the symphyseal tooth of the dentary is hypothesized to have been independently derived in those taxa.

40. *Presence or absence of distinct notch on posterior lamina of second or third tooth of dentary*: (0) distinct distal notch on tooth absent on posterior lamina of second and third teeth of dentary; (1) distinct distal notch divides posterior lamina of second or third tooth of dentary into anterior and posterior lobes (CI = 0.250; RI = 0.750).

As is the case with the symphyseal tooth of the dentary (see character 39), large distal notches occur in the second and/or third dentary teeth of *Abramites*, *Schizodon* and *Rhytiodus* (Figs 32B, D, E). Less developed notches are also present on the second tooth in *Leporinus* cf. *moralesi* (Fig. 32A), *Hypomasticus mormyrops* and *H. pachycheilus*, a pattern distinct enough to merit the recognition of this additional character.

No outgroups possess a posterior lamina or comparable notch of the dentary teeth. The final phylogenetic reconstruction indicates that the notched character state has evolved at least three times in the Anostomidae, with one occurrence in the lineage leading to *Rhytiodus* and *Schizodon* (clade 13), and a second in the lineage leading to *Hypomasticus mormyrops* and *H. pachycheilus* (clade 6). If the polytomy in clade 8 were to resolve with *L. cf. moralesi* as sister to clade 9, then the notch on the tooth in *L. cf. moralesi* could be optimized ambiguously as homologous with the condition in *Abramites*. Given that the majority rule consensus places *L. cf. ecuadorensis* as sister to clade 9, the potential homology of the notched dentary teeth in *L. cf. moralesi* and *Abramites* is not well supported.

41. *Cusping of main body of symphyseal tooth of dentary*: (0) distal margin of main body of symphyseal

tooth of dentary with straight incisiform margin and no apparent cusps; (1) distal margin of main (anterior) lobe of symphyseal tooth of dentary with only single cusp (posterior lobe, if present, may also possess one or more distinct cusps); (2) distal margin of main (anterior) lobe of symphyseal tooth of dentary with two distinct cusps (posterior lobe, if present, may also possess one or more distinct cusps); (3) distal margin of main lobe of symphyseal tooth of dentary with three distinct cusps (posterior lobe, if present, may also possess one or more distinct cusps); (5) distal margin of main lobe of symphyseal tooth of dentary with five distinct cusps (CI = 0.500; RI = 0.800).

Many anostomids have a single distinct cusp on the main body of the symphyseal tooth of the dentary (state 1). Such a single cusp encompasses various morphologies ranging from the blunt symphyseal dentary teeth of *Hypomasticus mormyrops* and *Anostomoides* (Fig. 32C) to the strongly pointed teeth of some species of *Leporinus* (e.g. *Leporinus* cf. *fasciatus*, fig. 31D) or *Synaptolaemus* (Fig. 31G) to the condition in *Abramites* which has only a single distinct cusp on the main lobe of the tooth despite a deep notch in the posterior lamina of the tooth (Fig. 32A). The following taxa possess state 1: *Abramites* (Fig. 32B), *Anostomoides* (Fig. 32C), *Hypomasticus* (with the possible exception of *H. despaxi*, see discussion of character 38), *Leporellus* (Fig. 31A), *Leporinus* (Fig. 31C, D), *Sartor* (Fig. 31H), *Synaptolaemus* (Fig. 31G), and adults of *Petulanos* (Fig. 31F). Conversely, *Anostomus*, *Gnathodolus*, *Pseudanos*, *Rhytiodus* and *Schizodon* have a multicuspid main body of the symphyseal tooth of the dentary. *Anostomus*, *Gnathodolus*, *Pseudanos*, *Rhytiodus*, *Schizodon isognathus* and *S. nasutus* possess two distinct cusps on the main lobe of the symphyseal tooth of the dentary (state 2), while *Schizodon knerii*, *S. fasciatus*, *S. scotorhabdotus* and *S. vittatus* possess three cusps (state 3). Adults of *Laemolyta* have a continuous incisiform edge across the dentary teeth, a morphology distinctly different from any other encountered within the Anostomidae (Fig. 31E). All four examined species of *Laemolyta* are coded as possessing state 0 for this character.

The species of *Laemolyta* and *Petulanos* require additional discussion due to the ontogenetic shifts in tooth cusping. Species of *Laemolyta* are notable for possessing multicuspid dentary teeth similar to the condition in *Pseudanos* and *Anostomus* as juveniles of under 40 mm SL (Mautari & Menezes, 2006: 31). Cusps on these teeth disappear during the ontogenetic replacement of the dentition (Géry, 1977; Mautari & Menezes, 2006) with distally truncate dentary teeth present in members of the genus throughout the later stages of ontogeny. The examined cleared and stained specimen of *L. proxima*



retains cusping on all four dentary teeth contrary to the lack of such cusping in the other examined congeners of similar size. Such cusping is a juvenile character in light of the lack of that feature in adults of the species (Mautari & Menezes, 2006). We consequently coded *L. proxima* as state 0 in keeping with the uncusped dentary teeth in adults of that species. This observation may be evidence that *L. proxima* retains cusps on its dentary teeth to a greater body size than do its congeners.

In the final phylogenetic hypothesis arrived at herein, *Laemolyta* is nested deeply within a clade of taxa with strongly multicuspid dentary teeth. That evidence, combined with the observed ontogenetic progression, reveals that the truncate, incisiform tooth morphology in *Laemolyta* is derived from a plesiomorphically multicuspid adult tooth.

*Petulanos intermedius* and *P. plicatus* also exhibit an ontogenetic reduction in the degree of cusping of the symphyseal tooth, having bicuspid teeth in juveniles smaller than about 60 mm SL and unicuspid teeth in adults (Winterbottom, 1980: 15, 55). In keeping with the observed adult morphology (Fig. 31F), these two taxa are coded as possessing state 1 (unicuspid teeth), but this condition is clearly derived from a bicuspid precursor. In this light and given the final phylogeny, the unicuspid symphyseal dentition of *Sartor* (Fig. 31H) and *Synaptolaemus* (Fig. 31G), which together with *Gnathodolus* form the sister clade to *Petulanos*, can also be understood as a derived character state modified from a bicuspid precursor and as such non-homologous with the unicuspid teeth present in some species of *Leporinus*.

The teeth of the Chilodontidae and Prochilodontidae in the proximate outgroups to the Anostomidae all have only a single cusp. A single cusp is also present in the larvae of the Curimatidae, the members of which lose all dentition ontogenetically (Vari, 1983: 8). *Parodon suborbitalis* has unicuspid dentary teeth and *Hemiodus ocellatus* lacks dentary teeth. Members of the Citharinidae and basal members of the Distichodontidae possess bicuspid teeth, and *Brycon falcatus* possesses pentacuspoid teeth (coded as the autapomorphic state 5).

In light of the final phylogenetic hypothesis, the presence of two cusps on the symphyseal tooth of the dentary (state 2) is a synapomorphy for clade 14, with a further modification to the incisiform, uncusped condition a synapomorphy for *Laemolyta* (clade 22). The possession of a unicuspid symphyseal dentary tooth (state 1) is a synapomorphy for clade 29, which is reversed in *Gnathodolus*. State 3 (tricuspid main body of symphyseal dentary teeth) optimizes as a synapomorphy for *Schizodon* that is reversed to the bicuspid condition in clade 19 (*Schizodon isognathus* + *S. nasutus*). We note that the potential resolution of

the polytomy within *Schizodon* such that clade 19 is basal within the genus would reverse the polarity of that state transition.

42. *Cusping of main body of second tooth of dentary*: (0) distal margin of main body of second tooth of dentary with straight incisiform margin and no apparent cusps; (1) distal margin of main lobe of second tooth of dentary with only single cusp (posterior lobe, if present, may also possess one or more distinct cusps); (2) distal margin of main lobe of second tooth of dentary with two distinct cusps (posterior lobe, if present, may also possess one or more distinct cusps); (3) distal margin of main lobe of second tooth of dentary with three distinct cusps (posterior lobe, if present, may also possess one or more distinct cusps) (CI = 0.333; RI = 0.727).

Most species in the Anostomidae have similar cusping patterns on the three dentary teeth located closest to the symphysis. Nonetheless, sufficient species in the family differ in the characteristic cusping patterns of the symphyseal, second and third teeth of the dentary as to merit a separate coding for each of these teeth. Species not discussed below are coded as for character 41. *Synaptolaemus* has a tricuspid second dentary tooth (Fig. 31G; state 3), which contrasts with the unicuspid morphology of the symphyseal dentary tooth in that taxon. *Leporinus* cf. *moralesi* (Fig. 32A) has a bicuspid main lobe of the second dentary tooth despite lacking a second cusp on the symphyseal tooth. *Gnathodolus* lacks the second tooth of the dentary and consequently cannot be coded for this character.

In the final phylogeny, this character yields the synapomorphies of equal inclusiveness and supports the same clades as does character 41. The cusping patterns observed in *Leporinus* cf. *moralesi* and *Synaptolaemus* are autapomorphic in the context of the analysed set of taxa, but may prove to be synapomorphies of *Synaptolaemus* or a portion of *Leporinus* when additional species of each genus are added to the analysis.

43. *Cusping of main body of third tooth of dentary*: (0) distal margin of main body of third tooth of dentary with straight incisiform margin and no apparent cusps; (1) distal margin of main lobe of third tooth of dentary with only single cusp (posterior lobe, if present, may also possess one or more distinct cusps); (2) distal margin of main lobe of third tooth of dentary with two distinct cusps (posterior lobe, if present, may also possess one or more distinct cusps); (3) distal margin of main lobe of third tooth of dentary with three distinct cusps (posterior lobe, if present, may also possess one or more distinct cusps) (CI = 0.429; RI = 0.810).

The species of *Petulanos* have tricuspid main lobes of the third tooth of the dentary (state 3) as opposed to the unicuspid adult dentition of the symphyseal and second teeth on that bone. The specimen of *Petulanos intermedius* that appears in the micrograph (Fig. 31F) has an anomalously rounded (worn?) third dentary tooth whereas the contralateral tooth on the left side of that individual is clearly tricuspid. This difference may represent different levels of wear if the species of the Anostomidae undergo the simultaneous complete replacement of the teeth on one side of the jaw such as occurs in various groups in the Characiformes (Roberts, 1967; Berkovitz, 1975; Berkovitz & Shellis, 1978). In support of that conjecture, several examined alcohol specimens of *Petulanos intermedius* (INPA 15184) are missing all but the symphyseal tooth in one side of the lower jaw. *Leporinus cf. moralesi* (Fig. 32A) has a unicuspid main body of the third tooth of the dentary (state 1) that contrasts with the distinctly bicuspid main lobe of the second tooth of the dentary in that taxon. *Rhytiodus argenteofuscus* has only a single cusp on the main lobe of the third tooth of the dentary (Fig. 32D), while *Pseudanos* (Fig. 32F), *Anostomus*, *Schizodon nasutus* and *S. isognathus* have three cusps on the main lobe of the third tooth of the dentary contrary to the two cusps that they possess on the symphyseal and second teeth of that bone. The third teeth of the dentary of *Synaptolaemus* (Fig. 31G) and *Sartor* (Fig. 31H) are reduced in size (note that the tiny third tooth in the figured specimen of *Sartor* has a damaged tip and is hardly visible), but are apparently unicuspid and coded as such (state 1). Taxa not cited above are coded as for character 42.

In the final hypothesis of relationships, state 1 is plesiomorphic within the Anostomidae. The possession of two cusps on the third tooth of the dentary is a synapomorphy linking *Rhytiodus lauzannei* and *R. microlepis* (clade 17). The presence of an incisiform third tooth (state 0) is a synapomorphy for *Laemolyta*. Optimization of character state 3 varies between ACCTRAN and DELTRAN reconstructions. Under ACCTRAN, state 3 evolved in the common ancestor of clade 14 with subsequent shifts in cusping in *Rhytiodus argenteofuscus*, clade 17, *Laemolyta* and clade 31. Under DELTRAN, state 1 is the plesiomorphic condition for clade 14 and the tricuspid third tooth of the dentary (state 3) evolved independently in *Schizodon* and clade 25, with additional state changes in *Laemolyta*, and clades 17 and 31.

44. *Presence or absence of cusps on posterior lobes of dentary teeth*: (0) posterior lobes of dentary teeth absent, or if posterior lobes present, no distinct cusp present on posterior lobes of tooth; (1) posterior lobes of dentary teeth with one or more distinct cusps (CI = 1.000; RI = 1.000).

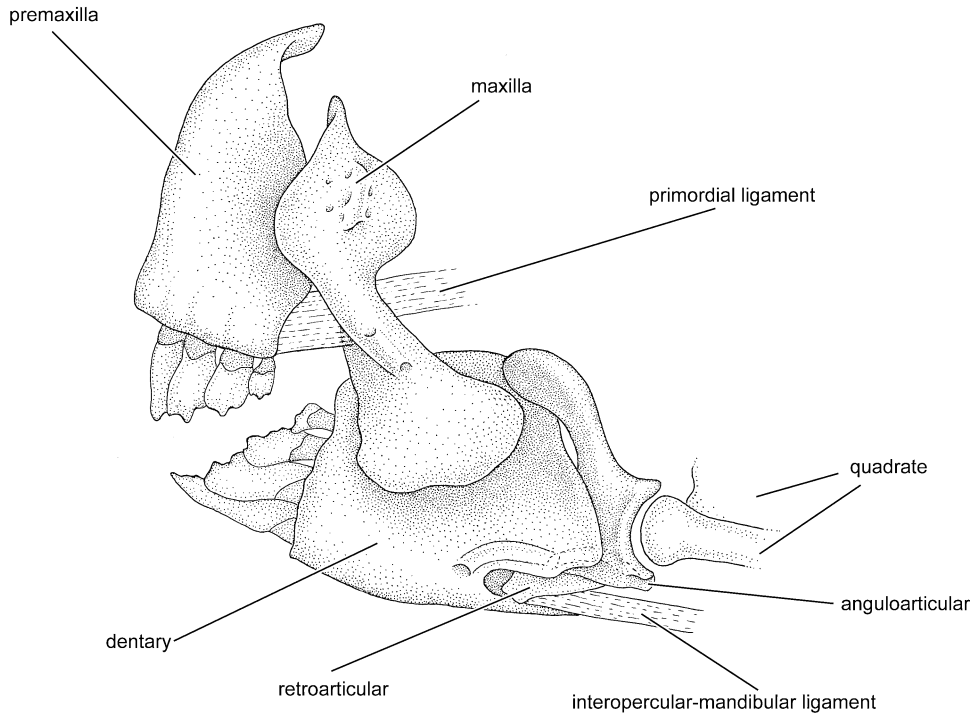
Most anostomids lack a posterior lobe of the dentary teeth delimited by a distinct notch along the posterior lamina of the tooth (see characters 39 and 40). Among those members of the family with a posterior lobe, only the species of *Rhytiodus* and *Schizodon* possess one or more distinct cusps on the distal margin of that posterior lobe (Fig. 32D, E). Most species in these genera possess a single cusp on this lobe, but *Schizodon isognathus* has two cusps. None of the examined outgroups possesses a posterior lamina, let alone a notch or posterior lobe of the dentary teeth; consequently, we did not code the outgroups for this character. The possession of a distinct posterior cusp on the dentary teeth is a synapomorphy for the clade containing *Rhytiodus* and *Schizodon* (clade 15) under the final phylogenetic hypothesis.

#### UPPER JAW

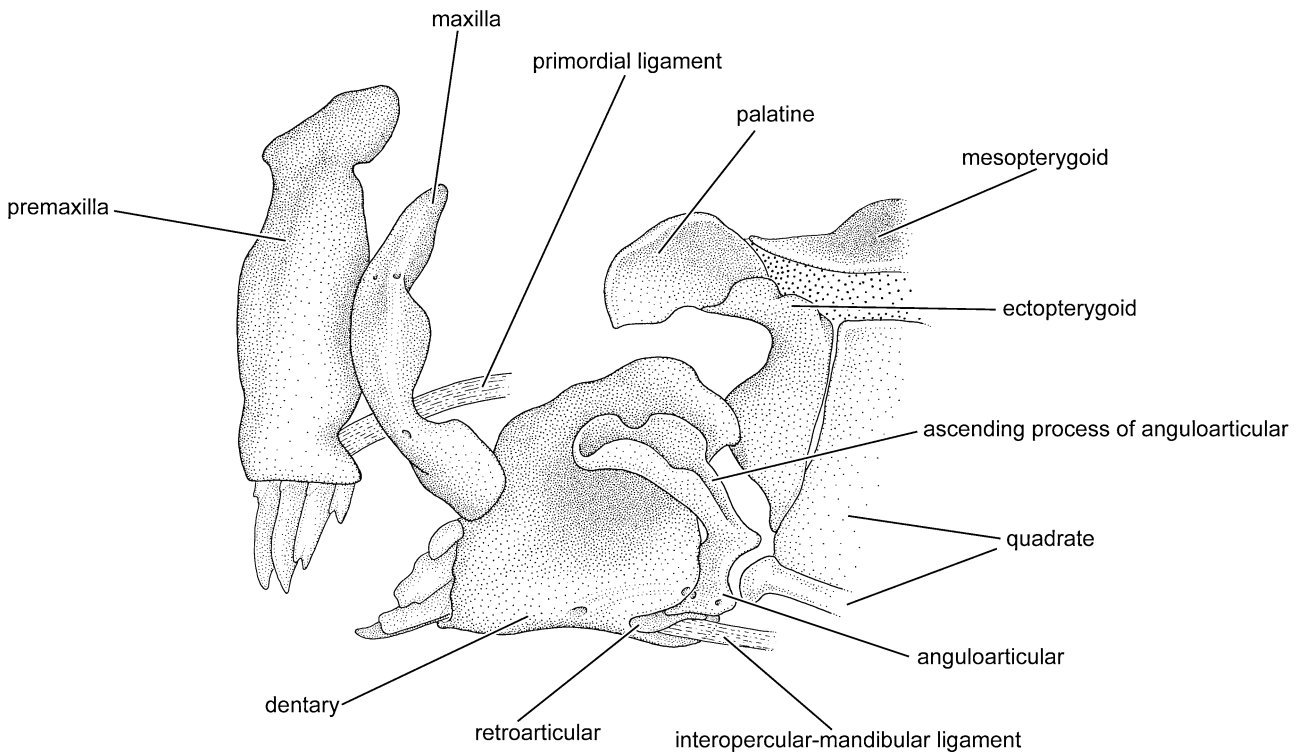
45. *Form of ascending process of premaxilla*: (0) either absent or slightly to moderately developed and slender; (1) large, well developed and distinctly triangular overall (CI = 0.500; RI = 0.917).

In all members of the Anostomidae as well as in the outgroup *Parodon suborbitalis*, the premaxilla is a very robust ossification with an enlarged ascending process that progressively expands from its tip towards the region where it joins the main body of the bone (state 1, Figs 33–37). The ascending process of the premaxilla has a resultant overall triangular form in lateral view and is less distinct from the main body of the premaxilla than in outgroups (see also comments in Vari, 1983: 10), which typically have an ascending process of the premaxilla that is notably narrower than, and quite distinct from, the main body of that bone (state 0). *Curimata inornata* and *Distichodus* sp. have deep, ventrally expanded premaxillae but no distinct ascending process and are coded as 0, while an apparent process in *Xenocharax spilurus* is medial in position and presumably non-homologous with that in the Anostomidae (also coded as 0). In the final reconstruction, the triangular form of the ascending process of the premaxilla is a synapomorphy for the whole Anostomidae (clade 1). *Parodon suborbitalis* is not the sister to the Anostomidae (Vari, 1983; results herein), and the triangular ascending process of the premaxilla in that species is a homoplasy relative to the presence of that feature in the family.

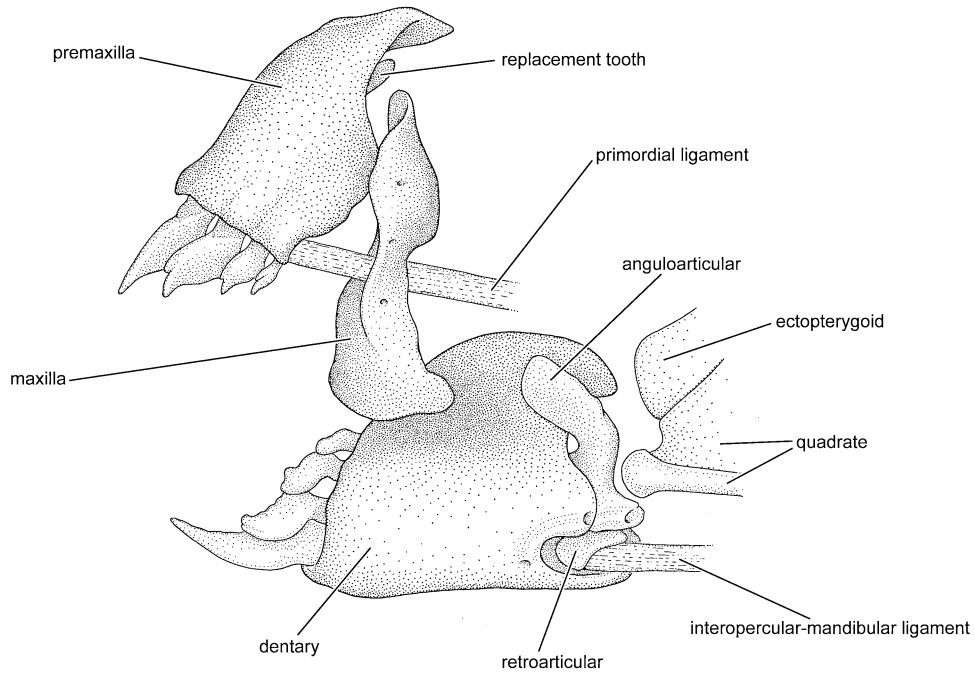
46. *Orientation of premaxilla*: (0) vertically or antero-dorsally inclined, with dorsal point of premaxilla situated immediately dorsal to, or anterior of, vertical through ventral point of premaxilla; premaxillary teeth directed ventrally or posteroventrally; (1) postero-dorsally inclined, with dorsal portion of premaxilla



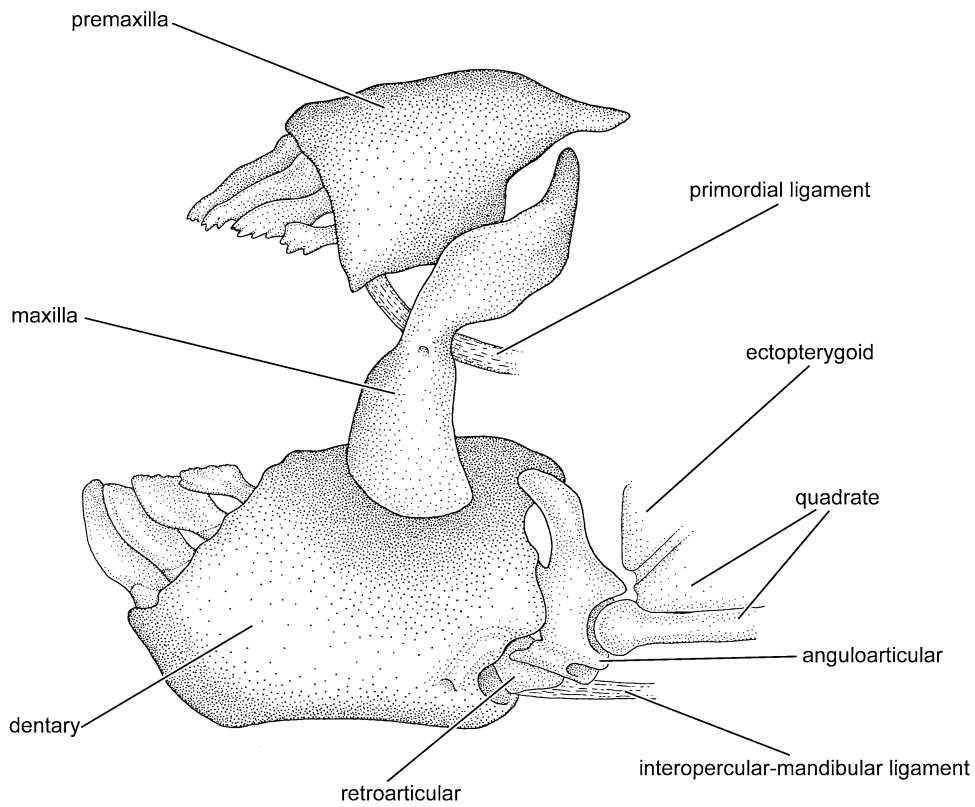
**Figure 33.** Left upper and lower jaws of *Leporellus vittatus*, INHS 56128, 78.2 mm SL; lateral view.



**Figure 34.** Left upper and lower jaws and anterior palatine arch, *Hypomasticus mormyrops*, USNM 318140, 104 mm SL; lateral view, jaws spread wider in drawing of dissected specimen than typical in life.

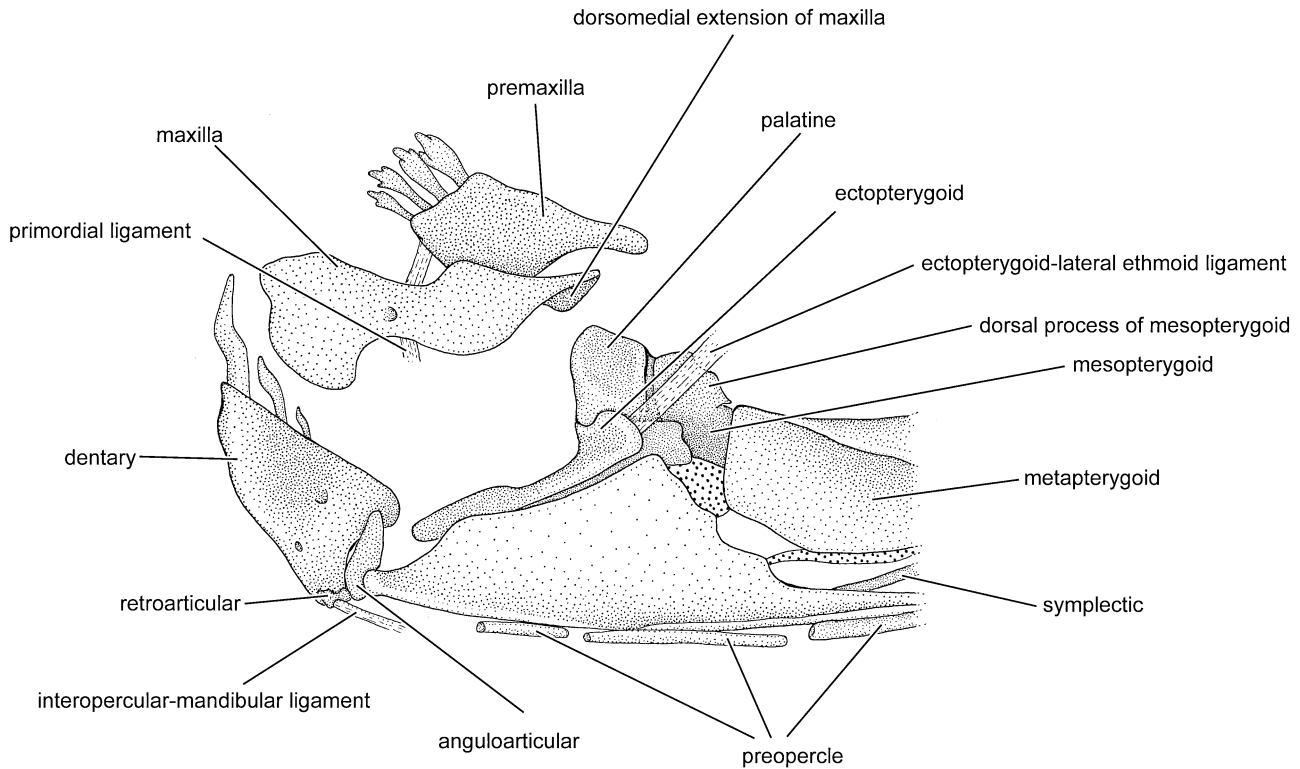


**Figure 35.** Left upper and lower jaws, *Leporinus fasciatus*, USNM 225991, 87.8 mm SL; lateral view, jaws spread wider in drawing of dissected specimen than typical in life.



**Figure 36.** Left upper and lower jaws, *Laemolyta taeniata*, USNM 280708, 72.9 mm SL; jaws spread wider in drawing of dissected specimen than typical in life.





**Figure 37.** Right upper and lower jaws, *Sartor elongatus*, INPA 1168 (paratype), 76.1 mm SL; lateral view, jaws spread wider in drawing of dissected specimen than typical in life, drawing reversed to place anterior at left.

situated far posterior of vertical through ventral margin of premaxilla; premaxillary teeth directed anteroventrally; (2) horizontally orientated premaxilla with points of premaxilla homologous with dorsal and ventral margins of premaxilla in states 0 and 1 situated along same approximate horizontal plane; premaxillary teeth directed anteriorly (CI = 0.400; RI = 0.893).

Species in the Anostomidae vary considerably in the orientation of the mouth and demonstrate considerable correlated variation in the alignment of the primary axis of the premaxilla when the mouth is closed. In one distinctive morphology (state 0), possessed by *Hypomasticus* (Fig. 34) and *Schizodon nasutus*, the mouth is downturned and the longest axis of the premaxilla is orientated vertically, with the premaxillary teeth directed ventrally or posteroventrally. Among these taxa, the most extreme downward rotation of the mouth occurs in *Hypomasticus mormyrops* and *H. pachycheilus* in which the mouth opens onto the ventral surface of the head. In *Abramites*, *Anostomoides*, *Leporellus* (Fig. 33), *Leporinus* (Fig. 35), *Rhytioidus*, *Schizodon isognathus*, *S. fasciatus*, *S. knerii*, *S. scotorhabdotus* and *S. vittatus* the mouth is terminal or slightly subterminal and the premaxilla is posterodorsally inclined with the teeth directed anteroventrally (state 1). Within this group of

taxa, the species of *Leporellus* along with *Schizodon isognathus* approach the vertically aligned premaxilla characteristic of state 0, but with the premaxilla in *Leporellus* and *S. isognathus* inclined sufficiently anterodorsally to merit coding in state 1. In *Anostomus*, *Gnathodolus*, *Laemolyta* (Fig. 36), *Petulanos*, *Pseudanos*, *Sartor* (Fig. 37) and *Synaptolaemus*, the mouth is upturned and the longest axis of the premaxilla has an overall horizontal orientation, with the plesiomorphously dorsal portion of the premaxilla now situated at the posterior limit of the bone and the premaxillary teeth directed anteriorly (state 2).

The cleared and stained specimens of *Rhytioidus*, which are all juveniles, have upturned mouths with horizontal premaxillae (state 2), whereas large adults of *Rhytioidus* (examined by way of radiographs) have the mouth opening facing anteriorly and the premaxilla with a posterodorsal orientation (state 1). An ontogenetic shift in the position of the mouth to an anterior position in *Rhytioidus* was documented by Santos (1980) and that genus is coded as having state 1 based upon the morphology of the mouth in adults of the genus. At least some species of *Schizodon* including *S. fasciatus*, *S. isognathus* and *S. scotorhabdotus* also undergo a similar ontogenetic shift in the position of the mouth, possessing horizontally aligned premaxillae as juveniles and posterodorsally inclined

premaxillae as adults (Santos, 1980; Sidlauskas *et al.*, 2007). All of the examined cleared and stained specimens of *Schizodon* are of a body size large enough to have already made the transition to the adult state of the mouth, with those species coded as having the states possessed by the examined cleared and stained material. *Schizodon isognathus*, *S. fasciatus*, *S. knerii*, *S. scotorhabdotus* and *S. vittatus* have posterodorsally inclined premaxillae as adults (state 1), while *S. cf. nasutus* has a vertically orientated premaxilla (state 0).

Among the examined outgroups, the different morphologies of the ascending process of the premaxilla relative to the condition typical of the Anostomidae (see character 45) renders this character difficult to code. Based on the orientation of the dentigerous surface of the premaxilla, character states 1 (posterodorsally inclined premaxilla) and 0 (vertical premaxilla) both occur in the outgroups. The species of the closest outgroup (Chilodontidae) appear to have posterodorsally inclined premaxillae (state 1), as does the distantly related *Distichodus* sp. In the Prochilodontidae of the second outgroup, in which the oral dentition is attached to the fleshy lips rather than the underlying bones, the overall structure of the premaxilla is very different from that present in the Anostomidae. This is also the case in the jaws of the genera of the edentulous Curimatidae. The presumably formerly dentigerous surface of the premaxilla in the Prochilodontidae and the Curimatidae is directed ventrally as it is in the members of the Anostomidae with premaxillae that have a vertical orientation of that bone (state 0). Consequently members of the Prochilodontidae and Curimatidae are also coded as possessing state 0 for this character. *Parodon suborbitalis* has a strongly downturned mouth with a posteroventral orientation of the premaxillary teeth and clearly meets the conditions for state 0, while the situation in the more distant outgroups *Hemiodus*, *Brycon*, *Xenocharax* and *Citharinus* is somewhat equivocal. We coded those four outgroups tentatively for state 0. Character state 2 is clearly absent in all of the examined outgroups.

In the final analysis, the plesiomorphic condition for the Anostomidae is state 1, a posterodorsally aligned premaxilla. A vertically aligned premaxilla is hypothesized to be a synapomorphy for clade 4 (*Hypomasticus*) with the similar morphology in *Schizodon nasutus* derived independently. The horizontal orientation of the premaxilla (state 2) is a synapomorphy for *Laemolyta*, *Pseudanos*, *Anostomus*, *Petulanos*, *Synaptolaemus*, *Sartor* and *Gnathodolus* (clade 17).

47. *Presence or absence of block-like anterodorsal process of premaxilla*: (0) anterodorsal portion of premaxilla not as in state 1; (1) premaxilla with large,

block-like anterodorsal process that fits above lateral process of mesethmoid (see character 16) (CI = 1.000; RI = 1.000).

The medial anterodorsal surface of the premaxilla in most species in the Anostomidae has a smoothly convex region positioned immediately dorsal to a distinct concavity on the premaxilla that accommodates the anterior process of the mesethmoid. In *Hypomasticus mormyrops* and *H. pachycheilus*, the anterodorsal portion of the premaxilla has instead a large anteriorly directed process with square corners that fits dorsal to the prominent lateral flanges of the mesethmoid (partially visible in lateral view, Fig. 34). The function of this process of the premaxilla is uncertain, but it is probably correlated functionally with the strongly subterminal position of the mouth in those two species; this location of the mouth does not occur in any other examined species of the Anostomidae.

Several species of *Leporinus* have a small knob on the anterodorsal margin of the premaxilla (e.g. *L. striatus*, *L. pellegrinii*, *L. gomesi*, *L. jatuncochi*) but the process in these species is much smaller than that present in *Hypomasticus mormyrops* and *H. pachycheilus*, lacks squared-off corners and does not extend over a lateral process of the mesethmoid. The process on the premaxilla of these *Leporinus* species is consequently considered non-homologous to the structures in the two *Hypomasticus* species. *Hypomasticus despaxi* and *H. megalepis* have a small knob-like process that does fit over a lateral process of the mesethmoid, but the overall form of the knob in these two species is more similar to the small process in that region present in *Leporinus striatus*, *L. pellegrinii*, *L. gomesi* and *L. jatuncochi* than it is to the very large process that occurs in *Hypomasticus mormyrops* and *H. pachycheilus*. As such the premaxillary processes in *H. despaxi* and *H. megalepis* are at most precursors of the large structures present in *H. mormyrops* and *H. pachycheilus* and are not coded as equivalent to these processes.

None of the examined species in the remaining genera within the Anostomidae and in the proximate outgroups to the Anostomidae (Chilodontidae, Curimatidae, Prochilodontidae) or more distant outgroups has the distinctive form of the anterodorsal process of the premaxilla comparable with that possessed by *Hypomasticus mormyrops* and *H. pachycheilus*. In the final hypothesis of relationships, possession of the block-like anterodorsal process of the premaxilla is a synapomorphy for clade 6.

48. *Orientation of maxilla*: (0) maxilla having anterodorsal orientation, with dorsal tip of maxilla situated distinctly anterior of ventral tip of bone; (1) maxilla having vertical or posterodorsal orientation, with

dorsal tip of maxilla situated directly dorsal to, or distinctly posterior of, ventral margin of bone (CI = 1.000; RI = 1.000).

Most characiforms including *Brycon* (Weitzman, 1962: fig. 8) and the basal members of the Distichodontidae [e.g. *Xenocharax* (Daget, 1960: fig. 7)] and Citharinidae (e.g. *Citharinus*) have the dorsal tip of the maxilla positioned anterior to the vertical through the ventral tip of the maxilla when the mouth is closed. This condition (state 0) is common to all examined outgroups, but within the Anostomidae it is limited to *Leporellus* and *Hypomasticus* (Figs 33, 34). The remaining members of the Anostomidae have a maxilla with a vertical or posterodorsal orientation in the closed mouth (state 1; Figs 35–37), which optimizes as a synapomorphy for clade 7 in the final phylogeny. The most extreme posterodorsal rotation of the maxilla is found in *Gnathodolus*, *Sartor* and *Synaptolaemus* (Fig. 37). The variation between the vertically and variably posterodorsally inclined orientations present in various anostomids is, however, continuous and no objective division between the diverse morphologies contained within state 1 was possible.

49. *Insertion of primordial ligament on medial surface of maxilla*: (0) area of attachment of ligament on medial surface of maxilla located at middle of longest axis of bone or slightly dorsal to that point; (1) area of attachment of ligament on medial surface of maxilla located within ventral half of longest axis of bone (CI = 0.333; RI = 0.846).

In the examined species of the Chilodontidae, Curimatidae and Prochilodontidae, the component of the adductor mandibulae muscle that serves to rotate the upper jaw posteroventrally attaches to the medial surface of the maxilla by way of the primordial ligament *sensu* Winterbottom (1974a: 232), termed the articular–maxillary ligament by Alexander (1964: 183). The primordial ligament in these taxa inserts at, or somewhat dorsal to, the vertical midpoint of the main body of the maxilla (for condition in the Curimatidae see Vari, 1989a: fig. 37). Within the Anostomidae, with the exception of *Leporellus* (Fig. 33) the insertion of this muscle is located distinctly ventral of the vertical midpoint of the maxilla (state 1, Figs 34–37; noting that the dorsal portion of the maxilla turns medially and is foreshortened in lateral view in the illustrations). In most anostomids (e.g. *Abramites*, *Laemolyta*, *Pseudanos*, *Schizodon*) the primordial ligament attaches very close to the ventral margin of the maxilla. In the other examined anostomids, particularly in taxa where the ventral flange of the maxilla is enlarged (*Petulanos*, *Gnathodolus*, *Sartor*, *Synaptolaemus*, see character 52) the primordial ligament inserts just ventral of the midpoint of the

maxilla. The maxillae of the available cleared and stained specimen of *Pseudanos irinae* are missing and that specimen could not be coded for this and several subsequent characters.

Under the most parsimonious hypothesis of relationships arrived at during this study, the relocation of the insertion of the primordial ligament to a more ventral position (or alternatively, the dorsoventral shortening of the ventral portion of the maxilla, which would achieve the same result) is a synapomorphy for the members of the Anostomidae exclusive of *Leporellus* (clade 3).

50. *Form of insertion of anterolateral flange of maxilla on flat ventral portion of maxilla*: (0) anterolateral flange of maxilla merges with ventral portion of maxilla on lateral face of ventral portion; (1) anterolateral flange of maxilla merges with ventral portion of maxilla on anterior edge of ventral portion (CI = 0.500; RI = 0.957).

In members of the Anostomidae, the maxilla has a distinct anterolateral flange that extends over the ventral portion of the posterior corner of the premaxilla (see, for example, *Leporinus fasciatus*, Fig. 35). In *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytidodus* and *Schizodon*, the anterolateral flange of the maxilla merges with the ventral portion of the maxilla posterior of the anterior edge in lateral view (state 0; distinctly so in most of the above genera, but only barely in *Laemolyta*). Alternatively, in *Anostomus*, *Petulanos*, *Pseudanos*, *Sartor*, *Gnathodolus* and *Synaptolaemus*, the anterolateral flange merges with the anterior edge of the ventral portion of the maxilla (state 1, Fig. 37). The anterolateral flange of the maxilla also merges with the anterior edge of the ventral flange of the maxilla in all examined outgroups (state 0).

Under the reconstruction of relationships arrived at in this study, state 0 (the extension of the flange onto the lateral surface of the main body of the maxilla) is a synapomorphy for the Anostomidae and is possessed by the most basal members of the family (e.g. *Leporellus*). State 1 is a synapomorphy for the clade consisting of *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 21).

51. *Rotation of ventral portion of maxilla relative to anterolateral flange of maxilla*: (0) anterolateral and ventral flanges of maxilla rotated relative to each other along main axis of bone with result that ventral portion of maxilla lies in parasagittal plane and anterolateral flange of bone lies in transverse plane; (1) anterolateral flange of maxilla and ventral portion of bone without rotation relative to each other, and both lying in parasagittal plane (CI = 0.333; RI = 0.857).



Most species in the Anostomidae have an obvious twist of the ventral portion of the maxilla (Figs 33–36) relative to the anterolateral flange of the maxilla. The extent of this torsion varies among the members of the family that demonstrate this modification, being well developed in *Abramites*, *Anostomoides*, *Hypomasticus* (Fig. 34), *Leporinus* (Fig. 35), *Rhytiodus* and *Schizodon*, and poorly developed, but still present, in *Anostomus*, *Leporellus* (Fig. 33), *Laemolyta*, (Fig. 36) *Petulanos* and *Pseudanos*. Torsion of the anterolateral flange of the maxilla relative to the ventral portion of the maxilla is absent in the species in *Gnathodolus*, *Sartor* and *Synaptolaemus*, all of which have these two components of the maxilla joined into a single continuous plate (Fig. 37).

Most examined outgroups also lack torsion of the anterolateral flange of the maxilla relative to the ventral portion of that bone (Chilodontidae, Characidae, Curimatidae, Citharinidae, Distichodontidae), although the highly modified maxilla in examined members of the Prochilodontidae exhibits considerable torsion and is coded as having state 0. Given the final hypothesis of relationships arrived at in this study, the torsion of the maxilla (state 0) evolved early in the history of the Anostomidae and is a synapomorphy for the family. Torsion of the maxilla was secondarily lost (state 1) during the evolution of the highly derived species of the genera *Gnathodolus*, *Sartor* and *Synaptolaemus*, which form a deeply nested clade in the family (clade 31) under both this reconstruction and that of Winterbottom (1980).

52. *Width of ventral portion of maxilla*: (0) ventral portion of maxilla narrow, only slightly expanded in axis transverse to long axis of bone; (1) ventral portion of maxilla very wide, greatly expanded in direction transverse to long axis of bone (CI = 0.250; RI = 0.824).

Most members of the Anostomidae [*Abramites*, *Anostomoides*, *Anostomus*, *Hypomasticus* (Fig. 34), *Laemolyta* (Fig. 36), *Leporinus* (Fig. 35), *Pseudanos*, *Rhytiodus* and *Schizodon*] possess relatively small and narrow ventral portions of the maxilla (state 0). This portion of the maxilla in the close outgroups, the Chilodontidae, Curimatidae and Prochilodontidae, is greatly expanded along both the long axis of the bone and the direction perpendicular to that axis (state 1) relative to the condition typical for the Anostomidae. *Leporellus*, *Gnathodolus*, *Petulanos*, *Synaptolaemus* and *Sartor* have the ventral flange of the maxilla greatly expanded in the direction perpendicular to the long axis of the maxilla in a mode similar to the outgroup condition (state 1; for condition in *Leporellus* see Fig. 33, for *Sartor* see Fig. 37).

Winterbottom (1980) cited a triangular expansion of the ventral portion of the maxilla as a synapomorphy

for *Gnathodolus*, *Sartor*, *Synaptolaemus* and all members of his concept of *Anostomus* (herein encompassing *Anostomus* plus *Petulanos*). We differ from his interpretation of the maxillae of *Anostomus anostomus* and *A. ternetzi*. Winterbottom considered the maxillae in those two species to be ventrally expanded, while we see no objective difference between the form of that portion of the bone in those species and the condition in *Pseudanos*, *Laemolyta* and other members of the Anostomidae (state 0).

Among more distant outgroups, *Brycon falcatus*, *Hemiodus ocellatus* and *Parodon suborbitalis* have the maxilla expanded along the long axis of the bone, but not along the perpendicular axis (for the condition in *Brycon* see Weitzman, 1962: fig. 8). These three taxa are coded as possessing state 0. Members of the Citharinidae and basal members of the Distichodontidae have greatly expanded ventral flanges of the maxilla relative to the condition typical of the Anostomidae and are coded as possessing state 1.

Under the final hypothesis of relationships presented herein, the widened ventral flange of the premaxilla is a symplesiomorphy shared by the proximate outgroups and *Leporellus*. The narrow form of the maxilla is a synapomorphy for clade 3, while the repeated evolution of a widened flange is, in turn, a synapomorphy for clade 20 (*Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*).

53. *Form of dorsal tip of maxilla*: (0) dorsal portion of maxilla rod-like, with tapered or pointed tip; (1) dorsal portion of maxilla in form of flat, medially directed plate (CI = 0.333; RI = 0.667).

In most species in the Anostomidae, including *Abramites*, *Anostomoides*, *Anostomus*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytiodus*, *Schizodon* and *Pseudanos trimaculatus* the dorsal portion of the maxilla has a rod-like form in the area where it contacts the anterior of the pair of cartilages that lie between the tip of the maxilla and the anterior portions of the palatine (state 0, Figs 33–36). In *Gnathodolus*, *Petulanos*, *Pseudanos gracilis*, *P. winterbottomi*, *Sartor* and *Synaptolaemus* the dorsal portion of the maxilla that approaches the palatine is alternatively distinctly flattened (state 1, Fig. 37). The maxillae of the available cleared and stained specimen of *Pseudanos irinae* are missing and that specimen could not be coded for this character. Of the seven examined anostomid species with the compressed plate-like morphology of this portion of the maxilla, the compression is least pronounced in *Pseudanos gracilis* and *P. winterbottomi* and most pronounced in *Sartor*.

The dorsal portion of the maxilla of *Brycon meeki* (Weitzman, 1962: fig. 2), the basal distichodontid *Xenocharax* (Daget, 1960: fig. 7), *Citharinus* sp., *Dis-*



*tichodus* sp., *Parodon suborbitalis*, *Hemiodus ocellatus* and most other members of the Characiformes has a distinct rod-like form with a tapered dorsal tip (state 0). Members of the Curimatidae have the dorsal portion of the otherwise plate-like maxilla extended into a long rod (Vari, 1982b: fig. 11; 1989a: fig. 43). A similar rod-like dorsal portion of the maxilla, albeit a very short one, is found in the species of the Chilodontidae. In the Prochilodontidae, the anterior portion of the maxilla, which is homologous to the dorsal portion of the maxilla in other characiforms, is also extended into a long rod and coded as state 0.

Although state 0 is clearly plesiomorphic, the optimization of the gain of state 1 on the final phylogeny is ambiguous due to the polytomies in the region of the phylogeny involving *Pseudanos* and the missing data for *Pseudanos irinae*. Under ACCTRAN the flattened dorsal region of the premaxilla evolved in the common ancestor of *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25) with subsequent reversions in *Pseudanos trimaculatus*, the species of *Anostomus* (clade 28) and possibly *Pseudanos irinae*. Under DELTRAN the compressed morphology of the dorsal portion of the maxilla represents a synapomorphy for clade 29, which is composed of *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*, with additional homoplastic gains within *Pseudanos*.

54. *Form of contact of dorsal portion of maxilla with anterolateral and posterior portions of maxilla*: (0) anterolateral and posterior portions of maxilla (if present) merge without interruption into dorsomedial process of maxilla that contacts cartilage of palatine; dorsal portion of maxilla not as in state 1; (1) anterolateral and posterior portions of maxilla merge to form flat plate orientated perpendicular to process of maxilla that contacts cartilage of palatine (CI = 1.000; RI = 1.000).

In most species of the Anostomidae, as well as in all examined outgroups, any flanges or bony plates associated with the dorsal portions of the maxilla grade smoothly into the dorsal process of the maxilla in the area where that bone contacts the cartilages associated with the palatine (e.g. *Laemolyta*, Fig. 36). In *Gnathodolus* and *Sartor*, these flanges alternatively form a broad, flat plate that is orientated perpendicular to the dorsal process of the maxilla that contacts the cartilages associated with the palatine (for condition in *Sartor*, see Fig. 37). *Leporellus* (Fig. 33) has a morphology of its maxilla with the dorsal process expanded into a broad plate which is superficially similar to that present in *Gnathodolus* and *Sartor*. In *Leporellus* this plate grades smoothly into the dorso-medial portions of the maxilla instead of being orien-

tated at right angles to that region as is the case in *Gnathodolus* and *Sartor*. No other modification of this portion of the maxilla in any anostomid or outgroup approaches the morphology of that bone found in *Gnathodolus* and *Sartor*, which is a synapomorphy linking those two genera (clade 30).

#### LOWER JAW

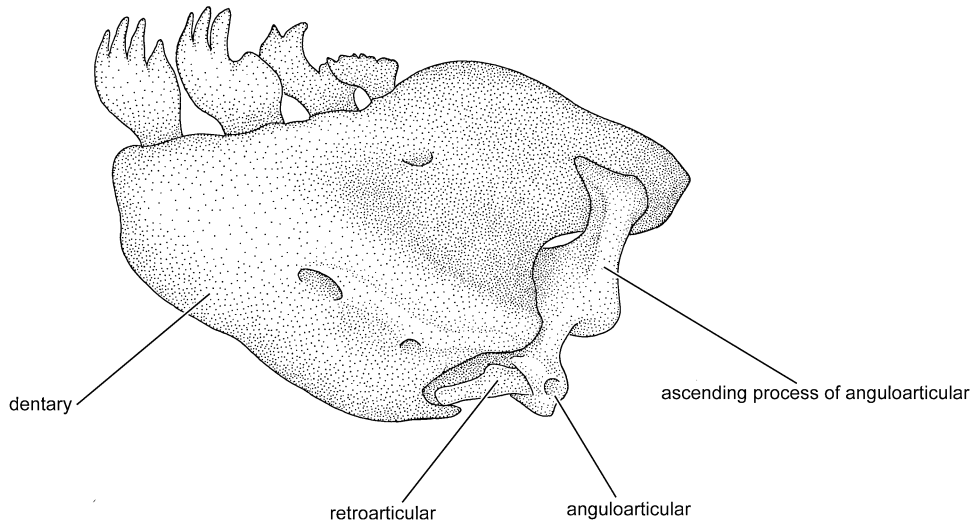
55. *Width of ascending process of anguloarticular*: (0) ascending process of anguloarticular narrow, not forming wide vertical ridge perpendicular to dentary; (1) ascending process of anguloarticular very wide, forming pronounced vertical ridge perpendicular to dentary (CI = 0.500; RI = 0.889).

In most members of the Anostomidae and all examined outgroups, the ascending process of the anguloarticular is a thin, narrow process of bone, closely associated with, and in the same plane as, the posterior portions of the dentary (e.g. *Leporellus*, Fig. 33; see also Figs 35–37). Two groups within the Anostomidae (*Schizodon* and *Hypomasticus*) instead have the ascending process of the anguloarticular greatly thickened and widened, forming a raised vertical ridge projecting laterally from the posterolateral surface of the dentary (for condition in *Hypomasticus* see Fig. 34; for *Schizodon* see Figs 38, 39). A few species of *Leporinus* (most notably *L. ortomaculatus*, *L. pellegrinii* and *L. striatus*) have a knob-like process near the dorsal margin of the ascending process of the anguloarticular with the ascending processes slightly thickened overall relative to those present in the other species of *Leporinus*. The width of the ascending process of the anguloarticular in these three species is much less pronounced than it is in *Schizodon* or *Hypomasticus*. *Leporinus ortomaculatus*, *L. pellegrinii* and *L. striatus* are consequently coded as possessing state 0 (narrow process) for this character.

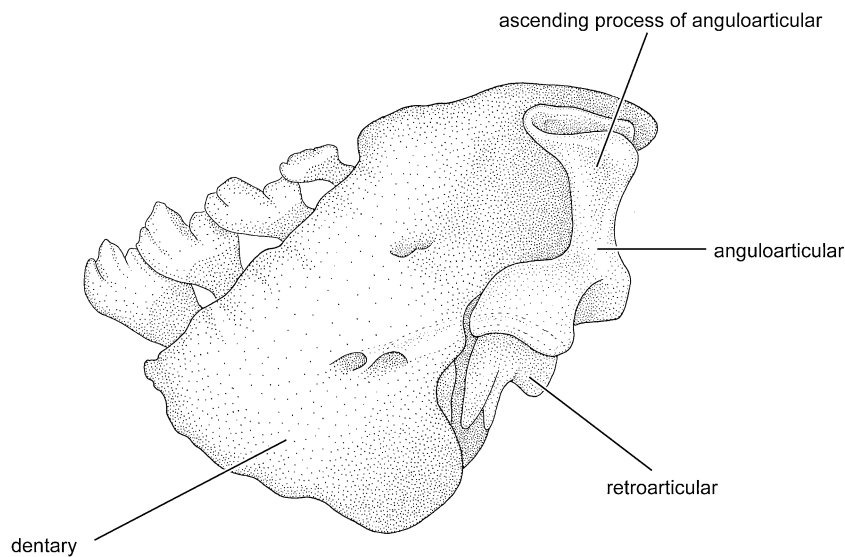
Under the final hypothesis of relationships arrived at under this study, the widened form of the anguloarticular evolved twice within the Anostomidae, once in a common ancestor of *Hypomasticus* (clade 4) and once in the lineage leading to *Schizodon* (clade 18).

56. *Presence or absence of trough-like form of dorsal portion of ascending process of anguloarticular*: (0) ascending process of anguloarticular not as in state 1; (1) dorsal portion of ascending process of anguloarticular in form of deep trough for passage of thick A1 component of adductor muscle that inserts on medial surface of maxilla by way of primordial ligament (CI = 0.500; RI = 0.750).

The morphology of the ascending process of the anguloarticular in the set of species with subterminal mouths within the Anostomidae is particularly strik-



**Figure 38.** Right lower jaw, *Schizodon fasciatus*, USNM 280739, 103.2 mm SL; lateral view, drawing reversed to place anterior at left.



**Figure 39.** Left lower jaw, *Schizodon nasutus*, USNM 326944, 111 mm SL; lateral view.

ing, even allowing for the notable variation in the form of this process across the family. In all examined species of *Hypomasticus* and also *Schizodon nasutus* (all of which possess the widened form of the ascending process, see character 55), the dorsal portion of the ascending process of the anguloarticular is modified into a deep trough through which a section of the anterior portion of the A1 portion of the adductor mandibulae muscle passes before continuing further anteriorly via the primordial ligament to an attachment on the medial surface of the maxilla (for condition in *Hypomasticus mormyrops* see Fig. 34; for *Schizodon nasutus* see Fig. 39). After passing anteriorly through the trough, the muscle and associated

ligament turn sharply ventrally to the insertion of the ligament on the medial surface of the maxilla. In *Schizodon nasutus* the trough is primarily a notch in the widened dorsal margin of the anguloarticular with limited anterior expansion (Fig. 39), while in *Hypomasticus* the notch is extended into an anteriorly elongate trough (Fig. 34). No other examined species in either the Anostomidae or any outgroup has the trough-like morphology of the ascending process of the angular possessed by the five cited species, although a slight depression in the widened ascending process of the anguloarticular occurs in *S. isognathus*. *Schizodon isognathus* is the reconstructed sister species to *S. nasutus* (clade 19), and the slight

depression in that species might represent an incipient form of the notch that is present in *S. nasutus*.

The trough or notch on the anguloarticular and the bend in the associated A1 component of the adductor mandibulae suggests that this system may function in a mode comparable with a pulley or block-and-tackle. If so, the trough may transfer the contractive force of the adductor mandibulae muscle from an anteroposterior direction to a dorsoventral direction prior to the attachment of the muscle via the primordial ligament to the maxilla. The trough appears in those species of *Hypomasticus* and *Schizodon* with downturned mouths lying far ventral of the ascending process of the anguloarticular and may be essential to functioning in a subterminal jaw position. Elucidation of the mechanics and function of these downturned jaws will require construction of a biomechanical model incorporating skeletal and muscular linkages (for example, Ferry-Graham *et al.*, 2001; Westneat, 2003).

This unusual morphology of the anguloarticular is particularly interesting as it represents a clear case of parallel evolution within the Anostomidae, being possessed by four members of *Hypomasticus* that form the relatively basal clade 4 and by the more derived *Schizodon nasutus* within clade 18, the only examined member of that genus that is characterized by a strongly subterminal mouth. These two groups are not closely related to one another (Fig. 5), yet the width of the ascending process and the depth of the notch in the two groups are similar (albeit with the process slightly wider and the notch slightly shallower and less extensive anteriorly in *S. nasutus* than they are in the four species of *Hypomasticus*). Given the potential adaptive value conferred by the trough, it is not particularly surprising that the two groups of anostomids with the most strongly subterminal mouths have evolved this morphology independently.

**57. Elongation of dentary:** (0) dentary block-like or in form of blunt triangle from lateral view; dentary not extremely slender; (1) dentary extraordinarily elongate, distance from joint with anguloarticular to tip of dentary three times or more height of dentary just anterior to ascending process of anguloarticular (autapomorphy).

Alone among the examined species in the Anostomidae and the outgroups, *Gnathodolus bidens* possesses a hyperelongate dentary (see Winterbottom, 1980: fig. 41). Not even *Sartor*, the sister taxon to *Gnathodolus* under Winterbottom's (1980) phylogenetic reconstruction and that arrived at herein, possesses a dentary as elongate as that of *Gnathodolus* (Fig. 37). While this morphology is an autapomorphy for the presently monotypic *Gnathodolus*, Winterbottom (1980: 21–22) suggested the presence of an unde-

scribed species in this genus. The character is included herein as a probable synapomorphy for *Gnathodolus* should future studies reveal the presence of more than one species in the genus.

**58. Form of anterior margin of dentary and angle of teeth:** (0) dentary triangular and without notable bend along anteroventral margin; teeth and anterior margin of dentary inflected so that line drawn through long axis of symphyseal tooth of dentary intersects joint of quadrate and anguloarticular; (1) dentary squarish or rhomboidal with notable bend midway along anteroventral margin; teeth and anterior margin of dentary inflected so that line drawn through long axis of symphyseal tooth of dentary passes distinctly anterior of joint of quadrate and anguloarticular (CI = 0.500; RI = 0.957).

In *Abramites*, *Anostomoides*, *Hypomasticus*, *Leporellus* and *Leporinus*, the dentary is an overall triangular bone with teeth set such that a line drawn through the long axis of the symphyseal tooth intersects the retroarticular or the joint of the quadrate with the anguloarticular (state 0, Figs 33–35). In *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytidodus*, *Sartor*, *Schizodon* and *Synaptolaemus*, the anteroposterior margin of the dentary has a distinct bend (somewhat less so in *Sartor* and *Gnathodolus*, which have rather slender dentaries) and the teeth are positioned in the jaw such that a line drawn through the long axis of the symphyseal tooth of the dentary passes distinctly anterior of the retroarticular and joint of the anguloarticular with the quadrate (Figs 36–39).

The state of this character in the outgroups is difficult to evaluate due to the absence of dentary teeth in adults (all Curimatidae, *Caenotropus labyrinthicus* in the Chilodontidae, *Hemiodus ocellatus* in the Hemiodontidae), the relocation of the teeth from the jaws to the fleshy lips (Prochilodontidae and the remainder of the species within the Chilodontidae), extreme restructuring of the dentary (Prochilodontidae, see Castro & Vari, 2004: figs 12, 13, 16) or the various fundamentally different tooth arrangements possessed by *Brycon*, *Citharinus*, *Distichodus*, *Parodon* and *Xenocharax*. Leaving aside the teeth and examining the ventral profile of the dentary, all examined outgroups except *Distichodus* sp. have fundamentally triangular dentary shapes with an essentially straight ventral profile to the dentary between the retroarticular and the anterior tip of the jaw. Any bend in the ventral profile in the outgroups (except *Distichodus*) occurs immediately proximal to the teeth [e.g. *Brycon* (Weitzman, 1962: fig. 10), *Xenocharax* (Vari, 1979: fig. 3A)], not midway along the ventral profile of the bone as in members of the Anostomidae coded as possessing state 1 (e.g.

*Laemolyta*, Fig. 36). The outgroups other than *Distichodus* sp. are coded consequently as possessing state 0. *Distichodus* sp. has a highly modified rectangular dentary with a distinct bend along the ventral margin (see Vari, 1979: fig. 3B) and is coded tentatively as possessing state 1.

The restructuring of the anterolateral margin of the dentary and the repositioning of the teeth on that bone constitutes an unambiguous synapomorphy for clade 14, formed by *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytidodus*, *Sartor*, *Schizodon* and *Synaptolaemus*. In most members of this clade the distal tip of the tooth is the primary cutting surface, being either incisiform (*Laemolyta* and to a lesser degree *Petulanos*) or strongly multicuspoid (*Anostomus*, *Gnathodolus*, *Pseudanos*, *Rhytidodus*, *Schizodon*), with the posterior blade-like lamina of the tooth reduced relative to the condition in other members of the Anostomidae (character 38). Members of anostomid genera with the more plesiomorphic tooth orientation tend to have dentary teeth with a single strong central cusp and a blade-like posterior lamina that appears to constitute much of the cutting surface of the tooth. The vector of force generated by the teeth when the mouth closes may change with shifts in the angle of the teeth relative to the joint of the lower jaw. If so, the correlated shift in the functional edge of the tooth from the posterior lamina to the distal tip would be unsurprising. Linkage models (e.g. Westneat, 2003, 2006) should be used to calculate force vectors, mechanical advantage and angles of jaw rotation and thereby determine if a major transition in jaw function occurs at the base of clade 14 as suggested by this character.

59. *Angle formed by long axis of dentary and long axis of anguloarticular*: (0) long axes of dentary and anguloarticular form right or acute angle; (1) long axes of dentary and anguloarticular form distinctly obtuse angle (CI = 0.333; RI = 0.333).

Most members of the Anostomidae possess dentaries and anguloarticulars orientated at approximate right angles or slightly acute angles (e.g. *Schizodon fasciatus*, Fig. 38). In *Schizodon isognathus*, *S. knerii* and *S. nasutus* (Fig. 39), there is a ventromedial displacement of the anterior portion of the dentary relative to the anguloarticular, resulting in an obtuse angle between the long axes of these two bones (see Sidlauskas *et al.*, 2007: fig. 8 for conditions in *S. isognathus* and *S. scotorhabdotus*). The restructuring of the dentary in these three taxa also results in a sigmoidal ventral margin of the lower jaw unique to these three species of *Schizodon* in the family.

Among the examined outgroups, only *Distichodus* sp. has an obtuse angle formed by the long axes of the

dentary and anguloarticular. The overall form of the lower jaw is extremely different between *Distichodus* and the Anostomidae (see Vari, 1979: fig. 3B) and given the considerable phylogenetic separation of these families the condition is clearly homoplastic. Nevertheless, *Distichodus* sp. is coded as state 1 in accordance with the above state definitions. The remaining outgroups all possess state 0 for this character.

Due to the polytomy within clade 18 (*Schizodon*), state 1 (obtuse angle between dentary and anguloarticular) optimizes as having evolved twice within the Anostomidae, once in *Schizodon knerii* and once in clade 19 (*Schizodon isognathus* and *S. nasutus*). If the polytomy in clade 18 were to resolve with *S. knerii* sister to clade 19, then state 1 would be inferred to have arisen only once within the Anostomidae.

60. *Form of dentary replacement tooth trench or crypt*: (0) small to moderate-sized and closed ventrally; (1) large and with distinct ventral fenestra; (2) extremely large and with posteromedial fenestra (CI = 0.667; RI = 0.750).

Most characiforms, including basal taxa such as *Xenocharax* (Daget, 1960: fig. 4), typically have a variably sized trench or in some instances an osseous crypt within the dentary. The trench or crypt serves as the area of development for the replacement teeth for the functional tooth row that attaches along the dorsal margin of the lower jaw. In various characiforms distributed across the phylogeny of the order, the anterior wall of the trench serves as the area of attachment on the jaw for the pleurodont functional teeth (e.g. *Leporinus obtusidens*, Trapani, 2001: fig. 6). Dentary replacement tooth trenches are absent in some groups of small to moderate body sizes that are either edentulous (e.g. Curimatidae) or have very small teeth not attached to the jaw (e.g. Chilodontidae). Such trenches are also lacking in some species of small overall body size such as *Lepidarchus* (Roberts, 1966: 213) and *Clupeocharax* (Zanata & Vari, 2005: 47) that, nonetheless, retain relatively well-developed teeth.

When present, the trench or crypt in most characiforms is ventrally enclosed and of small to moderate size (state 0). The Anostomidae differs from that general characiform condition in possessing a large trench with a well-developed ventral aperture through the dentary (state 1, see also comments in Vari, 1983: 10). A similar ventral opening of the dentary tooth trench also occurs in *Distichodus* sp., and that species is also included in state 1. A large fenestra opening extending from the trench through the wall of the dentary also occurs in members of the Prochilodontidae. That aperture of the tooth trench in that family is, however, situated on the posteromedial



surface of the highly restructured dentary (Vari, 1983: 10, fig. 2; Castro & Vari, 2004: 32, figs 12, 13, 15) and as such is non-homologous with the ventrally positioned opening into the dentary of the Anostomidae and is coded as state 2. This character does not apply to members of the Curimatidae and Chilodontidae or to *Hemiodus ocellatus*, all of which lack dentary tooth trenches. Those taxa were coded as possessing missing data for this character. The presence or absence of the trench was coded as a separate out-group character 131 in Appendix 2.

Under the final hypothesis of relationships, state 0 is plesiomorphic. Strictly speaking, the optimization of character states 1 and 2 at the node uniting the Anostomidae, Curimatidae, Chilodontidae and Prochilodontidae is equivocal because the Curimatidae and Chilodontidae were coded as having missing data. Nevertheless, the ventral opening of the tooth trench (state 1) is hypothesized to be a synapomorphy for the members of the Anostomidae (clade 1), while state 2 is hypothesized as a synapomorphy for the Prochilodontidae.

61. *Presence or absence of sensory canal of dentary*: (0) sensory canal of dentary greatly reduced or absent; (1) sensory canal of dentary present (CI = 0.500; RI = 0.500).

In the typical characiform morphology, the sensory canal segment within the preopercle communicates anteriorly with the sensory canal of the anguloarticular. The canal of the anguloarticular, in turn, communicates anteriorly with the sensory canal segment in the dentary. The dentary canal segment continues forward to terminate near the anterior tip of the dentary (for condition in *Brycon*, see Weitzman, 1962: fig. 9). Most members of the Anostomidae also possess a sensory canal segment of the dentary (state 0, Figs 33–36, 38, 39). Uniquely among the examined species of the Anostomidae, *Gnathodolus* and *Sartor* lack the portion of the sensory canal that runs through the dentary (state 1, Fig. 37). *Sartor elongatus* has a small pore on the lateral surface of the dentary in a position similar that of the pore present on one side of one specimen of *Gnathodolus*. The tiny canal associated with this pore in *Sartor* has an apparently dorsomedial orientation rather than being aligned towards the anguloarticular as is the case in other anostomids. It is uncertain whether this pore represents the remnant of the plesiomorphically present canal, a vast restructuring of that canal or a non-homologous feature. Even if homologous with the primitive laterosensory canal, the complete or nearly complete loss of the sensory canal in *Sartor* and *Gnathodolus* is different from the condition shared by all other members of the Anostomidae. Although the examined specimen of *Distichodus* sp. in the out-

groups also lacks a sensory canal of the dentary (although such a canal is present in adult congeners; Daget, 1959: fig. 6), the loss of the canal optimizes as an unambiguous synapomorphy for clade 32 within the Anostomidae.

62. *Length of sensory canal of dentary*: (0) dentary with elongate laterosensory canal segment extending from contact of dentary with ventral portion of anguloarticular to point close to symphysis of dentary; (1) dentary with short laterosensory canal segment, terminating at, or posterior to, approximate longitudinal midpoint of bone (CI = 0.500; RI = 0.900).

Most members of the Characiformes, including all examined species in the Chilodontidae, Curimatidae, Prochilodontidae and Anostomidae except *Gnathodolus* and *Sartor* (see character 61), have a dentary with an elongate laterosensory canal segment that connects posteriorly to the canal within the preopercle via a canal segment running through the ventral portion of the anguloarticular. The position of the anterior limit of the canal varies within these four families, with a relatively elongate canal that extends to within a short distance of the symphysis of the dentary being present in the Curimatidae (Vari, 1989a: fig. 39) and Chilodontidae (both state 0). The canal is shorter in all genera of the Prochilodontidae (state 1) in which the lower jaw is modified as a consequence of the massive expansion of the replacement tooth trench of the dentary that accommodates the increased number of replacement tooth rows (see Castro & Vari, 2004: figs 12, 13).

In all examined species in the Anostomidae, the canal segment within the dentary is truncated to some degree, with at least the portion of the canal anterior of the approximate midpoint of the dentary being absent (Figs 33–39). The canal is further reduced in *Gnathodolus* and *Sartor*, which completely lack a laterosensory canal segment within the dentary or have it dramatically reduced and altered (see character 61). The truncation of the sensory canal of the dentary appears to be a synapomorphy for the entire Anostomidae (clade 1), which was not reported by Vari (1983), and which arose independently in the Prochilodontidae based on available evidence as to the phylogenetic relationships of the Prochilodontidae and Anostomidae (Vari, 1983, 1989a; Castro & Vari, 2004).

63. *Presence or absence of pore on midlength of sensory canal segment of dentary*: (0) sensory canal segment of dentary without pore situated along midlength of canal segment in posterior half of dentary; (1) sensory canal segment of dentary with pore positioned along midlength of canal segment between posterior opening of canal proximate to

anguloarticular and anterior limit of canal and occurring in posterior half of length of dentary (CI = 0.500; RI = 0.889).

Within the Anostomidae, the truncated sensory canal situated in the posterior half of the dentary is typically a simple tube lacking a pore positioned in the middle of its length. This unpored condition is found in *Abramites*, *Anostomoides*, *Anostomus*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptolaemus*, and juveniles and adults of all species of *Leporinus* with the exception of adults of *L. cf. ecuadorensis*. In *Rhytiodus*, *Schizodon fasciatus* (Fig. 38), *S. isognathus* (Sidlauskas *et al.*, 2007: fig. 8A), *S. knerii*, *S. scotorhabdotus* (Sidlauskas *et al.*, 2007: fig. 8B), *S. vittatus* and the largest examined specimens of *Leporinus cf. ecuadorensis* and *Schizodon nasutus* (Fig. 39), a pore occurs along the midlength of the shortened sensory canal of the dentary that is typical of all members of the Anostomidae with the exception of *Gnathodolus* and *Sartor*, both of which completely lack the canal (see character 61). This pore is typically positioned midway along the dentary canal segment (Fig. 38), but in *Schizodon knerii*, *S. isognathus* and the largest examined specimen of *S. nasutus* (Fig. 39) the pore is more anteriorly positioned, being almost merged with the distal pore at the anterior limit of the canal with only a small lamina of bone separating the midlength pore from the distal pore. In the smaller cleared and stained specimen of *Schizodon nasutus* the large anterior opening of the canal encompasses the space occupied by both the anterior and midlength pores in *S. knerii*, *S. isognathus* and the larger specimen of *S. nasutus*. The apparent lack of a pore along the midlength of the sensory canal segment in the dentary of the smaller specimen of *S. nasutus* is probably comparable with the morphology of the canal segment in the remaining species of *Schizodon* (i.e. an enlarged pore homologous with both the distal and the medial pores of other *Schizodon* species) rather than with the more common morphology of the lack of a midlength pore observed throughout the rest of the family. *Schizodon nasutus* is consequently coded as possessing state 1 (medial pore present). The sensory canal segment in the dentary is completely absent in *Gnathodolus* and *Sartor* and those genera could not be coded for this character.

In both the proximate and the distant outgroups to the Anostomidae, the sensory canal of the dentary includes at least one pore between the anterior and posterior extremes of the canal, with some species (e.g. members of *Potamorhina*, Curimatidae) possessing multiple pores along this canal segment. The position of the pore along the middle of the sensory canal in the Chilodontidae, the closest outgroup to the Anostomidae, is approximately equivalent in its position on the overall dentary to the pore at the anterior

termination of the sensory canal in most members of the Anostomidae (Vari *et al.*, 1995: figs 2, 3). That positional fact and the nested location of the clade containing *Rhytiodus* and *Schizodon* (clade 15) within the Anostomidae in the final hypothesis of relationships independently make it clear that the pores along the midlength of the canal segment of the dentary in *Rhytiodus* and *Schizodon* are non-homologous with the pores present along the midlength of the canal segment of the dentaries in the outgroups. Rather, the positional information indicates that the distal anterior portion of the sensory canal of the dentary and associated anterior pore on the canal were lost in the common ancestor of the Anostomidae (see character 62) with the evolution of a new pore located in a more posterior position in the ancestor of *Rhytiodus* and *Schizodon* (clade 15). The midlength pore also appears to have been acquired independently by *Leporinus cf. ecuadorensis*.

64. *Form of retroarticular*: (0) retroarticular small, compact and cup-shaped, with its length in lateral view only slightly longer than its height and with interopercular–mandibular ligament attaching in cup-shaped depression at midlength of bone; (1) retroarticular elongate and cup-shaped, with its length in lateral view more than three times its height, with interopercular–mandibular ligament attaching in cup-shaped depression near anterior margin of bone; (2) retroarticular elongate and rod-shaped, with interopercular–mandibular ligament attaching at posterior margin of bone (CI = 0.667; RI = 0.889).

The typical morphology of the retroarticular in the Anostomidae is a small cup-shaped bone that serves as the attachment point for the interopercular–mandibular ligament and sits in a small cavity formed by the anguloarticular and dentary at the posteroventral margin of the lower jaw (state 0, Figs 34–39). In this condition, the retroarticular is very slightly longer along its anteroposterior axis than it is along its vertical extent. In the two examined species of *Leporellus*, the retroarticular is still cup-shaped but is also elongated along the anteroposterior axis and fits into a correspondingly elongate depression on the posterolateral portion of the dentary (state 1, Fig. 33). In *Leporellus* the attachment of the interopercular–mandibular ligament is near the anterior margin of the bone.

Among the outgroups, the Chilodontidae and the Prochilodontidae also possess small, cup-shaped retroarticulars (state 0, Vari, 1983: fig. 2A, C). The Curimatidae (Vari, 1983: fig. 2D), Citharinidae (Daget, 1962a: fig. 10), and Distichodontidae as well as *Hemiodus*, *Parodon* and *Brycon* (Weitzman, 1962: fig. 8) have a third morphology of the retroarticular in which the bone is approximately as elongate as in

*Leporellus*, but is rod-shaped rather than cup-shaped as in *Leporellus* and with the interopercular–mandibular ligament attaching at the posterior margin instead of in a distinct depression (state 2).

Under the final hypothesis of relationships, the plesiomorphic condition is state 2, with state 0 (cup-shaped retroarticular) ambiguously optimized as a synapomorphy either for the clade containing the Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae (with reversal in the Curimatidae) or for the clade containing the Anostomidae and Chilodontidae (with an additional gain in the Prochilodontidae). The elongate form of the retroarticular in combination with the anterior attachment of the interopercular–mandibular ligament in *Leporellus* (state 1) is a synapomorphy for that genus (clade 2) under this reconstruction.

65. *Relative position of retroarticular and dentary*: (0) retroarticular laterally situated in lower jaw and deeply recessed into pocket formed primarily by dentary and to lesser degree by anguloarticular; line drawn along ventral margin of retroarticular clearly bisects ventral portion of dentary; (1) retroarticular ventrally situated in lower jaw and forms part of ventral margin of lower jaw, line drawn along ventral margin of retroarticular barely, if at all, intersects ventral portion of dentary (CI = 0.333; RI = 0.909).

In all examined species of *Abramites*, *Hypomasticus*, *Leporellus* and *Leporinus* the retroarticular is recessed deeply into a lateral pocket situated in the posteroventral portion of the lower jaw (Figs 33–35). This pocket is formed primarily by the dentary and to a lesser degree by the anguloarticular. That condition differs from the placement of the retroarticular in *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon* and *Synaptolaemus*, in which the retroarticular forms part of the ventral margin of the lower jaw and rests in a much smaller pocket that is margined laterally approximately equally by the dentary and anguloarticular (Figs 36–39). *Anostomoides* and the species of *Schizodon* possess what might be a transitional morphology between these two conditions. In *Anostomoides* and *Schizodon* the retroarticular is ventrally positioned, but the dentary contributes more to the margin of the pocket that accommodates the retroarticular than does the anguloarticular. The line drawn along the ventral margin of the retroarticular in these two genera, furthermore, bisects a tiny portion of the ventral margin of the dentary (e.g. *Schizodon fasciatus*, Fig. 38). The condition in *Anostomoides* and *Schizodon* is much closer to the overall morphology of the pocket encompassing the retroarticular which is possessed by *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor* and *Synap-*

*tolaemus*, (state 1) than it is to the condition present in *Abramites*, *Hypomasticus*, *Leporellus* and *Leporinus* (state 0). *Anostomoides* and *Schizodon* are coded as state 1 for this character.

In the Chilodontidae (Vari, 1983: fig. 2A) and Curimatidae (Vari, 1983: fig. 2D, 1989a: fig. 89), the retroarticular forms part of the ventral margin of the lower jaw and species in these families are coded for state 1. Species in the Prochilodontidae have highly restructured lower jaws (Castro & Vari, 2004: figs 12, 13, 15) with a more laterally placed retroarticular that occupies a distinct pocket in the dentary. The members of the Prochilodontidae are coded as state 0. More distant outgroups (e.g. members of the Distichodontidae; Vari, 1979: fig. 3) also possess state 1.

The more laterally positioned retroarticular (state 0) optimizes as a synapomorphy for the Anostomidae (clade 1). The subsequent shift to a ventral placement of the retroarticular (state 1) is an unambiguously optimized and unreversed synapomorphy for *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon* and *Synaptolaemus* (clade 13).

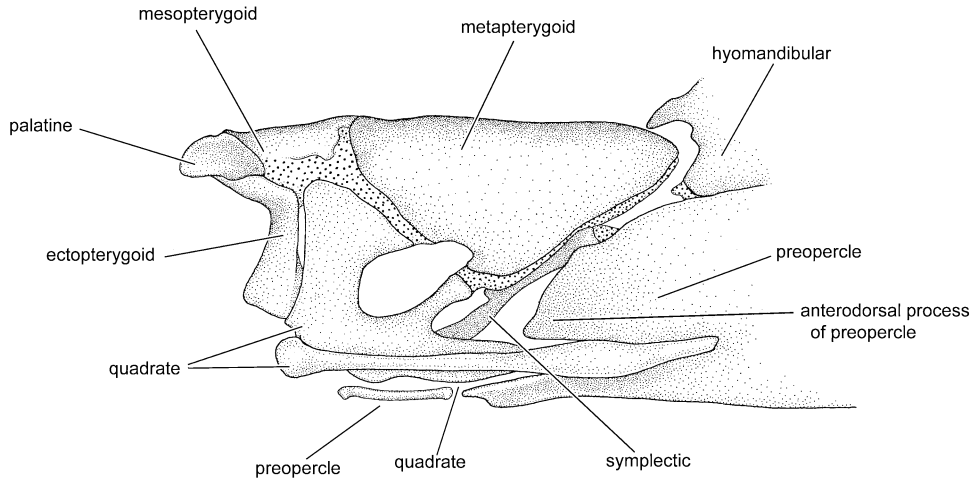
66. *Presence or absence of dermal papillae on lower lip*: (0) papillae absent; (1) papillae present (CI = 1.000; RI = 1.000).

Most species in the Anostomidae have either smooth lower lips or lips with varying degrees of ridging and buckling, with the irregularity perhaps a consequence of changes during fixation. As noted by Winterbottom (1980: 53), only *Gnathodolus*, *Sartor* and *Synaptolaemus* have the lip of the lower jaw covered with conical or hemi-cylindrical dermal papillae (see Myers & Carvalho, 1959: fig. 3). Such papillae are absent in all examined outgroups, and their presence is a clear synapomorphy for clade 31.

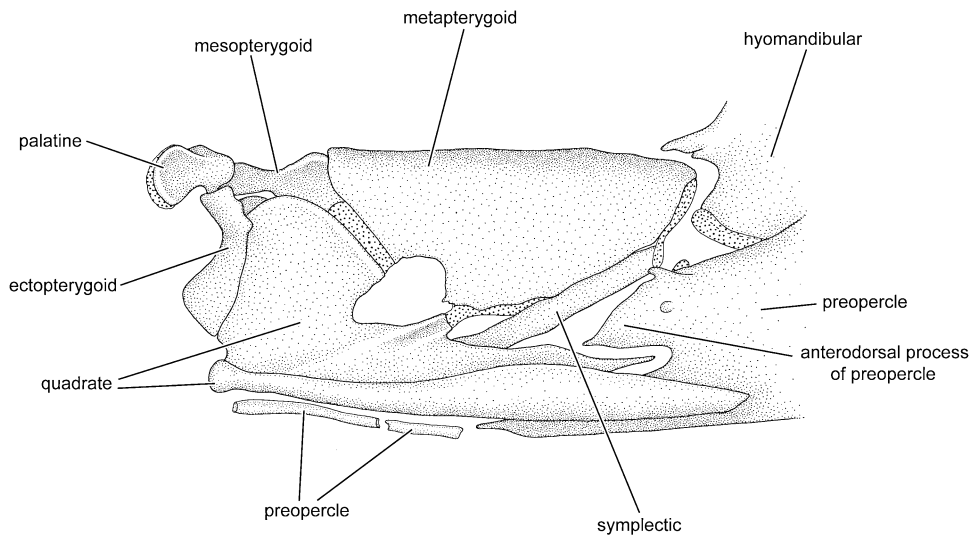
#### PALATINE ARCH

67. *Presence or absence of distinct process of palatine*: (0) palatine without distinct process extending away from main, rounded portion of bone cradled by dorsal portion of ectopterygoid; (1) palatine with distinct plate- or finger-like process extending away from main, rounded portion of bone cradled by dorsal portion of ectopterygoid (CI = 1.000; RI = 1.000).

Within the Anostomidae, members of *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytiodus* and *Schizodon* possess a distinct process extending anteriorly, anteroventrally or laterally from the main body of the palatine which is cradled by the dorsal portion of the ectopterygoid (state 1, Figs 34, 40, 41). Such a process of the palatine is absent in *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*, with



**Figure 40.** Anterior portion of left suspensorium, *Leporellus pictus*, USNM 302487, 115 mm SL; lateral view.



**Figure 41.** Anterior portion of left suspensorium, *Leporinus fasciatus*, USNM 225991, 87.8 mm SL; lateral view.

the palatine in these taxa having the form of a small block or plate (*Anostomus*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptolaemus*) or being restructured into a thin hourglass-shaped bone (*Gnathodolus*, see character 70) that lacks any distinct processes (state 0, see Fig. 37 for condition in *Sartor elongatus*).

Palatine shape varies widely across the outgroups, and the shallow bowl-like palatines possessed by the proximate outgroups in the Chilodontidae and Curimatidae (e.g. *Steindachnerina argentea*, Vari, 1989a: fig. 40B) and the small plate-like palatine possessed by members of the Prochilodontidae (e.g. Castro & Vari, 2004: fig. 19) are so different from the condition in the Anostomidae that we refrained from homologizing these morphologies *a priori*. Consequently, we

did not code the outgroups for this character or for characters 68 and 69.

Under the final hypothesis of relationships arrived at herein, the loss of the process of the palatine represents an unambiguous synapomorphy for the species of *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25).

68. *Orientation of process of palatine*: (0) process of palatine anteriorly directed without noticeable lateral or ventral orientation; (1) process of palatine with distinct lateral, anterolateral or anteroventral orientation (CI = 1.000; RI = 1.000).

Most species in the Anostomidae possess a palatine with a distinct process that connects to various car-



tilages and soft tissues proximate to the maxilla and mesethmoid (character 67). The morphology of that lateral process varies considerably across the Anostomidae. In many species in the family (*Anostomoides*, *Laemolyta*, *Leporinus agassizi*, *L. cf. niceforoi*, *L. cf. ecuadorensis*, *L. fasciatus*, *L. cf. fasciatus*, *L. friderici*, *L. gomesi*, *L. ortomaculatus*, *L. pellegrinii*, *L. striatus*, *Rhytiodus* and *Schizodon*) this process of the palatine has a primarily lateral orientation (e.g. *Leporinus fasciatus*, Fig. 41), while in others (*Abramites*, *Hypomasticus*, *Leporinus jatuncochi* and *L. tigrinus*), the process of the palatine is directed anterolaterally, anteroventrally or anteroventrolaterally with only slight deviation of the body of the process from the parasagittal plane (e.g. *Hypomasticus mormyrops*, Fig. 34). The species of *Hypomasticus* as well as *Leporinus jatuncochi* have the process notably ventrally slanted (Fig. 34). Unfortunately all the variation in *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporinus*, *Rhytiodus* and *Schizodon* forms a continuum, and it proved impossible to parse the range of morphologies among these genera into discrete character states. All these taxa are coded as state 1.

The two examined species of *Leporellus* have a process of the palatine that is aligned fully anteriorly without deviation from the parasagittal plane (Fig. 40). This is a unique condition within the Anostomidae and is coded as state 0. The species of *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* lack any indication of a process of the palatine and have overall morphologies of that bone that are highly modified relative to the form of the ossification in other anostomids and characiforms. Those five genera cannot be coded for this character.

Proximate outgroups to the Anostomidae all have significant modifications of the form of the palatine relative to the condition present in many groups within the Characiformes, a situation that complicates comparisons between the palatine morphologies present in the Anostomidae and the outgroup species. The most common morphology of the palatine among the outgroup species is an anteriorly and anterolaterally directed plate or spoon-shaped bone that underlies a well-developed cartilage. None of the species in the Anostomidae possesses a palatine morphology similar to that condition and none of the outgroups was formally coded for this character. The anterior and anterolateral orientation of the palatines in the Chilodontidae and Curimatidae (Vari, 1989a: fig. 40) does, however, evoke the primarily anteriorly directed process of the palatine that occurs in *Leporellus* (Fig. 40), *Abramites* and some species of *Leporinus*.

Because we could not code the outgroups for this character and because *Leporellus* appears as the most basal anostomoid, the state reconstruction for this character at the base of the anostomid phylogeny is

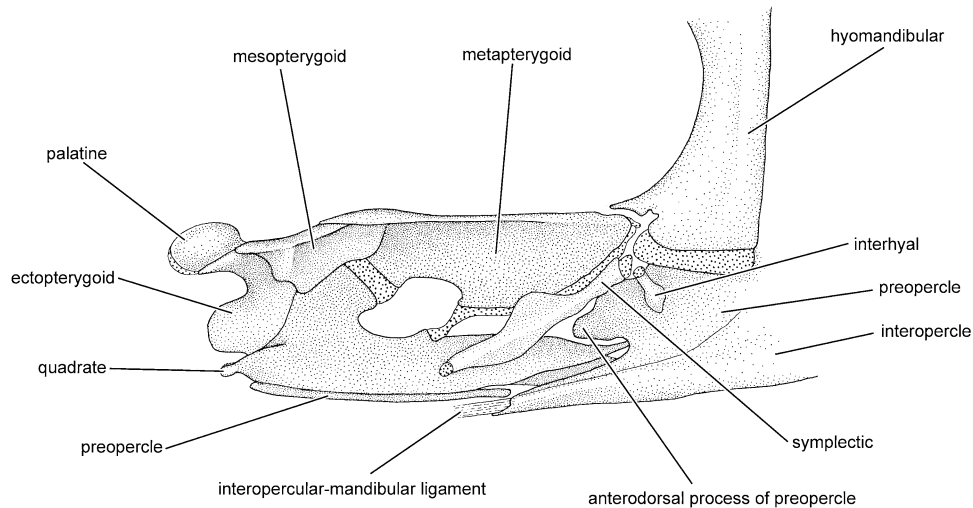
ambiguous. A palatine with a directly anteriorly orientated process may be a synapomorphy for the two examined species of *Leporellus* (clade 2). Alternatively, the angled palatine characteristic of the remainder of the Anostomidae may be a synapomorphy for clade 3. It is equally possible that either of these conditions represents the primitive condition for the Anostomidae, or that both are derived relative to the very distinctive morphologies possessed by the outgroups.

Nevertheless, there is a trend in increasingly more derived members of the Anostomidae for the process of the palatine to shift from having a slight anterolateral orientation (e.g. *Hypomasticus mormyrops*, Fig. 34) through a distinctly anterolateral orientation (e.g. *Leporinus fasciatus*, Fig. 41) to an almost fully lateral orientation in *Schizodon*, *Laemolyta* and *Rhytiodus*. In that light, the fully anterior orientation of the palatine in *Leporellus* (Fig. 40) could also be seen as the starting point of a trend towards increasing lateralization of the process in the Anostomidae prior to the loss of the process in the modified palatine characteristic of the species in clade 25.

69. *Length of process of palatine*: (0) process of palatine moderately to weakly developed, length of process about 1.5 times width or less; (1) process of palatine very long, length of process approximately two or more times width of process (CI = 1.000; RI = 1.000).

The length of the process of the palatine varies considerably within the Anostomidae, being short in *Leporellus* (Fig. 40), moderate in *Abramites*, many species of *Leporinus* (e.g. *L. fasciatus*, Fig. 41), *Hypomasticus* (e.g. *H. mormyrops*, Fig. 34) and *Laemolyta*, and slightly longer (length approximately 1.5 times width) in *Leporinus cf. ecuadorensis*, *L. friderici*, *Anostomoides*, *Rhytiodus*, *Schizodon isognathus*, *S. knerii*, *S. nasutus* and *S. scotorhabdotus*. Variation is continuous across all of the above conditions, which are all coded consequently as state 0. In *Schizodon fasciatus* and *S. vittatus* the length of the process reaches its extreme within the Anostomidae, with the length of the process approximately twice its width (state 1). Palatine morphologies vary considerably in the outgroups (see discussion in characters 68 and 69) and the outgroups were not formally coded for this character. Nevertheless, no examined outgroup species possess a palatine with a long laterally directed process comparable with that present in *S. fasciatus* and *S. vittatus*. The extreme elongation of the process is a synapomorphy for these two species under the final hypothesis of relationships (clade 20).

70. *Shape of palatine*: (0) main portion of palatine in form of block or plate; (1) palatine in shape of dorsoventrally elongate hourglass, with triangular dorsal



**Figure 42.** Anterior portion of left suspensorium, *Schizodon nasutus*, USNM 326944, 111 mm SL; medial view, drawing reversed to place anterior at left.

and ventral portions connected by thin thread of bone (autapomorphy).

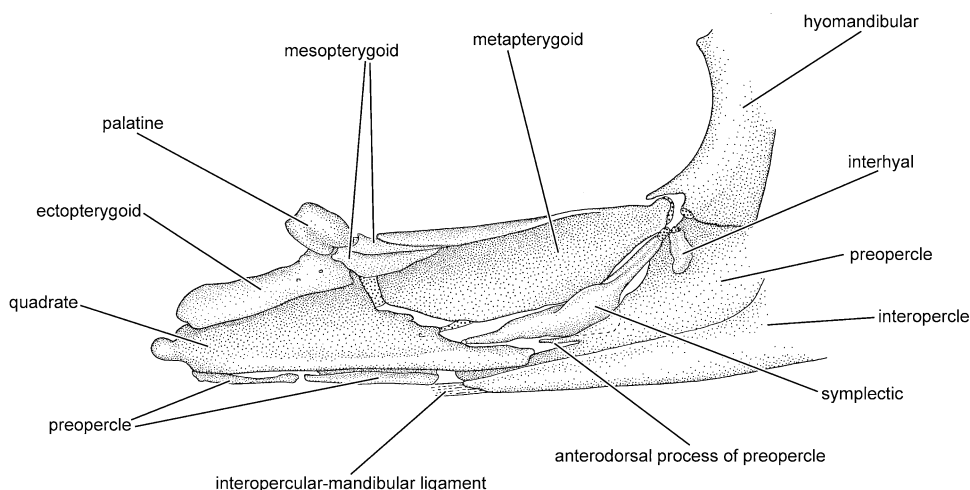
*Gnathodolus* has a strikingly modified palatine that in lateral view is divided into upper and lower triangular lobes connected by a narrow thread of bone (see Winterbottom, 1980: fig. 41). The form of the palatine in *Gnathodolus* is an autapomorphic modification not encountered elsewhere in the outgroup comparisons, and is among the most distinctive modifications of the suspensorium within the Characiformes. *Sartor elongatus*, a member of the sister-clade to *Gnathodolus*, has a dorsoventrally elongate palatine that might represent a precursor to the modification found in *Gnathodolus* (Fig. 37). *Sartor*, however, shares neither the bilobed palatine morphology of the palatine nor the thin connecting thread of bone between those lobes found in *Gnathodolus*. Although the form of palatine is autapomorphic for the presently monophyletic *Gnathodolus*, it has been suggested that at least one additional species occurs in that genus (Winterbottom, 1980: 21). This character is included as a potential synapomorphy for such a more complex *Gnathodolus*.

71: *Morphology of anterodorsal process of ectopterygoid*: (0) with distinct anterodorsal process of ectopterygoid running ventral to palatine; (1) with very small anterodorsal process of ectopterygoid running ventral to palatine or process absent; (2) portion of ectopterygoid running under palatine extensive but extent of process unclear due to lack of bend between this portion of bone and portion contacting quadrate (CI = 1.000; RI = 1.000).

The species of *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytidodus*,

*Pseudanos* and *Schizodon* have a dorsal portion of the ectopterygoid with an anteriorly directed process that runs ventral to, and cradles, the palatine (state 0, Figs 34, 40–42). *Pseudanos gracilis*, *P. irinae*, *P. trimaculatus* and especially *P. winterbottomi* have an anterodorsal process of the ectopterygoid that is relatively smaller than that occurring in the taxa cited above, although still obvious. *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus* have the process either represented by a tiny nubbin of bone smaller than the process in the species of *Pseudanos*, or absent entirely (state 1, Figs 37, 43). For the condition in *Pseudanos trimaculatus* and *P. gracilis*, see Winterbottom (1980: figs 33–35).

The members of the Chilodontidae have a pronounced anterodorsal process of the ectopterygoid larger than any present within the Anostomidae. In the Curimatidae and Prochilodontidae (Vari, 1983: fig. 27; Castro & Vari, 2004: fig. 19), the very elongate ectopterygoid clearly underlies the palatine and is nearly straight, with only a slight bend at the approximate position where the anterodorsal process of the ectopterygoid joins the main body of the ectopterygoid in the Chilodontidae. It is possible that the anterodorsal process of the ectopterygoid in the Chilodontidae and Anostomidae was formed by an expansion of the plesiomorphically shallowly bent ectopterygoid found in the Curimatidae and Prochilodontidae, but this homology is uncertain. More distant outgroups [e.g. *Brycon* (Weitzman, 1962: fig. 10)] have essentially straight ectopterygoids. In recognition of this fundamentally different morphology, the Prochilodontidae, Curimatidae and more distant outgroups are coded as state 2, which does not occur within the Anostomidae.



**Figure 43.** Anterior portion of left suspensorium, *Petulanos plicatus*, USNM 225396, 95.3 mm SL; medial view, drawing reversed to place anterior at left.

The acquisition of the anterodorsal process of the ectopterygoid (state 1) is a previously undocumented synapomorphy for the clade formed by the Anostomidae and Chilodontidae, with the pronounced reduction or loss of the anterodorsal process of the ectopterygoid a synapomorphy for *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus* (clade 27).

72. *Alignment of ectopterygoid*: (0) ectopterygoid anterodorsally inclined, with vertical through anterodorsal limit of ectopterygoid passing anterior to anterior limit of ventral portion of ectopterygoid; (1) ectopterygoid vertically orientated with vertical through anterodorsal limit of ectopterygoid passing through ventral portion of ectopterygoid; (2) ectopterygoid posterodorsally inclined with vertical through anterodorsal limit of ectopterygoid passing distinctly posterior of ventral portion of ectopterygoid (CI = 0.500; RI = 0.938).

In *Leporellus* (Fig. 40), *Leporinus* cf. *niceforoi*, *Hypomasticus* (Fig. 34), *Schizodon isognathus* and *Schizodon nasutus* (Fig. 42) within the Anostomidae, the anterodorsal limit of the ectopterygoid is positioned anterior to the vertical through the anterior margin of the ventral portion of the ossification (state 0). In most of these species, the dorsal portion of the ectopterygoid is located distinctly anterior of the ventral portion of the ectopterygoid, although in *Leporinus* cf. *niceforoi* the dorsal portion of the ectopterygoid is located only very slightly anterior of the vertical through the anterior limit of the ventral portion of that bone. The remaining species in the Anostomidae have the ventral portion of the ectopterygoid more anteriorly positioned relative to the dorsal process of that ossification. In *Abramites*, *Anos-*

*tomoides*, *Laemolyta*, *Rhytiodus* and the species of *Leporinus* and *Schizodon* not listed above (Fig. 41) the ectopterygoid has an approximately vertical alignment, with the vertical through the anterior portion of the dorsal process of the ectopterygoid touching the anterior margin of the ventral portion of the ectopterygoid or passing through the ventral portion of the ectopterygoid (state 1). A final condition of this character (state 2) is found in *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*. In these six genera the ventral portion of the ectopterygoid is positioned far anterior of the originally dorsal portion of the ectopterygoid, with the primary axis of the ossification lying nearly parallel to the longitudinal axis of the fish (Figs 37, 43).

All examined members of the outgroups have a distinctly anterodorsal inclination of the ectopterygoid [state 0; e.g. Distichodontidae (Daget, 1960: fig. 10); Characidae (Weitzman, 1962: fig. 10)]. In the final hypothesis of relationships arrived at in this study the vertical orientation of the ectopterygoid (state 1) is a synapomorphy for a clade containing all members of the Anostomidae except *Leporellus* and *Hypomasticus* (clade 7), with a reversal to state 0 in clade 19 (*Schizodon nasutus* and *S. isognathus*) and *Leporinus* cf. *niceforoi*. The posterodorsally aligned morphology of the ectopterygoid (state 2) is an unambiguous synapomorphy for *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Synaptolaemus* and *Sartor* (clade 25).

73. *Presence or absence of distinct process on posterolateral surface of the ectopterygoid*: (0) absent; (1) present (CI = 0.500; RI = 0.929).

All examined anostomids with the exception of *Gnathodolus* have a thick, cord-like ligament that

connects the posterodorsal portion of the ectopterygoid to the lateral ethmoid (see character 23). The attachment area of this ligament onto the ectopterygoid has the form of a distinct process on the posterolateral surface of that ossification (Vari, 1983: fig. 26). This elaboration of the ectopterygoid has not been encountered in examined outgroups. Both the ligament and the process on the ectopterygoid are lacking in *Gnathodolus*, with these losses apparently correlated with the dramatic alternations of a number of components of the suspensorium in that genus (see characters 20, 57, 70). Winterbottom (1980: 50) indicated that a dorsal process of the ectopterygoid is present in species of *Anostomus* (including *Petulanos*) and *Pseudanos* but absent in *Gnathodolus*, *Sartor* and *Synaptolaemus*. Assuming that Winterbottom's dorsal process corresponds to the structure described by Vari (1983), we differ from Winterbottom's interpretation of the character, as our examined specimens of *Sartor* and *Synaptolaemus* possess the process in question (Fig. 37). In the final hypothesis of relationships, possession of this process on the ectopterygoid is a synapomorphy for the entire Anostomidae (clade 1) that is reversed in *Gnathodolus*.

74. *Posteriorly directed dorsolateral process of mesopterygoid*: (0) absent; (1) present (CI = 0.333; RI = 0.500).

The examined species of *Anostomus*, *Petulanos* and *Sartor* possess a posteriorly directed process on the lateral surface of the mesopterygoid that is absent in all other examined species of the Anostomidae (Fig. 37). In the dissected cleared and stained specimens of these genera, a small amount of connective tissue remains attached to the medial surface of this process of the mesopterygoid, suggesting that it may serve as an attachment point for a muscle or ligament. The species of *Anostomus* have the process of the mesopterygoid situated medial to the well-developed ligament connecting the ectopterygoid to the lateral ethmoid in most members of the Anostomidae (character 23) and is difficult to see the process without extensive dissection. In *Sartor* the process is similarly positioned but more highly developed, forming a lateral ridge that abuts the lateral surface of the dorsally elongate palatine (Fig. 37). No trace of the process of the mesopterygoid is present in *Gnathodolus* or *Synaptolaemus*. The mesopterygoid of *Gnathodolus* is modified and elongated dorsoventrally relative to the typical anostomoid condition (Winterbottom, 1980: fig. 41), and it is possible that the dorsolateral process in *Gnathodolus* has become incorporated into the rest of the mesopterygoid as it expanded dorsally. Alternatively, it may have been lost.

Species of *Pseudanos* have a small bump on the mesopterygoid in the same position as the posteriorly

directed process which is present in that region in *Anostomus*, *Petulanos* and *Sartor*. While *Pseudanos* is coded as state 0 (process absent) in light of its lack of a distinct process, this bump on the mesopterygoid of *Pseudanos* may, nonetheless, represent a rudimentary form of the more highly developed process which occurs in *Anostomus*, *Petulanos* and *Sartor*. If that homology is correct, this character would be applicable at a higher level of inclusiveness. No other examined species, including all outgroups, possesses a dorsolateral process of the mesopterygoid.

Optimization of this character on the final phylogeny is ambiguous. Either the mesopterygoid process in question evolved once in clade 27 and was lost independently in *Synaptolaemus* and *Gnathodolus*, or it evolved three times in total, once each in *Anostomus* (clade 28), *Petulanos* (clade 30) and *Sartor*.

75. *Association of quadrate with mesopterygoid*: (0) mesopterygoid with well-developed ventral triangular process that significantly overlaps ossified portion of medial surface of quadrate; (1) mesopterygoid lacking ventral process overlapping quadrate or process, if present, much smaller than in state 0 and not significantly overlapping ossified portion of medial surface of quadrate (CI = 0.250; RI = 0.857).

In *Abramites*, *Hypomasticus*, *Leporellus*, *Leporinus*, *Rhytidodus* and *Schizodon* the mesopterygoid has a triangular, ventral process that overlaps the medial surface of the quadrate (e.g. *Schizodon nasutus*, Fig. 42). *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* either lack this triangular process or have it much smaller in size relative to the condition present in the above cited species (e.g. *Petulanos plicatus*, Fig. 43). A lack of contact of the ventral margin of the mesopterygoid with the quadrate characterizes *Anostomoides*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*, with all these taxa coded as state 1. In *Anostomus ternetzi* the ventral margin of the mesopterygoid barely contacts the ossified dorsal margin of the quadrate. *Synaptolaemus*, *Laemolyta* and *Anostomus anostomus* have the small ventral flange of the mesopterygoid approaching or contacting the cartilaginous dorsal portion of the quadrate. *Synaptolaemus*, *Laemolyta*, *Anostomus anostomus* and *A. ternetzi* are all coded as possessing state 1 (ventral flange of mesopterygoid small or absent).

Species in the Chilodontidae (the immediate outgroup of the Anostomidae) possess a large ventral flange of the mesopterygoid that overlaps the quadrate in a mode similar to that in *Leporinus* and the other taxa possessing a ventral flange of the mesopterygoid (see Vari *et al.*, 1995: fig. 4 for illustration of the condition in the Chilodontidae). Among the components of the second outgroup to the Anostomidae,



an overlap of the quadrate by the mesopterygoid is absent in the Prochilodontidae (Vari, 1983: fig. 28). Members of the Curimatidae appear to lack such an overlap of these two elements, although the situation in that family is frequently difficult to evaluate due to the expansion of the various cartilages located throughout the region of the palatine and adjoining structures (e.g. *Potamorhina latior*, Vari, 1983: fig. 27). Among more distant outgroups, the overlap of the mesopterygoid and quadrate is clearly present in *Brycon* (Weitzman, 1962: fig. 10), *Hemiodus ocellatus* and the distichodontids *Xenocharax spilurus*, *Distichodus* sp. and *Paradistichodus dimidiatus*. No overlap of these two elements is apparent in *Parodon suborbitalis*, and the condition in *Citharinus* sp. was difficult to evaluate due to the small size and poor staining of the specimen (coded as missing data).

Optimization of this character on the final phylogeny is ambiguous. The plesiomorphic condition within the Anostomidae optimizes as state 0 (overlap of quadrate by mesopterygoid). Either the overlap between the quadrate and mesopterygoid was lost in a common ancestor of *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytidodus*, *Sartor*, *Schizodon* and *Synaptolaemus* (clade 13) and re-evolved in the lineage leading to *Rhytidodus* and *Schizodon* (clade 15), or the loss occurred twice, once in *Anostomoides* and once in the lineage leading to *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 21).

76. *Form of association of posterodorsal and posterior processes of quadrate*: (0) processes separated with length of separate portion of posterodorsal process approximately twice width of process or greater; (1) processes entirely or almost entirely joined by thin intervening plate of bone with length of separate portion of posterodorsal process much less than twice width of process (CI = 0.250; RI = 0.667).

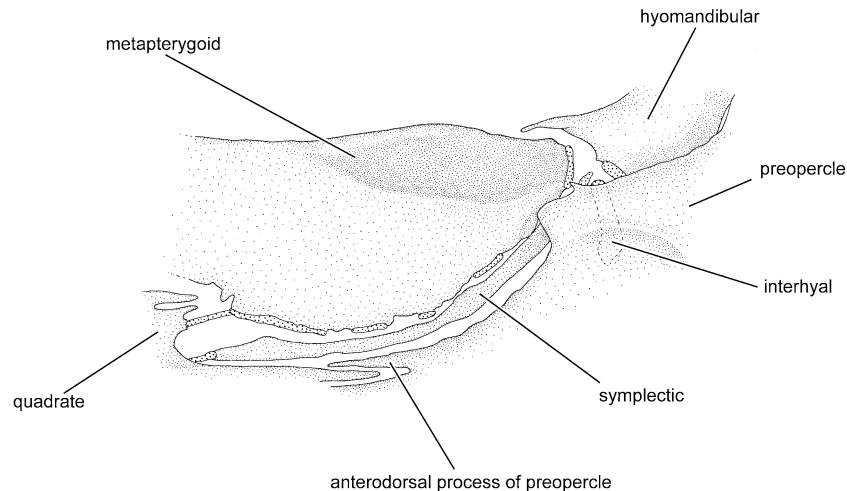
The posterior and dorsal regions of the quadrate of most groups in the Characiformes have three main processes: a dorsal process that articulates along its anterior margin with the ectopterygoid and dorsally with the mesopterygoid, a posterodorsal process that forms the ventral margin of the metapterygoid–quadrate fenestra, and a posterior process that extends ventral to the symplectic (for condition in *Brycon*, see Weitzman, 1962: fig. 10). In the examined proximate outgroups to the Anostomidae along with *Leporellus* in that family (Fig. 40), the posterodorsal process of the quadrate is separated posteriorly from the posterior process of the quadrate. There is an anteriorly directed indentation between the two processes and the length of the posterodorsal process is two or more times the width of the posterodorsal process. The indentation is less developed in the

species of the Anostomidae other than *Leporellus* in which all, or almost all, of the plesiomorphically open space between the posterodorsal and posterior processes of the quadrate is variably filled by a thin bony plate (see also Roberts, 1973). Most of the species with that condition have the space completely filled, with only the position of the cartilage joining the quadrate and metapterygoid and the position of the symplectic serving to delimit the position of the posterodorsal process of the quadrate (Figs 37, 42). A small notch in the bony plate is present in *Hypomasticus despaxi*, *H. megalepis*, *H. mormyrops*, *Leporinus agassizi*, *L. cf. ecuadorensis*, *L. friderici*, *L. pellegrinii*, *L. cf. moralesi*, *L. jatuncochi*, *L. fasciatus* (Fig. 41), *L. cf. fasciatus*, *L. gomesi*, *L. ortomaculatus*, *L. tigrinus*, *Petulanos plicatus* (Fig. 43) and *Synaptolaemus cingulatus* (Fig. 44). All anostomid species except *Leporellus* are coded as possessing state 1 for this character.

In the outgroups, the notch between the posterodorsal and posterior processes of the quadrate is clearly present (state 0) in *Brycon falcatus*, *Parodon suborbitalis*, *Xenocharax spilurus* and members of the Chilodontidae and Prochilodontidae (for the condition in Prochilodontidae see Vari, 1983: fig. 28). The notch is absent in *Citharinus* sp., *Distichodus* sp. and *Hemiodus ocellatus* (state 1). Our examined specimens of the Curimatidae have the notch present but very small (coded as state 1); however, some members of the Curimatidae have the notch well developed (e.g. *Potamorhina latior*, Vari, 1983: fig. 27). Under the final hypothesis of the relationships, the loss of a deep notch between the posterodorsal and posterior portions of the quadrate (state 1) is an unambiguous and unreversed synapomorphy for the Anostomidae exclusive of *Leporellus* (clade 3).

77. *Posterior extent of lateral shelf of quadrate*: (0) lateral shelf of quadrate elongate, extending posteriorly past posterior margin of symplectic to terminate ventral to hyomandibular; (1) lateral shelf of quadrate moderate in length, extending posteriorly past midpoint of the symplectic but not beyond posterior limit of symplectic; (2) lateral shelf of quadrate short, extending posteriorly to point short of midpoint of symplectic (CI = 0.333; RI = 0.789).

Species of the Anostomidae have a distinct, laterally positioned, teardrop-shaped shelf of the quadrate that serves as an area of attachment for the ventral portions of the adductor mandibulae muscles (Winterbottom, 1980: fig. 35; Vari, 1983: fig. 29). Such a process also appears in the Chilodontidae, Prochilodontidae and in *Distichodus* sp. (presence or absence coded as character 132, see Appendix 2). Members of the Anostomidae vary widely in the degree of development of this process of the quadrate. In *Abramites*,



**Figure 44.** Right metapterygoid, symplectic, quadrate, interhyal, preopercle and hyomandibular of *Synaptolaemus cingulatus*, FMNH 103455, 64.3 mm SL; lateral view, drawing reversed to place anterior at left.

*Anostomoides*, *Gnathodolus*, *Hypomasticus*, *Leporellus*, *Leporinus* and *Schizodon*, this lateral process of the quadrate is quite long, extending posteriorly well past the posterior limit of the symplectic to terminate under the hyomandibular (state 0, Figs 40, 41). In *Laemolyta* and *Rhytiodus* the shelf is shorter, reaching posteriorly past the vertical through the midpoint of the symplectic but falling short of the vertical through the posterior margin of that bone (state 1). In *Anostomus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*, in turn, the lateral shelf of the quadrate is distinctly shorter, terminating at, or anterior to, the vertical through the midpoint of the symplectic (state 2; see Winterbottom, 1980: figs 33, 35, 36).

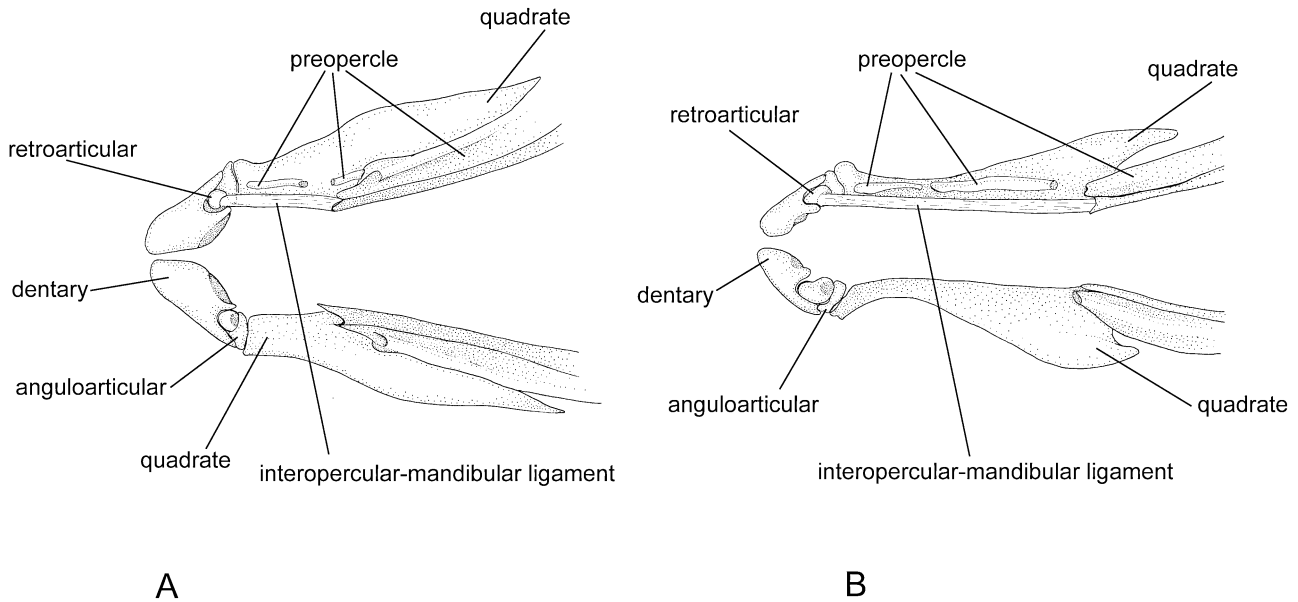
Among the outgroups that possess a lateral shelf of the quadrate, all three of these states are observed. Members of the Chilodontidae have an anteroposteriorly shorter form of the lateral shelf of the quadrate, but due to the more anterior position of the symplectic the flange reaches posteriorly past the midpoint of the symplectic. *Chilodus* and *Caenotropus* are coded consequently as having the intermediate condition (state 1). The flange in the Prochilodontidae is somewhat longer, with its tip reaching posteriorly barely past the vertical through the anterior limit of the hyomandibular (state 0; see Vari, 1983: fig. 28). The flange is very short in *Distichodus* sp. (state 2).

State 0 (flange elongate) optimizes as plesiomorphic within the Anostomidae. State 2 (short flange) is a synapomorphy for clade 25 that is reversed to state 0 in *Gnathodolus*. State 1 (moderate flange) is ambiguously optimized, either originating on the common ancestor of clade 14 with a reversal to state 0 in *Schizodon* (clade 18) or evolving independently in *Rhytiodus* and *Laemolyta*.

78. *Anterior extent of lateral shelf of quadrate*: (0) lateral shelf of quadrate complete anteriorly to articular condyle; (1) lateral shelf of quadrate terminates anteriorly prior to reaching articular condyle. (CI = 1.000; RI = 1.000)

Members of the Anostomidae vary in the anterior extent of the lateral shelf of the quadrate that serves as an attachment point for the ventral portions of the adductor mandibulae. In most species, the shelf is complete to the lateral surface of the articular condyle of the quadrate with the anguloarticular (state 0), although narrowing anteriorly in most taxa (e.g. *Leporinus* cf. *ecuadorensis*, Fig. 45A). In *Petulanos* (Fig. 45B), *Sartor* and *Synaptolaemus*, the lateral shelf terminates posterior of the condyle (state 1) and very far posterior of the condyle in *Gnathodolus* (also coded as state 1). In *Anostomus anostomus* and *A. ternetzi* the shelf narrows considerably as it approaches the condyle but is still apparent at the transverse through the condyle and is coded accordingly as state 0 (complete) in those two taxa. Our coding differs from Winterbottom's (1980: 50) use of the character, which he cited as a synapomorphy for all members of *Anostomus* (including *Petulanos*), *Gnathodolus*, *Sartor* and *Synaptolaemus*, excluding *Pseudanos*. In our estimation the development of the lateral shelf of the quadrate in *Anostomus* in the more restricted sense of this paper is not distinguishable from that in *Pseudanos*, and the character state distinctions are most obvious as coded above.

All of the outgroups that possess a lateral shelf of the quadrate (see outgroup character 132, Appendix 2) have the shelf complete to the articular condyle (state 0). In the final hypothesis of relationships,



**Figure 45.** Ventral view of lower jaw and anterior portions of suspensorium in (A) *Leporinus cf. ecuadorensis*, FMNH 102198, 96.7 mm SL; (B) *Petulanos plicatus*, USNM 225396, 75.8 mm SL.

state 1 optimizes as a synapomorphy for clade 29 containing *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*.

79. *Aspect ratio of metapterygoid–quadrate fenestra*: (0) metapterygoid–quadrate fenestra shorter along axis running parallel to quadrate–metapterygoid joint than along axis perpendicular to that joint; (1) metapterygoid–quadrate fenestra longer along axis running parallel to quadrate–metapterygoid joint than along axis perpendicular to that joint (CI = 0.500; RI = 0.857).

Most members of the Anostomidae have a metapterygoid–quadrate fenestra that is a wide opening formed by deep, U-shaped depressions in the posterodorsal portion of the quadrate and/or the anteroventral region of the metapterygoid. These depressions together form a usually ovoid fenestra with the longest axis of the fenestra aligned perpendicular to the joint between the quadrate and the metapterygoid [state 0, Figs 40–42, see also Sidlauskas & Santos (2005: fig. 5A) for condition in *Pseudanos gracilis*]. In a small number of species (*Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor*, *Synaptolaemus*, *Pseudanos winterbottomi* and one side of one specimen of *P. irinae*) the depressions in the margins of the quadrate and metapterygoid are proportionally less extensive, resulting in a relatively much smaller fenestra whose longest axis is orientated parallel to the quadrate–metapterygoid joint [state 1, Fig. 43, see also Sidlauskas & Santos (2005: fig. 5B) for condition in *P. winterbottomi*]. *Pseudanos*

*trimaculatus* and both sides of the other examined specimen of *P. irinae* retain a deep depression in the quadrate and at most a small matching depression in the margin of the metapterygoid (Winterbottom, 1980: fig. 34) or completely lack such a depression. The resulting fenestrae in *P. trimaculatus* and *P. irinae* nevertheless meet the criteria for state 0 and are coded accordingly.

The variation underlying this character was recognized by Winterbottom (1980), who cited the reduction or loss of the fenestra as a synapomorphy for *Anostomus* (including *Petulanos*), *Pseudanos*, *Gnathodolus*, *Synaptolaemus* and *Sartor*. We agree that the size of the fenestra is small in all those genera versus large in many other anostomids [e.g. *Schizodon* (Fig. 42), *Anostomoides*]. Other species not examined by Winterbottom (e.g. *Leporinus gomesi*) also have, however, small fenestrae, and the variation in the size of the fenestra across the family is continuous and impossible to break into discrete states. Redefining the character as a change in the aspect ratio of the opening allows the objective coding outlined above.

Variation in the form of the metapterygoid quadrate fenestra is extensive across the outgroups. For example, species of the Curimatidae have very large depressions in the margins of the quadrate and metapterygoid and correspondingly extensive metapterygoid–quadrate fenestrae (Vari, 1983: fig. 27, 1989a: fig. 41). In the Chilodontidae, the quadrate retains the indentation in the region occupied by the anteroventral portion of the fenestra in many charac-

forms [e.g. *Brycon meeki* (Weitzman, 1962: fig. 10)]. The metapterygoid in the Chilodontidae has a distinctive anterior process that largely (*Chilodus*) or completely (*Caenotropus*) fills the indentation in the posterior portion of the quadrate (Vari *et al.*, 1995: fig. 4). Members of the Prochilodontidae have increased mobility within the suspensorium (Vari, 1983) and an associated change in the overall form of the metapterygoid which now has a relatively straight margin in the area proximate to the quadrate (Roberts, 1973: fig. 11; Vari, 1983: fig. 28). It is impossible to determine whether the lack of the component of the fenestra formed by the metapterygoid in the Prochilodontidae represents the lack of the indentation or the loss of the processes of the metapterygoid that extend towards the quadrate in those characters with a fully developed fenestra. Because of the high degree of variability across the outgroups and the difficulty in homologizing those conditions with the morphologies observed within the Anostomidae, we elected to not code the outgroups for this character.

Optimization of this character on the final phylogeny is unclear because of the lack of complete resolution for the species of *Pseudanos*. Assuming the polytomy in clade 25 to be hard, either the shift in the aspect ratio of the metapterygoid–quadrate fenestra occurred independently in *Pseudanos winterbottomi* and clade 27, or the shift is a synapomorphy for clade 25 that was reversed in clade 27. If, instead, the polytomy is resolved with *Pseudanos* paraphyletic as suggested by the majority rule consensus (Fig. 6), then the shift in aspect ratio of the metapterygoid–quadrate fenestra is a synapomorphy for a clade containing *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos winterbottomi*, *Sartor* and *Synaptolaemus*.

80. *Length of cartilage body spanning ventral section of metapterygoid–quadrate fenestra*: (0) short and plug-like; metapterygoid and quadrate barely separated by cartilage; (1) long and rod-like; metapterygoid and quadrate clearly separated by thin bridge of cartilage (CI = 0.250; RI = 0.824).

Members of the Anostomidae demonstrate two distinct morphologies of the cartilage that bridges the gap along the ventral portion of the metapterygoid–quadrate fenestra between the ossified proximate portions of the quadrate and metapterygoid. In *Abramites*, *Hypomasticus*, *Leporellus*, *Leporinus agassizi*, *L. aripuanaensis*, *L. cf. ecuadorensis*, *L. fasciatus*, *L. friderici*, *L. gomesi*, *L. cf. moralesi*, *L. cf. niceforoi*, *L. ortomaculatus*, *L. striatus* and *Schizodon vittatus*, the cartilage that bridges the very short gap between the quadrate and metapterygoid has a plug-like morphology (Figs 40, 41). In *Anostomoides*, *Anostomus*, *Laemolyta*, *Leporinus cf. fasciatus*, *L.*

*jatuncochi*, *L. pellegrinii*, *L. tigrinus*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Synaptolaemus* and the species of *Schizodon* not cited above, the cartilage bridges a much wider gap and has a rod-like morphology (Figs 42, 43; see also Sidlauskas & Santos, 2005: fig. 5)

As discussed under character 79, the metapterygoid/quadrate region is significantly restructured in the outgroups relative to the Anostomidae, with an accompanying high level of variation in the apparent length of the cartilage of interest. Both *Chilodus* and *Caenotropus* in the Chilodontidae have a considerable gap between the ossified postero-dorsal process of the quadrate and the proximate portion of the metapterygoid, with this gap bridged by an elongate cartilage (see Vari *et al.*, 1995: fig. 4) The Prochilodontidae and Curimatidae, the second outgroup, alternatively have short cartilages that cap the process of the quadrate within the relatively small gap between the quadrate and the metapterygoid (see Vari, 1989a: fig. 41). There is a large gap between the quadrate and metapterygoid in *Brycon meeki* (Weitzman, 1962: fig. 10) with the space filled by an elongate cartilage. *Xenocharax*, the basal member of the Distichodontidae, similarly has an elongate cartilage in the region. Overall, the outgroup condition relative to the Anostomidae is ambiguous and we elected to leave all the outgroups uncoded for this character.

Based on the basal position under the final hypothesis of relationships of *Hypomasticus* and *Leporellus*, both of which have the plug-like morphology of the cartilage in question, it appears that state 0 is plesiomorphic within the Anostomidae and the rod-like morphology (state 1) is derived. Optimization of this character on the strict consensus tree suggests that state 1 evolved two or three times. Under ACCTRAN state 1 evolves once in clade 10 and once in clade 12, with a reversal in *Leporinus fasciatus*. Under DELTRAN state 1 evolves in *Leporinus cf. fasciatus*, and clades 11 and 12. Because these groups are all components of the large polytomy in clade 8, future analysis may reveal the rod-like cartilage to be a synapomorphy linking two or all three clades. Indeed, if the majority rule consensus (Fig. 6) is correct, state 1 is a synapomorphy linking clades 10 and 12 with *Leporinus pellegrinii*, with subsequent reversal in *Leporinus fasciatus*. Regardless of the choice of optimization, *Schizodon vittatus* is nested within clade 12; the possession of state 0 by that taxon is also a reversal.

81. *Faceting of metapterygoid*: (0) metapterygoid with two distinct facets; vertical sheet of bone dorsal to quadrate and symplectic and horizontal or medially curved dorsal portion that contacts mesopterygoid; (1) metapterygoid with three distinct facets; vertical



sheet dorsal to quadrate and symplectic, horizontal or medially curved portion that contacts mesopterygoid, and inclined plane proximate to hyomandibular that meets other facets along well-defined margins (CI = 1.000, RI = 1.000).

The metapterygoid of members of the Anostomidae has a primarily vertical orientation, with the dorsal portion curving at least slightly medially to form a horizontal facet that meets the dorsal portions of the mesopterygoid. Members of *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytidodus* and *Schizodon* have just the vertical and horizontal facets on the bone (state 0, Figs 40, 41). Species in *Anostomus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* have an inclined third facet proximate to the hyomandibular that meets the other two facets along well-defined margins that are visible in lateral view (state 1, Fig. 44). *Gnathodolus* has a restructured metapterygoid that appears to retain only the posterior portions of the bone. The vertical and inclined facets are clearly present in *Gnathodolus*, but the horizontal facet proximate to the mesopterygoid appears to have been lost. *Gnathodolus* is tentatively coded as possessing state 1 for this character based on the presence of the inclined facet.

The condition in *Laemolyta*, although coded for state 0, may in truth represent a transitional condition. In species of *Laemolyta* the horizontal facet of the metapterygoid slopes laterally anterior to the hyomandibular to create an inclined area where the horizontal facet grades into the vertical facet. Only the lack of a clear division between the inclined portion of the bone and the other two facets excludes *Laemolyta* from state 1.

This character was noticed by Winterbottom (1980: 50), who discussed a medial slope of the metapterygoid as a synapomorphy for *Anostomus* (including *Petulanos*), *Gnathodolus*, *Pseudanos*, *Sartor* and *Synaptolaemus*. Our examination of specimens from across the family reveals that all anostomids have at least a slight medial slope of the metapterygoid, particularly in the region proximate to the mesopterygoid (what we call our horizontal facet). Winterbottom's medial slope most probably corresponds to our concept of the additional inclined facet of the metapterygoid.

The typical outgroup condition for the metapterygoid (possessed by all examined outgroups except *Parodon*) is a more or less vertical sheet of bone with a slight medial bend at the dorsal extreme and is coded as state 0. *Parodon suborbitalis* has a drastically restructured and abbreviated metapterygoid. We were unable to determine whether it possesses an inclined facet of the metapterygoid and coded that species as possessing missing data.

Under the final hypothesis of relationships the possession of an additional inclined facet of the metap-

terygoid is a synapomorphy for clade 25 containing *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*. *Laemolyta* is reconstructed as the sister to clade 25, suggesting that the sloped morphology of the metapterygoid in that genus as described above is indeed an intermediate or precursor to the inclined metapterygoid facet characteristic of the species in clade 25.

82. *Presence or absence of lateral shelf on metapterygoid*: (0) lateral surface of metapterygoid without well-developed lateral shelf; (1) lateral surface of metapterygoid with well-developed lateral shelf (autapomorphy).

Uniquely among the examined members of the Anostomidae and outgroups, *Sartor elongatus* possesses a well-developed lateral shelf on the metapterygoid (anterior portion visible in Fig. 37), resulting in a T-shaped bone in cross-section. Although the character is an autapomorphy in the current dataset, there are two other described species of *Sartor* that were unavailable for inclusion in this analysis. When these are examined osteologically, it may be found that the lateral shelf is a synapomorphy for the genus.

#### SYMPLECTIC, HYOMANDIBULAR AND OPERCULAR SERIES

83. *Length of interopercular–mandibular ligament*: (0) ligament very short, anterior tip of interopercle in close proximity to posterior of retroarticular; (1) ligament elongate, interopercle notably separated from retroarticular (CI = 0.500; RI = 0.909).

The interopercular–mandibular ligament in the Characiformes runs from the anterior tip of the interopercle to the retroarticular, typically bridging a very small gap between these elements in the area just ventral to the anterior portion of the quadrate [see *Brycon meeki* (Weitzman, 1962: fig. 10) and *Xenocharax* (Daget (1960: fig. 7)]. The condition in *Brycon meeki* and *Xenocharax* is shared by *Hemiodus ocellatus*, *Parodon suborbitalis*, *Distichodus* sp., *Citharinus* sp. and all examined members of the Chilodontidae and Curimatidae, although *Chilodus punctatus* possesses a ligament of slightly greater length than that possessed by the remaining outgroups. In all examined members of the Anostomidae and Prochilodontidae, the gap between the interopercle and retroarticular is large and as a consequence the interopercular–mandibular ligament is more elongate than in the typical characiform condition (Fig. 45), spanning a length comparable with, or greater than, the diameter of the eye in some of the more derived members of the Anostomidae (*Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptolaemus*).

Given that the Anostomidae and Prochilodontidae are not sister taxa (Fig. 5, see also Vari, 1983: fig. 41; Castro & Vari, 2004: fig. 26), the elongation of the interopercular–mandibular ligament in the Anostomidae is a homoplasy relative to the condition in the Prochilodontidae. The elongation of the interopercular–mandibular ligament optimizes as a clear synapomorphy for the Anostomidae which was not previously enumerated by Vari (1983), although that author did discuss at some length the ossified sensory tubes of the preopercular canal that are associated with the expanded ligament in the Anostomidae and Prochilodontidae (Vari, 1983: 31–32, 52). The presence or absence of those tubes is coded in outgroup character 134 (Appendix 2).

84. *Presence or absence of large shelf on lateral surface of preopercle that serves as origin for portion of adductor mandibulae muscle*: (0) absent; (1) present (CI = 0.500; RI = 0.909).

The adductor musculature associated with the upper jaw in the Anostomidae arises from a broad region on the lateral surface of the quadrate and preopercle. This area of attachment is, in part, formed by a lateral shelf that arises from the main body of the ventral arm of the preopercle and which laterally contacts a posteriorly directed process of the posterolateral portion of the quadrate (see character 77 and outgroup character 132, Appendix 2). The preopercular shelf continues posteriorly as a gradually diminishing ridge beyond the posterior terminus of the quadrate. Such a modification of the preopercle is absent in proximate outgroups to the Anostomidae except for the members of the Prochilodontidae, which possess a very small shelf on the preopercle. A lateral shelf on the preopercle, albeit of somewhat different form, is also present in some more distantly related characiforms including a subgroup of the Distichodontidae that is not incorporated into the outgroup analysis in this study (see Vari, 1979: fig. 18). Under the final hypothesis of relationships the possession of a lateral shelf on the preopercle optimizes as a synapomorphy for the entire Anostomidae (clade 1).

85. *Form of anterodorsal process of preopercle*: (0) anterodorsal process of preopercle that extends between symplectic and quadrate well developed with broad triangular or rhomboidal form; (1) anterodorsal process of preopercle with thin, needle-like form; (2) anterodorsal process of preopercle absent entirely (CI = 0.667; RI = 0.952).

All examined members of the Anostomidae and Prochilodontidae possess an anterodorsal process of the preopercle that extends into the space between the symplectic and the dorsal border of the quadrate.

This process is absent in examined members of the Chilodontidae, Curimatidae, Characidae, Citharinidae and Distichodontidae (state 2). In the Anostomidae, two distinct morphologies of this process were observed. In the more common morphology shared by *Abramites*, *Anostomoides*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Rhytidodus* and *Schizodon*, the process is large and either triangular or rhomboidal (state 0, Figs 40–42). A similar morphology is present in members of the Prochilodontidae (Vari, 1983: fig. 28). In *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*, the process is present but much smaller, being represented only by a very thin, anteriorly directed extension from the main body of the preopercle (state 1, e.g. *Petulanos plicatus*, Fig. 43).

The presence of the process optimizes as a synapomorphy for the Anostomidae (clade 1) and the reduction of the process from the triangular to the needle-like morphology is a synapomorphy for the clade consisting of *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25). The Prochilodontidae is not sister to the Anostomidae (Fig. 5; Vari, 1983, 1989a; Castro & Vari, 2004), and the presence of the anterodorsal process of the preopercle in these two families is a homoplasy.

86. *Form of anterior margin of ascending arm of preopercle*: (0) anterior margin of ascending arm of preopercle without distinct triangular process overlapping joint between interhyal, hyomandibular, metapterygoid and symplectic in lateral view; (1) anterior margin of ascending arm of preopercle with distinct triangular process overlapping joint between interhyal, hyomandibular, metapterygoid and symplectic in lateral view (CI = 0.500; RI = 0.667).

In *Gnathodolus*, *Synaptolaemus* and *Sartor*, the anterior margin of the ascending arm of the preopercle has a distinctly pointed triangular process that overlaps the joint of the interhyal, hyomandibular, metapterygoid and symplectic in lateral view [state 1, Fig. 44; see also Winterbottom (1980: figs 39, 41)]. One side of one of the examined specimens of *Pseudanos gracilis* (FMNH 103454) also has such a process, but that species is coded as lacking the process in keeping with the typical morphology of the preopercle for the species. No other examined species in the Anostomidae possess such a process, although some species of *Leporinus* (*L. gomesi*, *L. ortomaculatus*, *L. striatus*) have a somewhat widened and rounded morphology of this region of the preopercle that, however, lacks a distinct pointed process. Interestingly, *Chilodus punctatus* in the Chilodontidae (but not the examined species of *Caenotropus*) also has a triangular process on the anterior margin of the ascending arm of the preopercle. No other examined

members of the outgroups possess a process in this region of the bone.

According to the final hypothesis of relationships, the presence of the process optimizes as a synapomorphy for *Gnathodolus*, *Sartor* and *Synaptolaemus* (clade 31). *Gnathodolus*, *Sartor* and *Synaptolaemus* are quite derived relative to *Chilodus* within the clade formed by the Anostomidae plus Chilodontidae. *Chilodus* furthermore shares an extensive series of synapomorphies with, and is most closely related to, *Caenotropus* (Vari, 1983; Vari *et al.*, 1995). Thus, the presence of the process in *Chilodus* in the Chilodontidae versus *Gnathodolus*, *Synaptolaemus* and *Sartor* is judged to be homoplastic.

87. *Length of symplectic*: (0) symplectic short, with posterior margin of bone separated from anterior point of ventral margin of hyomandibular by noticeable gap; (1) symplectic long with posterior margin of bone situated proximate to ventral margin of hyomandibular (CI = 0.250; RI = 0.727).

All anostomids with the exception of *Leporellus* have an elongate symplectic whose posterior margin closely adjoins the hyomandibular (state 1, Figs 41–44). As the interhyal is closely associated with the posterior cartilaginous cap of the symplectic, the interhyal of all anostomids except *Leporellus* is also situated proximate to the hyomandibular. *Leporellus* and members of the Chilodontidae and Prochilodontidae as well as *Potamorhina laticeps*, *Curimata inornata*, *Parodon suborbitalis*, *Hemiodus ocellatus* and *Citharinus* sp. have a distinct gap between the posterior terminus of the symplectic and the anteroventral corner of the hyomandibular (exclusive of the associated cartilages), with the interhyal positioned near the symplectic and distant from the hyomandibular [for *Leporellus*, see fig. 40; for *Potamorhina* see Vari (1983: fig. 27); for condition in the Prochilodontidae see Castro & Vari (2004: fig. 20)]. The longer form of the symplectic (state 1) also occurs in *Brycon* (Weitzman, 1962: fig. 10), *Curimatopsis microlepis*, *Distichodus* sp. and *Xenocharax spilurus*.

In the final phylogeny arrived at herein, *Leporellus* is the basal member of the Anostomidae, and the elongation of the symplectic and the associated relocation of the interhyal to a position proximate to the hyomandibular serves as a synapomorphy for *Abramites*, *Anostomoides*, *Anostomus*, *Gnathodolus*, *Hypomasticus*, *Laemolyta*, *Leporinus*, *Petulanos*, *Pseudanos*, *Rhytidodus*, *Sartor*, *Schizodon* and *Synaptolaemus* (clade 3).

88. *Shape of ventral lamina of symplectic*: (0) ventral lamina of symplectic narrow and not triangular; (1) ventral lamina of symplectic broad and triangular (CI = 1.000; RI = 1.000).

Species in the Anostomidae typically possess a symplectic with at most a narrow, ossified lamina extending ventrally from the main body of the bone (Figs 40–42, 44). As noted by Winterbottom (1980: 37–38), *Petulanos intermedius* and *P. plicatus* (assigned therein to *Anostomus*) have that lamina expanded into a broad triangular sheet [Fig. 43; see also Winterbottom (1980: fig. 36)] extending ventrally medial to the adjoining portion of the horizontal arm of the preopercle. That expansion of the symplectic is absent elsewhere in the Anostomidae and also in all examined outgroups and represents an unambiguous synapomorphy for *P. intermedius* and *P. plicatus* (clade 30).

89. *Position of joint of interhyal, metapterygoid, symplectic and hyomandibular*: (0) joint of interhyal, metapterygoid, symplectic and hyomandibular positioned at approximately same horizontal plane as anterior portion of lateral shelf of metapterygoid; (1) joint of interhyal, metapterygoid, symplectic and hyomandibular positioned significantly ventral of horizontal plane of anterior portion of lateral shelf of metapterygoid (CI = 1.000; RI = 1.000).

Among members of the Anostomidae, the cartilaginous joint linking the interhyal, metapterygoid, hyomandibular and symplectic is typically positioned ventral of the horizontal plane of the shelf formed by the bending medially of the dorsal portion of the metapterygoid (state 1, Figs 41, 42). That condition was also observed in all outgroups [e.g. *Brycon* (Weitzman, 1962: fig. 10)]. In *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor*, and *Synaptolaemus*, this joint is positioned more dorsally, being located along approximately the same horizontal plane as the anterior portion of the medial shelf of the metapterygoid [state 0; Figs 43, 44; see also Winterbottom (1980: fig. 41)]. The more dorsal location of this joint is an apomorphic condition defining a clade consisting of *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus* (clade 27).

90. *Form of posterodorsal margin of opercle*: (0) with slight or pronounced concavity; (1) continuously convex or straight and completely lacking concavity (CI = 0.333; RI = 0.857).

Most examined species in the Anostomidae have some degree of concavity to the posterodorsal margin of the opercle. Species with the concavity (state 0) include those in *Abramites*, *Anostomus*, *Gnathodolus*, *Hypomasticus*, *Leporellus*, *Leporinus*, *Petulanos*, *Sartor* and *Synaptolaemus* as well as some specimens of *Pseudanos gracilis*. In some of the species of these genera, the concavity is highly developed [e.g. *Synaptolaemus cingulatus* (Winterbottom, 1980: fig. 39) and *Leporinus agassizi* (Fig. 14)] whereas in the rest of



the species, the concavity is very slightly developed [e.g. *Abramites* (Fig. 15), *Leporinus ortomaculatus*, *L. pellegrinii* and *Gnathodolus bidens*]. *Anostomoides*, *Laemolyta*, *Rhytiodus* and *Schizodon* as well as *Pseudanos irinae*, *P. trimaculatus*, *P. winterbottomi* and some specimens of *P. gracilis* have fully convex or straight posterodorsal margins of the opercle [state 1, for condition in *P. trimaculatus* see Winterbottom (1980: fig. 33)]. *Pseudanos gracilis* is polymorphic for this character. Two cleared and stained specimens of the species (CAS 68314, one of FMNH 103454) have distinct, albeit small, convexities along the posterodorsal margin of both opercles, whereas the two other cleared and stained specimens (USNM 270309, the other of FMNH 103454) have straight posterodorsal margins to their opercles. All four specimens of *P. gracilis* are approximately the same size, and this intraspecific variation probably does not reflect ontogenetic variation in the form of the opercle.

Winterbottom (1980: 51) discussed a concave opercular margin as a synapomorphy for *Anostomus* (including *Petulanos*), *Gnathodolus*, *Sartor* and *Synaptolaemus*. We agree with his basic conclusion, although we differ in our observation of *Pseudanos gracilis* (polymorphic in our material) and the interpretation of *Abramites*, which we found to have a slightly concave margin in our material (state 0, Fig. 15) but which was cited by Winterbottom (1980: 51) as possessing a straight opercular margin (state 1).

Conditions of the posterodorsal margins of the opercle vary among the outgroups. *Parodon suborbitalis* in the Parodontidae and *Xenocharax spilurus* in the Distichodontidae (Daget, 1960: fig. 7) have moderate concavities along the anterodorsal margin of the opercle. The remaining outgroups have convex or straight margins of the opercle.

The most basal species in the Anostomidae have a distinct concavity in the posterodorsal margin of the opercle (*Abramites*, *Hypomasticus*, *Leporellus*, *Leporinus*), and possession of the concavity optimizes as a synapomorphy for the Anostomidae. A transition to the continuously convex or straight morphology of the margin is a synapomorphy of clade 13 and the subsequent re-evolution of the concave margin is a synapomorphy for clade 27 (*Anostomus*, *Gnathodolus*, *Petulanos*, *Synaptolaemus* and *Sartor*).

#### GILL ARCHES AND PHARYNGEAL JAWS

91. *Presence or absence of curved anterior process of third epibranchial that extends medially over dorsal surface of fourth infrapharyngobranchial*: (0) absent; (1) present (CI = 0.500; RI = 0.917).

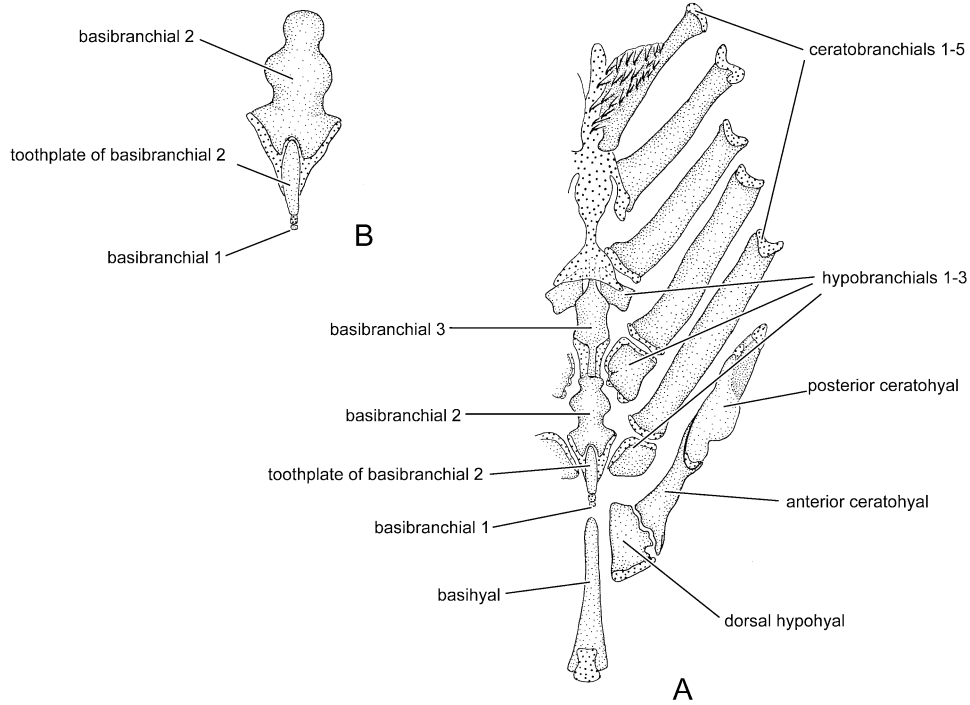
The anterior portion of the third epibranchial in both proximate and distant outgroups to the Anosto-

midiae is typically only somewhat wider in the approximately horizontal plane than is the slightly more distal region of that bone situated between the anterior articular surface and the dorsally directed uncinuate process of the third epibranchial (state 0; e.g. *Brycon meeki*, Weitzman, 1962: fig. 11; *Curimata vittata*, Vari, 1983: fig. 17). Members of the Anostomidae have the anterior portion of the third epibranchial significantly expanded into a broadly curving, anteriorly cartilage-capped process that extends medially over the dorsal surface of the cartilaginous fourth infrapharyngobranchial (state 1; e.g. *Anostomus*, Vari, 1983: fig. 18). A similar morphology occurs in the distant outgroup *Parodon suborbitalis* (coded as state 1). *Xenocharax spilurus* has a curved anterior process on the third epibranchial but that process does not extend medially over the fourth infrapharyngobranchial (coded as 0). Otherwise, the morphology of the third epibranchial characteristic of the Anostomidae has not been encountered elsewhere among examined characiforms, and optimizes as a synapomorphy for the family (clade 1) in the final reconstruction arrived at herein.

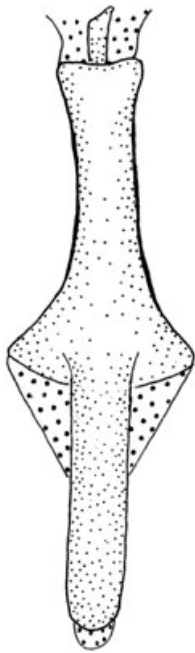
92. *Presence or absence of ossified first basibranchial*: (0) absent; (1) present (CI = 0.100; RI = 0.550).

Vari (1983: 14) noted that within the four family assemblage consisting of the Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae, the loss of an ossified first basibranchial is a synapomorphy for the Curimatidae, but that certain taxa within the Anostomidae (*Rhytiodus*, *Pseudanos*) also appear to have lost that element. During the course of this study it was discovered that within the Anostomidae an ossified first basibranchial is present in *Anostomus*, *Gnathodolus*, *Hypomasticus*, *Laemolyta*, *Leporellus* (Fig. 46), *Petulanos*, *Sartor*, *Schizodon nasutus* and all examined *Leporinus* except *L. cf. niceforoi* (state 1). An ossified first basibranchial is absent in *Anostomoides* (Fig. 47), *Leporinus cf. niceforoi*, *Pseudanos*, *Rhytiodus*, *Synaptolaemus*, all examined species of *Schizodon* except *S. nasutus*, and all but one specimen of *Abramites hypselonotus* (state 0). The *Abramites* specimen in USNM 164036 possesses a tiny ossified first basibranchial, while the other five examined specimens lack that element; *Abramites* is coded as lacking the element (state 0). The element is possibly absent in *Leporinus jatuncochi*; the specimen at hand is poorly cleared, weakly stained and incompletely ossified, making the state of this character impossible to determine in that species (coded as missing data). The element that Winterbottom (1980: fig. 50) labelled as the first basibranchial in his illustration of the lower gill arches of *Synaptolaemus cingulatus* is in fact a thin lamina of bone situated dorsal to a cartilage at the front of the second





**Figure 46.** *Leporellus vittatus*, INHS 56128, 78.2 mm SL: A, dorsal view of ventral portion of gill arches; B, close up of basibranchials 1 and 2.



**Figure 47.** Basibranchial 2 of *Anostomoides laticeps*, INHS 53677, 106.6 mm SL; ventral view.

basibranchial and fused to that element in our material of the specimen. This bony plate appears to be a portion of the second basibranchial, with the first basibranchial absent in *Synaptolaemus*.

Taxa within the Anostomidae that possess an ossified first basibranchial frequently have that element reduced to tiny ball of bone (e.g. *Leporellus*, Fig. 46) relative to the condition in the first outgroup, the Chilodontidae, in which the first basibranchial is a comparatively massive rod-like ossification (Vari, 1983: fig. 9) similar to that present in many outgroup characiforms including *Brycon* (Vari, 1983: figs 3, 4) and the basal distichodontid *Xenocharax*. Among the other outgroups, members of the Prochilodontidae as well as *Distichodus* sp. and *Hemiodus ocellatus* also possess ossified first basibranchials, while *Citharinus* sp. and *Parodon suborbitalis* appear to be lacking this ossification.

In light of the final phylogeny for the Anostomidae arrived at herein, the first basibranchial is plesiomorphically present within the family. The subsequent evolution of the character is extraordinarily homoplastic, necessitating no fewer than seven character state transitions within the Anostomidae. Losses of the ossification occur in *Leporinus* cf. *niceforoi*, *Abramites* and clade 13. Within clade 13, ossification of this element re-evolves in *Schizodon nasutus*, *Laemolyta* and clade 27. Within clade 27, *Synaptolaemus*, in turn, has lost the first basibranchial.

In the Anostomidae the first basibranchial is small even when present and it is possible that the feature is ontogenetically variable. If the bone appears later in the development of some species that lack the bone

in our representative cleared and stained material, this could explain some of the apparent homoplasy.

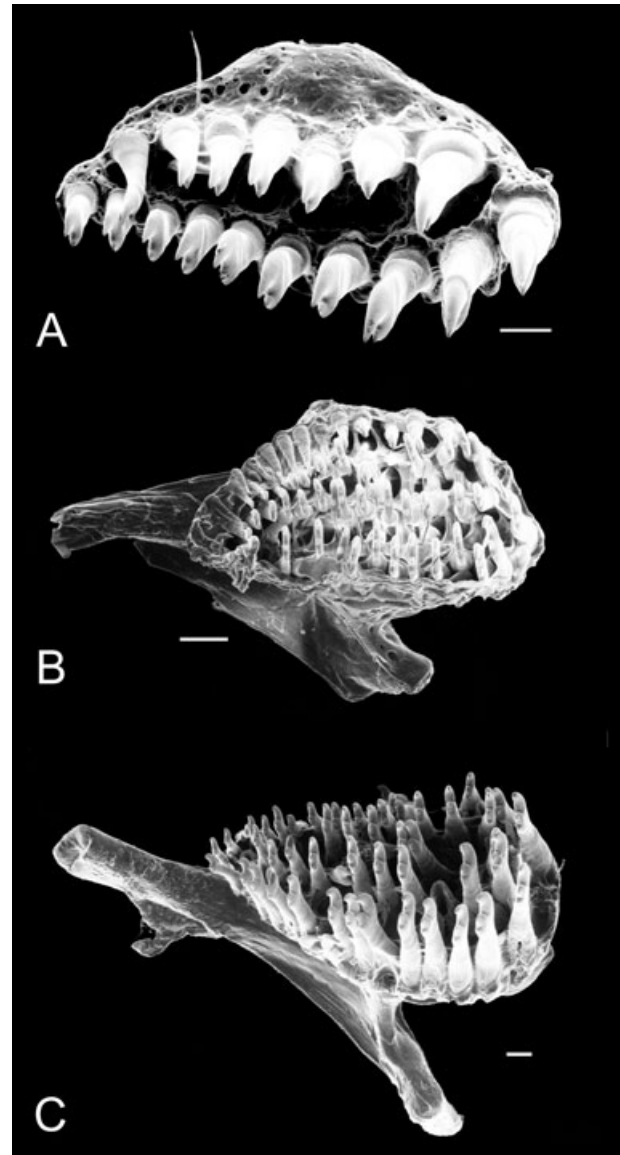
93. *Morphology of second basibranchial*: (0) second basibranchial rod-like, lacking prominent lateral flanges; (1) second basibranchial with prominent lateral flanges resulting in overall shape resembling violin (CI = 1.000; RI = 1.000).

In all examined members of the Anostomidae except *Leporellus*, the second basibranchial has the form of a thin rod with a slight to moderate lateral expansion along its anterior portion, resulting in an ossification resembling the letter 'T' from dorsal view (e.g. *Anostomoides laticeps*, Fig. 47). In the two examined species of *Leporellus*, the bone has an additional lateral flange on each side (Fig. 46). This flange is most developed anteriorly and posteriorly with a definite transverse constriction at the midlength of the bone, giving the second basibranchial the general shape of the body of a violin from dorsal view. No examined members of any outgroup family possess such elaborations of these lateral flanges, which represent an unambiguous synapomorphy for *Leporellus* (clade 2).

94. *Number of full tooth rows on fifth upper pharyngeal tooth-plate*: (0) fifth upper pharyngeal tooth-plate edentulous in adults; (1) one or two full rows of teeth on fifth upper pharyngeal tooth-plate; (2) three or more full rows of teeth on fifth upper pharyngeal tooth-plate (CI = 0.286; RI = 0.773).

For the purposes of this character, a full tooth row was considered to contain at least three teeth. The fifth upper pharyngeal tooth-plate is a relatively small ossification bearing two distinct rows of teeth (state 1) in *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Pseudanos*, *Petulanos*, *Sartor*, *Synaptolaemus* and all examined species in *Leporinus* except *L. gomesi* (e.g. *L. cf. ecuadorensis*, Fig. 48A). More than two tooth rows on the fifth upper pharyngeal tooth-plate are present in several other members of the family (all coded in state 2). *Abramites*, *Hypomasticus despaxi*, *H. megalepis*, *Leporellus*, *Leporinus gomesi*, *Rhytiodus lauzannei* and *R. microlepis* all possess three full tooth rows on this ossification. *Hypomasticus mormyrops*, *H. pachycheilus*, *Rhytiodus argenteofuscus* (Fig. 48B) and *Schizodon nasutus* all possess four full rows of upper pharyngeal dentition. *Schizodon fasciatus* possesses five rows of teeth on the fifth upper pharyngeal tooth-plate (Fig. 48C), while *S. isognathus*, *S. knerii*, *S. scotorhabdotus* and *S. vittatus* all have six full rows on that ossification.

Although it would have been possible to break this character into six discrete states, that practice would excessively subdivide the character and would obscure the broader underlying pattern of evolution.



**Figure 48.** A, right fifth upper pharyngeal tooth-plate and associated dentition of *Leporinus cf. ecuadorensis*, FMNH 102198; B, left fourth epibranchial and associated fifth upper pharyngeal tooth-plate and dentition of *Rhytiodus argenteofuscus*, INHS 67453, image reversed; C, right fourth epibranchial and associated fifth upper pharyngeal tooth-plate and dentition of *Schizodon fasciatus*, FMNH 111351; ventral views, scale bar = 200  $\mu$ m.

We elected to break the character into the two dentigerous character states described above, plus a third (state 0) to mark the absence of the dentition on the fifth upper pharyngeal tooth-plate in some outgroups.

Among the proximate outgroups to the Anostomidae, species in the Chilodontidae possess two rows on the upper pharyngeal tooth-plate (state 1), although we note that the species of *Caenotropus* have two

teeth in a third row, one tooth short of being included in state 2. Species in the Curimatidae with the exception of *Curimatopsis* lack dentition on the fifth upper pharyngeal tooth-plate as adults (Vari, 1983: 19, 1989a: 20). *Curimatopsis* species have only one or two rows of conical teeth on that ossification, with that number of tooth rows also present in larvae of the members of the family that have been studied ontogenetically (Vari, 1989a: fig. 7). Species in the Prochilodontidae also lack upper pharyngeal teeth as adults (Castro & Vari, 2004: 17). The distant outgroups *Parodon*, *Brycon*, *Hemiodus*, *Xenocharax* and *Distichodus* possess many small unicuspid teeth on the fifth upper pharyngeal tooth-plate. Although these teeth are not arranged in neat rows, were they so arranged there would be at least three complete rows. As such, these five outgroup taxa are coded for state 2. *Citharinus* sp. has an edentulous fifth upper pharyngeal tooth-plate.

Based on the final phylogeny, the plesiomorphic condition within the Anostomidae is the possession of three rows of upper pharyngeal teeth (state 2). A reduction to two rows is a synapomorphy for clade 8 that is reversed independently in *Abramites* and clade 15 containing *Schizodon* and *Rhytiodus*, the members of which have three to six full rows of upper pharyngeal dentition.

95. *Form of cusping of teeth on fifth upper pharyngeal tooth-plate*: (1) all teeth on fifth upper pharyngeal tooth-plate unicuspid; (2) most teeth on fifth upper pharyngeal tooth-plate bicuspid but with occasional teeth unicuspid; (3) at least some teeth on fifth upper pharyngeal tooth-plate tricuspid and other teeth bicuspid (CI = 0.333; RI = 0.714).

Most species in the Anostomidae have largely bicuspid teeth on the fifth upper pharyngeal tooth-plate, with some teeth being unicuspid [state 2, Fig. 48A; see also Vari (1983: fig. 11A)]. Uniquely within the Anostomidae, *Leporellus pictus* appears to have only unicuspid teeth on this ossification (state 1), whereas its congener, *L. vittatus*, possesses bicuspid upper pharyngeal teeth. *Rhytiodus argenteofuscus* (Fig. 48B), *Schizodon nasutus*, *S. knerii*, *S. isognathus*, *S. fasciatus* (fig. 48C) and *S. vittatus* have three cusps on some of the teeth on the fifth upper pharyngeal tooth-plate, particularly on those teeth positioned proximate to the posterior margin of the ossification. No tricuspid teeth on this tooth-plate were observed in *Schizodon scotorhabdotus*, *Rhytiodus microlepis* or *R. lauzannei*.

Species in the Prochilodontidae and all genera in the Curimatidae except for *Curimatopsis* lack upper pharyngeal dentition as adults but have unicuspid teeth with swollen bases on the fifth upper pharyngeal tooth-plate as larvae (Roberts, 1973: 219; Vari,

1989a: fig. 7). Because the adult state is edentulous, species in these taxa are coded as having missing data. A distinct patch of unicuspid teeth on the fifth upper pharyngeal tooth-plate occurs in adults of *Curimatopsis* (Vari, 1989a: fig. 5), and these are coded as state 1. Interestingly, species in the closest outgroup to the Anostomidae, the Chilodontidae, have several tricuspid teeth on the fifth upper pharyngeal tooth-plate (state 3; see Vari, 1983: fig. 11B, C).

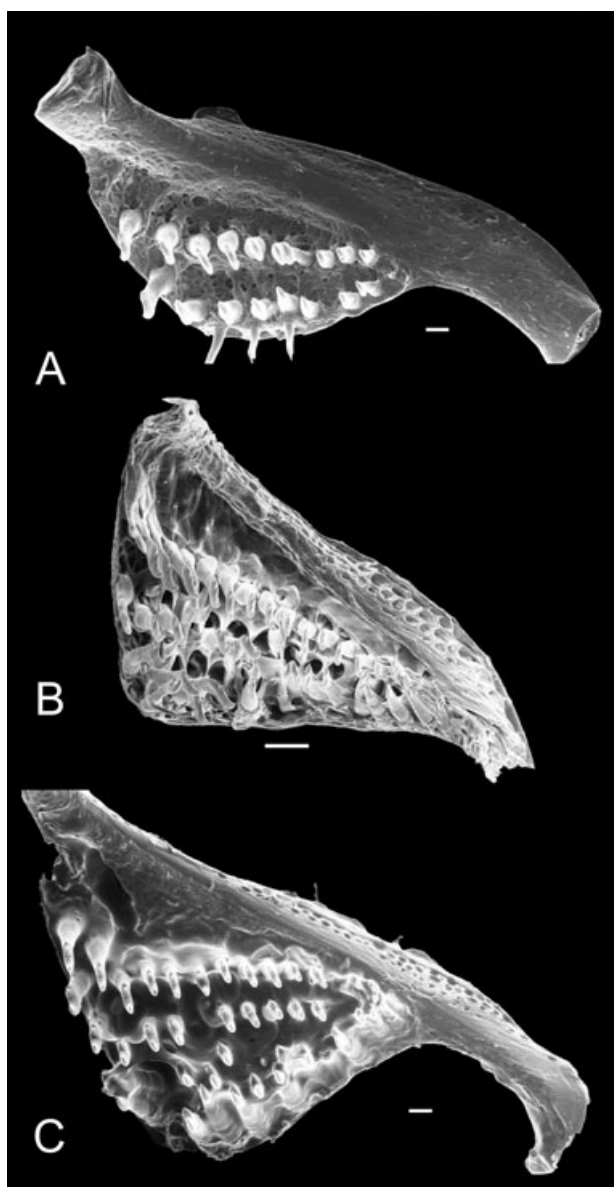
Given the derived position of *Rhytiodus* and *Schizodon* (clade 15) in the final hypothesis of relationships obtained by this study, the tricuspid upper pharyngeal dentition present in the Chilodontidae is derived independently of the tricuspid upper pharyngeal dentition possessed by some species of *Rhytiodus* and *Schizodon*. Within clade 15 the optimizations are equivocal. Under ACCTRAN the tricuspid upper pharyngeal dentition evolved in the common ancestor of clade 15 with a reversal to bicuspid dentition in clade 17 (*Rhytiodus lauzannei* and *R. microlepis*) and *Schizodon scotorhabdotus*. Under DELTRAN the tricuspid upper pharyngeal dentition evolved independently in *Rhytiodus argenteofuscus* and *Schizodon* (clade 18), again with a reversal to solely bicuspid dentition in *S. scotorhabdotus*.

96. *Number of complete rows of teeth on tooth-plate of fifth ceratobranchial*: (0) tooth-plate edentulous; (1) one or two complete rows of teeth; (2) three or more complete rows of teeth (CI = 0.286; RI = 0.773).

For the purposes of this character, a complete row of teeth on the fifth ceratobranchial was considered to consist of five or more teeth spanning the dentigerous portion of the bone. The few teeth placed erratically along the posterior margin of the bone in some taxa (e.g. *Leporinus* cf. *ecuadorensis*, Fig. 49A) were not counted as a full tooth row.

The majority of species in the Anostomidae possess two complete rows of teeth on the tooth-plate of the fifth ceratobranchial (state 1), including the species of *Abramites*, *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Leporinus* (Fig. 49A), *Petulanos*, *Pseudanos*, *Sartor*, *Synaptolaemus*, *Rhytiodus lauzannei*, *R. microlepis*, *Hypomasticus despaxi* and *H. megalepis*. In contrast, the species of *Leporellus* and *Schizodon* as well as *Hypomasticus mormyrops*, *H. pachycheilus* and *Rhytiodus argenteofuscus* have three or more rows of teeth on the fifth ceratobranchial tooth-plate. *Leporellus*, *Hypomasticus pachycheilus* and *Rhytiodus argenteofuscus* (Fig. 49B) possess three full rows, while *Hypomasticus mormyrops*, *Schizodon knerii*, *S. nasutus*, *S. fasciatus* (Fig. 49B) and *S. vittatus* have four full rows. *Schizodon isognathus* and *S. scotorhabdotus* possess five full rows of teeth on the fifth ceratobranchial. As with character 82, we chose to break this character into





**Figure 49.** A, right fifth ceratobranchial and associated dentition of *Leporinus cf. ecuadorensis*, FMNH 102198; B, left fifth ceratobranchial and associated dentition of *Rhytiodus argenteofuscus*, INHS 67453, image reversed, tip of left posterior process damaged and missing; C, right fifth ceratobranchial and associated dentition, *Schizodon fasciatus*, FMNH 111351, some teeth in second and third rows missing; dorsal views, scale bar = 200  $\mu\text{m}$ .

fewer discrete character states than maximally possible so as to avoid obscuring the general evolutionary pattern, namely that some taxa possess more rows of teeth on the lower pharyngeal jaw than is typical for most members of the family. All the species possessing three or more full rows of lower pharyngeal teeth were included in state 2.

Among the outgroups, members of the Chilodontidae possess three full rows of teeth on the fifth ceratobranchial and are coded as possessing state 2. Members of the Curimatidae, Prochilodontidae and Citharinidae lack teeth on the fifth ceratobranchial as adults (Vari, 1983) and are coded as possessing state 0, an edentulous fifth ceratobranchial, except for some *Curimatopsis* species, which retain a tiny patch of teeth on that ossification as adults and are coded as state 1. *Brycon falcatu*s (Weitzman, 1962: 35), *Distichodus* sp., *Hemiodus ocellatus* and *Xenocharax spilurus* possess many teeth arranged irregularly on the fifth ceratobranchial. Given that these would form at least three full rows if so arranged, these taxa were included tentatively in state 2.

Based on the evidence from the Chilodontidae, which forms the sister group to the Anostomidae, and the basal position of *Leporellus* in the final reconstruction of relationships herein, the plesiomorphic condition within the Anostomidae is state 2, the possession of three or more full tooth rows on the fifth ceratobranchial. Subsequent evolution of the character is homoplastic on the final phylogeny and optimization is ambiguous. Under ACCTRAN, state 1 evolves at the base of clade 3, with reversals to state 2 in clades 6 (*Hypomasticus mormyrops* and *H. pachycheilus*) and clade 15 (*Rhytiodus* and *Schizodon*) and a reversal in that clade to state 1 in clade 17 (*Rhytiodus lauzannei* and *R. argenteofuscus*). Under DELTRAN, state 1 evolves independently in clades 5 (*Hypomasticus despaxi* and *H. megalepis*) and 7, with reversals to state 1 in *Schizodon* and *Rhytiodus argenteofuscus*.

#### HYOID AND BRANCHIOSTEGAL RAYS

97. Length of dorsal margin of anterior ceratohyal (0): relatively long, approximately half length of ventral margin or longer; (1) very short, approximately one-third length of ventral margin (Autapomorphy).

Winterbottom (1980: 51) discussed an increase in the angle of the joint between the anterior and posterior ceratohyals as a synapomorphy of *Anostomus* (including *Petulanos*), but that character proved impossible to code objectively across the Anostomidae due to the presence of continuous intermediates (see unutilized characters). Nevertheless, in *Petulanos plicatus* the approximately 45° incline of the joint between the anterior and posterior ceratohyals is accompanied with a longitudinal foreshortening of the anterior ceratohyal. These combined modifications result in a very short dorsal margin of the anterior ceratohyal, which is approximately one-third the length of the ventral margin of that bone (state 1). Other examined anostomids, including *Anostomus anostomus*, *A. ternetzi* and *Petulanos intermedius*, have a dorsal margin of the anterior ceratohyal that is at least half as long as the



ventral margin, and many species have the two margins approximately of equal length. Although the dorsally shorter morphology of the anterior ceratohyal in *Petulanos plicatus* is unique among the examined anostomids and outgroups, it is shared with *P. spiloclistron* (Winterbottom, 1980: fig. 46A) and would presumably optimize as a synapomorphy for those two taxa in a future comprehensive analysis.

98. *Presence or absence of inflection point in joint between anterior and posterior ceratohyals and corresponding process of anterior ceratohyal running ventral to posterior ceratohyal*: (0) absent; (1) present (CI = 1.000, RI = 1.000).

The two examined species of *Leporellus* possess a distinct inflection in the angle of the joint between the anterior and posterior ceratohyals. The inflection of the joint produces a thin process of the anterior ceratohyal that runs ventral to the posterior ceratohyal. Many species in the Anostomidae have a steep angle to the joint between the ceratohyals [e.g. *Petulanos spiloclistron* (Winterbottom, 1980: fig. 46A, the epihyal and ceratohyal of that author) and *Synaptolaemus cingulatus* (Winterbottom, 1980: fig. 47)] but no others have a strong point of inflection in the joint or a similar ventral process. Inflection of this joint and the presence of a ventral process of the anterior ceratohyal were not observed in the outgroups, and possession of the inflection and process is a synapomorphy for *Leporellus* in the final phylogenetic reconstruction.

99. *Height of, and angle between, dorsal and ventral margins of urohyal*: (0) urohyal low, dorsal and ventral margins meet at an angle equal to or less than 45°; (1) urohyal high, dorsal and ventral margins meet at an angle greater than 45° (CI = 0.500, RI = 0.667).

Winterbottom (1980: 55, Fig. 46B) cited a high (deep) urohyal as a synapomorphy for *Petulanos intermedius*, *P. plicatus* and *P. spiloclistron*. We agree with that observation; these three species have a very high urohyal with the dorsal and ventral margins meeting at approximately a 60° angle. We also note that *Synaptolaemus* and *Gnathodolus* possess an urohyal almost as high as that in the *Petulanos* species, with margins meeting at approximately 50–55° angle. Under the definition of character states above, *Gnathodolus*, *Petulanos* and *Synaptolaemus* are all coded as possessing state 1. The remaining species in the Anostomidae have shallower urohyals with the dorsal and ventral margins meeting along a 45° angle or less (state 0). *Abramites*, *Leporellus*, *Sartor* and *Leporinus gomesi*, *L. jatuncochi*, *L. pellegrinii* and *L. tigrinus* have somewhat deep urohyals with margins meeting along an angle of approximately 40–45°. Species in

*Anostomus*, *Anostomoides*, *Hypomasticus*, *Pseudanos*, *Rhytiodus* and *Schizodon* as well as the members of *Leporinus* not cited above have even shallower urohyals, typically with margins meeting at approximately a 30° angle. Examined members of the outgroups all have urohyals with dorsal and ventral margins meeting at less than a 45° angle [e.g. *Brycon* (Weitzman, 1962: fig. 11B)]. Under the final hypothesis of relationships arrived at herein, possession of a high urohyal (state 1) optimizes as a synapomorphy for clade 29 (*Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*) that is reversed in *Sartor*.

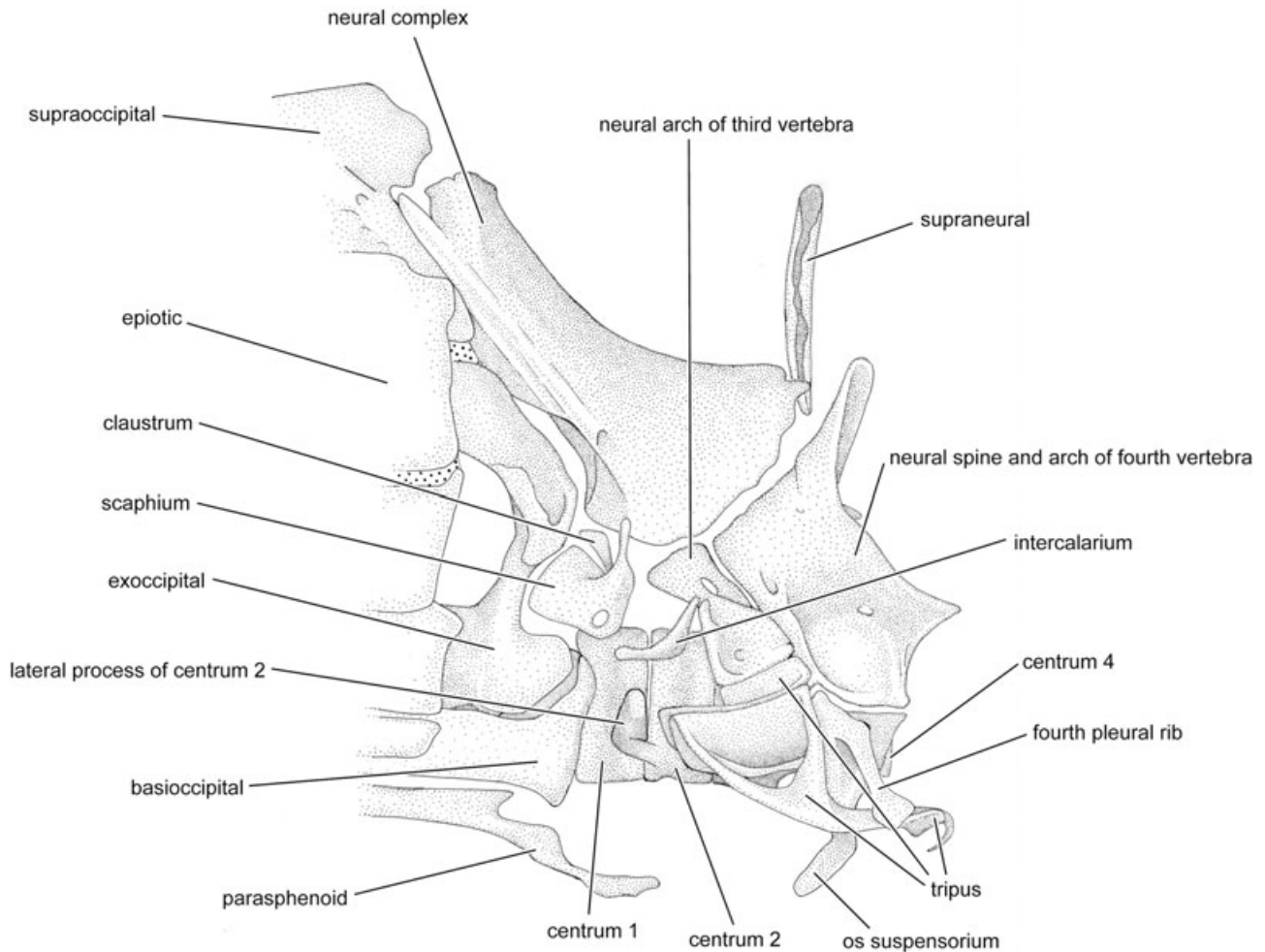
100. *Number of branchiostegal rays*: (0) three; (1) four (CI = 0.250; RI = 0.400).

Many groups in the Characiformes have four pairs of branchiostegal rays (Roberts, 1969: 422) albeit with variation from that number in various taxa. All examined outgroups in this study possess four branchiostegal rays, and that number of rays is also present in most species within the Anostomidae. *Abramites hypselonotus*, *Anostomoides laticeps*, *Anostomus ternetzi*, *Pseudanos gracilis*, *P. irinae* and *P. trimaculatus* lack the medial-most pair of branchiostegal rays, leaving a total of three pairs of rays (Winterbottom, 1980: fig. 42). *Anostomus anostomus* and *Pseudanos winterbottomi* are reported to be polymorphic for this character, with most specimens possessing four pairs of branchiostegal rays (Winterbottom, 1980: 11; Sidlauskas & Santos, 2005: 114) but occasional specimens possessing three pairs of rays. In accordance with the state possessed by the majority of specimens (four rays), *Pseudanos winterbottomi* and *Anostomus anostomus* are coded as possessing state 1 for this character.

Under the final phylogenetic hypothesis arrived at herein, possession of four branchiostegal rays is clearly the plesiomorphic condition within the Anostomidae. A reduction to three rays appears to have occurred four times in the family: once in *Abramites*, once in *Anostomoides*, once in *Anostomus ternetzi* and once in clade 26 (*Pseudanos gracilis*, *P. irinae* and *P. trimaculatus*). The concentration of species with only three branchial pairs of rays in *Pseudanos* and *Anostomus*, and the known polymorphism in *Pseudanos winterbottomi* and *Anostomus anostomus*, which appear to be relatively basal members of the clade containing *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* (clade 25) suggests that the common ancestor of that clade may also have been polymorphic for this character.

#### WEBERIAN APPARATUS AND SUPRANEURALS

101. *Presence or absence of anteriorly directed process of fourth pleural rib*: (0) absent; (1) present (CI = 0.500; RI = 0.750).

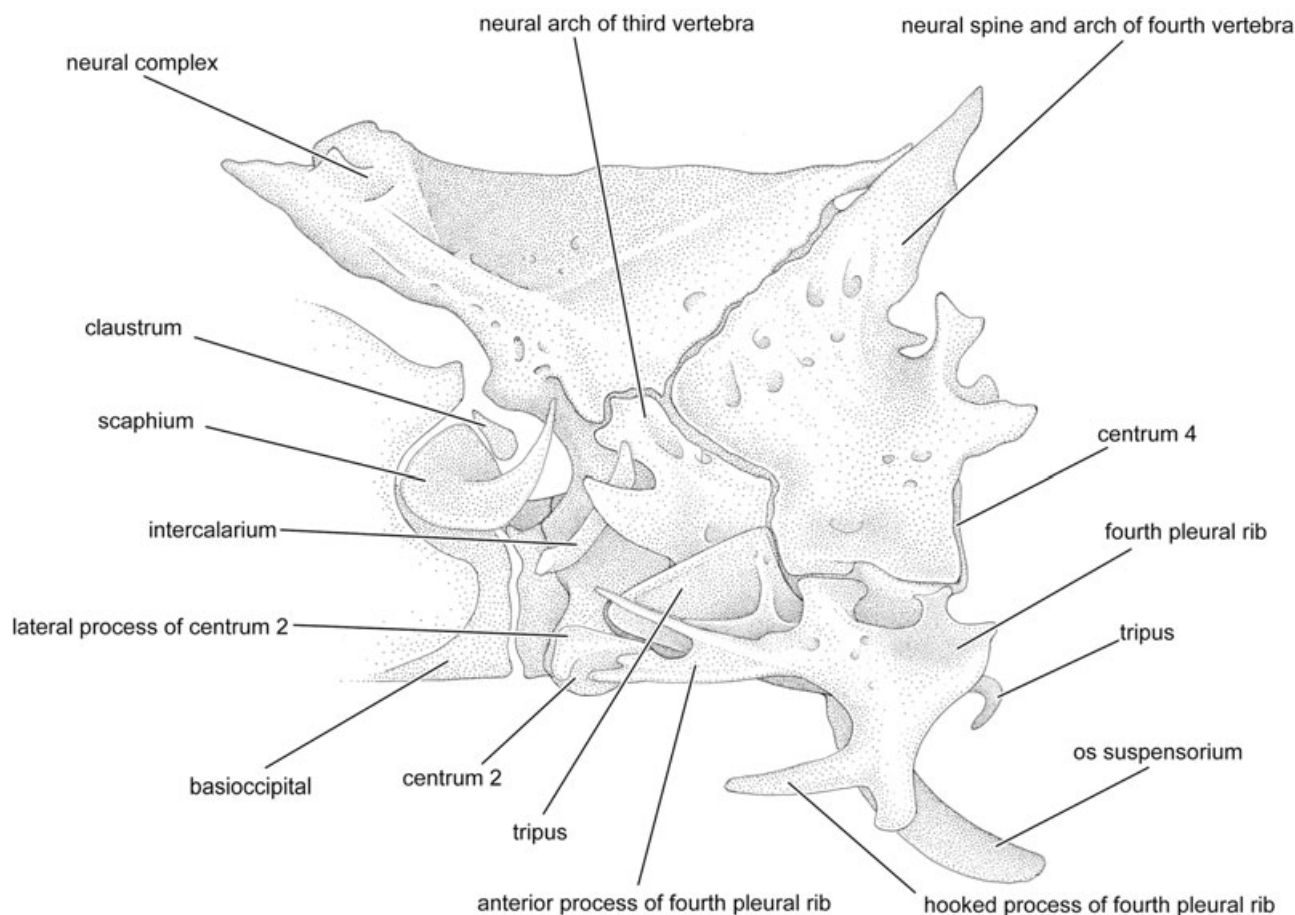


**Figure 50.** Right side of Weberian apparatus of *Leporellus vittatus*, INHS 56128, 78.2 mm SL; lateral view; drawing reversed to place anterior at left.

In most members of the Anostomidae, the modified fourth pleural rib is a small and unelaborated ossification located posterior of the tripus within the Weberian apparatus (state 0; e.g. *Leporellus*, Fig. 50). All three examined species of *Rhytiodus* instead possess a novel anteriorly directed process on the modified fourth pleural rib (state 1, Fig. 51). In *Rhytiodus argenteofuscus* the process is relatively small and triangular, while in *R. microlepis* and *R. lauzannei* the process is large and forked and passes lateral to the tripus, with one branch of the fork joining with the lateral process of centrum 2 and the other directed towards the ventral portions of the scaphium (Fig. 51). No other examined anostomid possesses an anteriorly directed process of the fourth pleural rib, although anostomids in general do possess a thick band of soft tissue connecting the fourth pleural rib to the lateral process of centrum 2. The condition in *Rhytiodus* appears to represent a full or partial ossi-

fication of this band of tissue, similar to the ossification of the connecting tissue sheath underlying the pars sustentaculum that occurs in the families Citharinidae and Distichodontidae (Vari, 1979: 305–310). The function, if any, of this unusual modification is unknown. Interestingly, the species of *Caenotropus* in the Chilodontidae also possess a small anterior projection of the fourth rib that also appears to represent a partial ossification of the same band of connective tissue. We know of no other characiform with a comparable modification. Under the final hypothesis of relationships, the possession of an anteriorly directed process on the fourth pleural rib optimizes as a synapomorphy for *Rhytiodus* (clade 16) that is independently derived, albeit with a lesser degree of development, in the distantly related *Caenotropus*.

102. *Curvature of fourth pleural rib*: (0) fourth pleural rib straight, without anteriorly directed distal hook;



**Figure 51.** Left side of Weberian apparatus of *Rhytiodus lauzannei*, INPA 21604, 260 mm SL; lateral view, gap between basioccipital and centrum 1 indicates a post-mortem disassociation of these elements, claustrum, scaphium and intercalarium and tripus dislodged in illustrated specimen, positions of these elements in illustration based on *Rhytiodus microlepis*, USNM 389694, 91 mm SL.

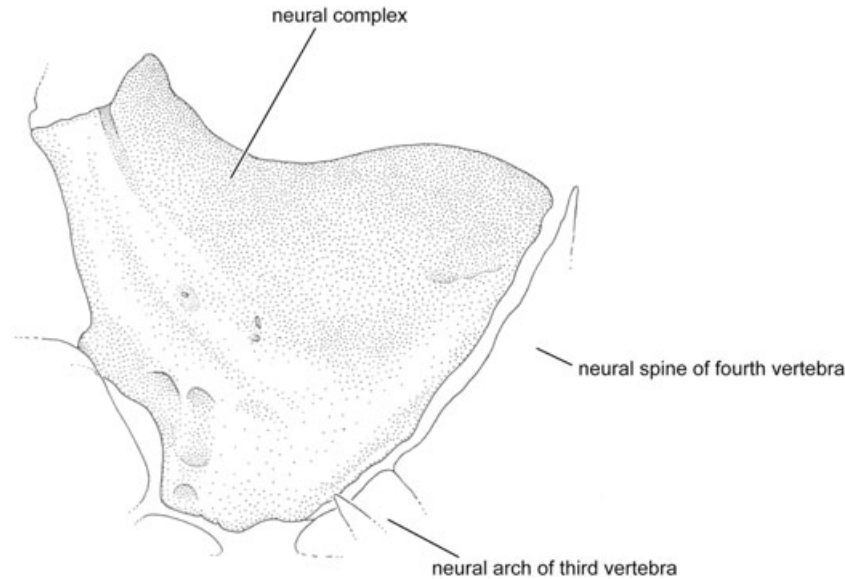
(1) fourth pleural rib with anteriorly directed distal hook (CI = 0.500; RI = 0.750).

The three examined species of *Rhytiodus* all possess an anteriorly directed hook on the distal portion of the fourth pleural rib (state 1). The hook is least pronounced in *Rhytiodus argenteofuscus* but, nevertheless, present. It is very obvious in *R. lauzannei* and *R. microlepis* (Fig. 51). All other examined members of the Anostomidae and all outgroups except for the species of *Caenotropus* possess laterally or posteriorly directed fourth pleural ribs without a distal hook (e.g. *Leporellus*, Fig. 50). Like *Rhytiodus*, *Caenotropus* has an anteriorly directed hook on the distal portion of the fourth pleural rib and is coded for state 1. As with the more dorsally positioned anterior process of the fourth pleural rib described in character 101, the function of the distal hook on that element is unknown. Nevertheless, possession of the hook optimizes as a synapomorphy for *Rhytiodus* (clade 16) that occurs independently in *Caenotropus*.

103. *Development and curvature of os suspensorium*: (0) os suspensorium small and straight, not cupping anterior portion of swim bladder; (1) os suspensorium very well developed ventrally with distinct posterior curvature around anterior portion of swim bladder (CI = 1.000; RI = 1.000).

The os suspensorium of most anostomids is a small, anteroventrally directed process of the fourth vertebral centrum (state 0, see condition in *Leporellus*, Fig. 50). *Rhytiodus microlepis* and *R. lauzannei* conversely possess a modified os suspensorium that is greatly expanded ventrally and that curves around and cups the anterior portion of the swim bladder (Fig. 51). *Rhytiodus argenteofuscus* possesses the more typical, uncurved condition of the os suspensorium. No examined specimen of the outgroups possesses a comparable modification to the os suspensorium, although larger individuals of *Citharinus* have a ventrally expanded os suspensorium (Vari, 1979: fig. 31). In the final phylogeny, the ventral





**Figure 52.** Right side of neural complex of *Abramites hypselonotus*, FMNH 97711, 76.0 mm SL; lateral view, drawing reversed to place anterior at left.

expansion and curvature of the os suspensorium optimizes as a synapomorphy for *Rhytiodus lauzannei* and *R. microlepis* (clade 17).

104. *Shape of neural complex and angle of dorsal margin of neural complex relative to anterior–posterior axis of fish:* (0) neural complex in form of elongate triangle with distinctly angled dorsal margin; (1) neural complex in form of elongate triangle with nearly horizontal dorsal margin; (2) neural complex in form of equilateral triangle with nearly horizontal dorsal margin (CI = 1.000; RI = 1.000).

In *Anostomoides*, *Anostomus*, *Gnathodolus*, *Hypomasticus*, *Laemolyta*, *Leporellus*, *Leporinus*, *Petulanos*, *Pseudanos*, *Sartor*, *Schizodon* and *Synaptolaemus* as well as the examined outgroups, the neural complex of the Weberian apparatus is an anteroposteriorly elongate bone with a distinctly angled dorsal margin angling posteroventrally away from the supraoccipital crest (state 0, Fig. 50). In species of *Rhytiodus* the neural complex retains the form of an elongate triangle, but the bone is rotated so that dorsal margin has a much more gradual slope that is nearly horizontal relative to the main body axis of the fish (state 1, Fig. 51). In *Abramites* the shape of bone is modified relative to state 0, with the posterior portion of the bone developing further dorsally than in other anostomids. The overall shape of the bone in *Abramites* is of an equilateral triangle with a nearly horizontal dorsal margin (state 2, Fig. 52).

The modifications to the neural complex seen in *Rhytiodus* and *Abramites* appear to be correlated with the shifts in overall body morphology that character-

ize the two genera. *Rhytiodus* species are by far the most elongate and fusiform members of the Anostomidae (Fig. 1) while *Abramites* species are deeper bodied than other members of the family (Fig. 2). The more horizontal orientation of the dorsal margin of the neural complex in *Rhytiodus* could be generated by stretching the form of the bone typical for anostomids along the anteroposterior axis. The morphology in *Abramites* could be obtained by a deepening of the more posterior portions of the neural complex concurrent with the increase in the depth of the body in that genus. As such we coded the conditions in *Abramites* and *Rhytiodus* as separate states to refrain from hypothesizing their homology *a priori*.

In the final hypothesis of relationships arrived at herein, the elongate triangular form of the neural complex with a horizontal dorsal margin (state 1) is a synapomorphy for the species of *Rhytiodus* (clade 16). The neural complex in the form of an equilateral triangle is an autapomorphy for the single species of *Abramites* incorporated in this analysis, but may be found to be a synapomorphy for the genus in a future analysis incorporating *A. eques*, the second nominal species in the genus (see Vari & Williams, 1987).

105. *Presence or absence of dorsal process of third vertebra overlapping neural complex laterally:* (0) absent; (1) present (CI = 0.083; RI = 0.607).

A small dorsal process of the third centrum within the Weberian apparatus that barely overlaps the ventral portion of the neural complex is present in *Abramites*, *Anostomoides*, *Schizodon*, *Rhytiodus*, *Hypomasticus megalepis*, *H. mormyrops*, *Laemolyta*



*garmani*, *L. orinocensis*, *L. proxima*, *Leporinus agasizi*, *L. aripuanaensis*, *L. cf. ecuadorensis*, *L. fasciatus*, *L. cf. fasciatus*, *L. friderici*, *L. gomesi*, *L. jatuncochi*, *L. cf. niceforoi* and *L. ortomaculatus*. The process is particularly well developed in the species of *Rhytiodus* and *Schizodon* (Figs 51, 52). The process is absent in the species of *Anostomus*, *Gnathodolus*, *Leporellus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* along with *Laemolyta proxima*, *Hypomasticus despaxi*, *H. pachycheilus*, *Leporinus cf. moralesi*, *L. pellegrinii*, *L. striatus* and *L. tigrinus* (Fig. 50). Among the outgroups such a process is present in *Brycon falcatus*, *Hemiodus ocellatus* and *Prochilodus rubrotaeniatus*. It is absent in the remaining examined outgroups.

Although the evolution of this character on the final phylogenetic hypothesis arrived at herein is homoplastic and ambiguously optimized within the Anostomidae, the character does appear to index considerable synapomorphy. The absence of the process (state 0) is the plesiomorphic condition present in *Leporellus* and the proximate outgroups. Under ACCTTRAN, possession of the process (state 1) is a synapomorphy for clade 3 that is reversed in *Hypomasticus despaxi*, *H. pachycheilus*, *Leporinus cf. moralesi*, *L. striatus*, *Laemolyta proxima* and clade 25 containing *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*. Under DELTRAN, state 1 evolves independently in *Hypomasticus megalepis*, *H. mormyrops* and clade 7, again with reversals to state 0 in *Leporinus cf. moralesi*, *L. striatus*, *Laemolyta proxima* and clade 25.

106. *Presence or absence of supraneural dorsal to Weberian apparatus*: (0) supraneural absent; (1) supraneural present (CI = 0.375; RI = 0.800).

In some species of the Anostomidae, a thin bone lies within the midsagittal plane dorsal to the posterodorsal portion of the Weberian apparatus (e.g. *Leporellus*, Fig. 50). Under the terminology for the bones of the Weberian apparatus suggested by Weitzman (1962), the bone in question, when present, is positioned posterior to the neural complex and slightly anterior to the neural spine of the fourth vertebrae. The positioning of this bone just anterior to a neural spine along the midsagittal plane suggests that the ossification is serially homologous with the supraneural series.

A supraneural positioned above the Weberian apparatus is present in *Anostomus*, *Gnathodolus*, *Hypomasticus*, *Leporellus*, *Petulanos*, *Synaptolaemus*, most species of *Leporinus* and most specimens of *Pseudanos*. No supraneural lies above the Weberian apparatus in *Abramites*, *Anostomoides*, *Laemolyta*, *Rhytiodus*, *Sartor*, *Schizodon* or *Leporinus striatus*. Two species, *Leporinus cf. ecuadorensis* and *Pseu-*

*danos irinae*, are polymorphic for this character. In the case of *Leporinus cf. ecuadorensis*, seven cleared and stained specimens were examined, with the supraneural missing in the largest and two of the smallest examined individuals, present as a tiny cartilaginous ball or rod in two other small specimens, and fully present, although small, in two specimens of intermediate size. Of the two examined specimens of *Pseudanos irinae*, one has a well-developed supraneural positioned dorsal to the Weberian apparatus while the bone is absent in the second individual. Both specimens had been previously extensively dissected and it is possible that the accessory supraneural was lost in the second specimen of *P. irinae* in the course of those dissections. In neither case does either state occur in a clear majority of specimens and both are coded as possessing a polymorphism for this character.

Among the examined outgroups, *Brycon falcatus*, *Citharinus* sp., *Distichodus* sp., *Hemiodus ocellatus* and *Xenocharax spilurus* possess a supraneural above the Weberian apparatus (state 1). *Parodon suborbitalis* as well as all examined members of the proximate outgroups (Chilodontidae, Curimatidae, Prochilodontidae) lack a supraneural or supraneural-like element located dorsal to the Weberian apparatus. Our specimen of *Potamorhina laticeps* (Curimatidae) does possess an odd finger-like dorsal extension from the anterior dorsal margin of the neural complex. We are unsure of the homology of this element (it may simply be an anomaly of the specimen) but based on its more anterior position it is probably not homologous with the supraneural above the Weberian apparatus possessed by some members of the Anostomidae. *Potamorhina laticeps* is coded as possessing state 0.

The supraneural dorsal to the Weberian apparatus was gained and lost several times in the evolution of the Anostomidae. Presence of the supraneural in question optimizes as a synapomorphy for the Anostomidae (clade 1) with subsequent loss occurring in clade 9 (*Abramites* and *Leporinus striatus*) and clade 13. Within clade 13 the ossification is reacquired in clade 25 and again lost in that clade in *Sartor*.

#### RIBS

107. *Presence or absence of two or more intercostal ligaments uniting in total four or more of anterior full ribs*: (0) absent; (1) present (CI = 1.000; RI = 1.000)

As discussed in Vari (1983), anostomids have distinct, anterodorsally aligned intercostal ligaments that join the mid and upper sections of the anterior-most pleural ribs. The ventral-most of these ligaments arises from the posterior margin of the first rib, extends posterodorsally to attachments on the medial margins of the second and third ribs and terminates posteriorly at an attachment on the anterior border of

the fourth rib. A second more dorsally positioned ligament extends between the first and third ribs, with an intervening attachment to the medial surface of the second rib. The described pattern of intercostal ligaments is the least extensive in the family, with some anostomids having increased numbers of ligaments and in some instances a larger number of involved ribs. Although comparable intercostal ligaments also occur in the Chilodontidae (Vari, 1983: 41, fig. 36), the bands in the latter family are limited to only the anterior-most three pleural ribs. Intercostal ligaments were not observed among the outgroups with the exception of the Chilodontidae. In our final reconstruction, possession of two or more intercostal ligaments uniting at least four ribs optimizes as a synapomorphy for the entire Anostomidae (clade 1).

#### DORSAL FIN

108. *Modal number of branched dorsal-fin rays*: (0) eight or nine branched dorsal-fin rays; (1) ten branched dorsal-fin rays; (2) 13 or more branched dorsal-fin rays (CI = 0.667; RI = 0.750).

Characiforms demonstrate a considerable range in the number of branched dorsal-fin rays, with basal groups in the order (Citharinidae, Distichodontidae) having high numbers of rays. Within the Citharinidae, species of *Citharinus* possesses 11–15 branched rays (Daget, 1962b: 84) and *Citharidium* 13–15 branched rays (Daget, 1962a: 506). Within the Distichodontidae, *Xenocharax* possesses 14–18 branched rays (Daget, 1960: 32), *Paradistichodus* 12–15 branched rays (Daget, 1958: 1362) and *Ichthyborus* 11–14 branched rays (Daget, 1967: 140). The majority of characiforms, by contrast, have lower numbers of branched dorsal-fin rays. In their discussion of a subgroup of the Characidae, Malabarba & Weitzman (2003: 82) noted that eight or nine branched dorsal-fin rays were typical for that group. This condition was observed in the outgroups in *Brycon* (Weitzman, 1962: fig. 16), *Hemiodus ocellatus* (Vari, 1982a), *Curimatopsis microlepis* (Vari, 1982b), *Curimata inornata* (Vari, 1989b) and all examined members of the Chilodontidae. In contrast, all members of the Anostomidae possess (other than in a few individuals) a tenth set of pterygiophores and a tenth branched dorsal-fin ray (state 1). Among the examined outgroups ten branched dorsal-fin rays also occur in *Parodon suborbitalis* (Pavanelli, 1999) and *Semaprochilodus insignis* (Castro & Vari, 2004). *Potamorhina laticeps* and *Prochilodus rubrotaeniatus* are polymorphic for this character, with nine or ten branched dorsal-fin rays present in *Potamorhina laticeps* (Vari, 1984) and seven to ten branched dorsal-fin rays present in *Prochilodus rubrotaeniatus* (Castro & Vari, 2004).

Although constant within the Anostomidae, this character is ambiguously optimized among the out-

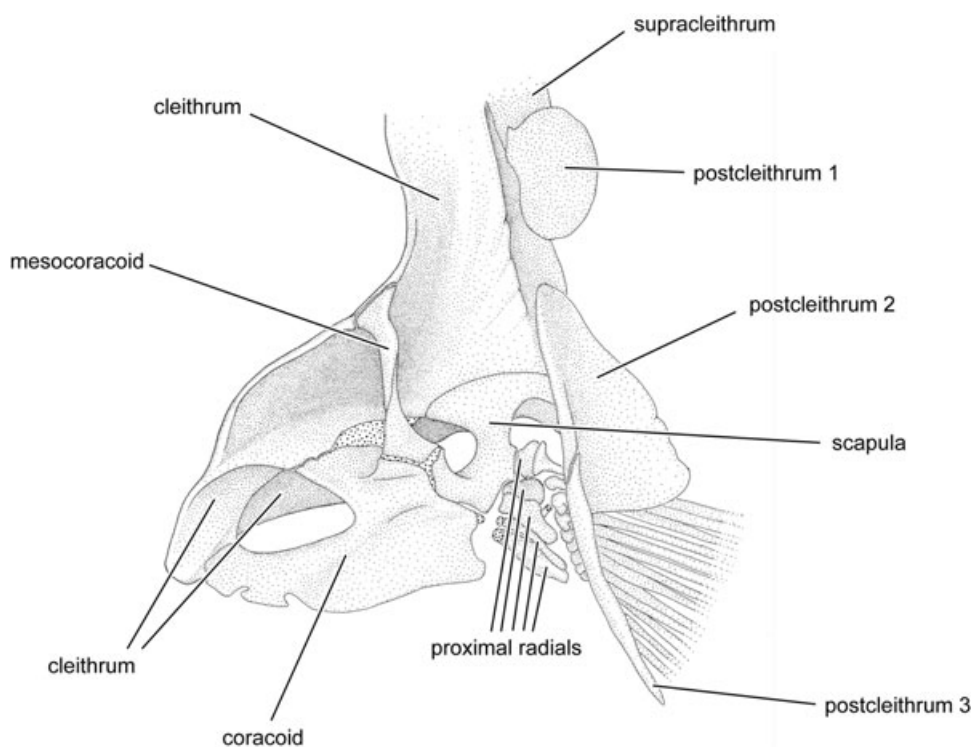
groups in our final phylogenetic hypothesis. Under DELTRAN the possession of ten branched dorsal fin rays (state 1) is a previously undocumented synapomorphy for the Anostomidae (clade 1) with independent evolution of character state 1 in elements of the Curimatidae, Prochilodontidae and Parodontidae. Under ACCTAN state 1 evolves in the common ancestor of the Anostomidae, Curimatidae, Chilodontidae, Parodontidae and Prochilodontidae with reversal to state 0 in the Chilodontidae and elements of the Prochilodontidae and Curimatidae.

#### PECTORAL GIRDLE

109. *Development of dorsomedial flange of mesocoracoid*: (0) dorsomedial flange of mesocoracoid weakly developed or absent; (1) dorsomedial flange of mesocoracoid very strongly developed (CI = 0.500; RI = 0.833).

All examined members of the Anostomidae exhibit a distinct twist to the mesocoracoid, with the plesiomorphically anteroventral margin of the bone which joins the coracoid rotating to become the posterodorsal margin of the bone where it joins the dorsal margin of the cleithrum. The medial ridge or flange created by this torsion is typically indistinct and small in most anostomids, but in the species of *Schizodon* and most examined specimens of *Abramites hypselonotus*, that flange is very well developed, obscuring much of the lateral portion of the bone in medial view (state 1, Fig. 53). The development of the flange varies within *Abramites* and is independent of the size of the specimen, but the flange is noticeable in all but one examined specimen and very well developed in most individuals. *Abramites* is coded as possessing the flange.

Examined members of the outgroups have untwisted or weakly twisted mesocoracoids [e.g. *Brycon* (Weitzman, 1962: fig. 19)] and lack the pronounced medial flange of the mesocoracoid possessed by the species of *Schizodon* and some specimens of *Abramites*. The degree of torsion of the mesocoracoid appears to be increased in all members of the Anostomidae relative to the outgroup condition and is a possible synapomorphy for the family. That character, however, is difficult to define objectively and is not proposed herein formally as a defining characteristic for the Anostomidae. More importantly, the increase in the development of the dorsomedial flange of the mesocoracoid in *Schizodon* is a synapomorphy for the genus (clade 18). *Abramites* is not the sister group to *Schizodon* under the final hypothesis of relationships, and the increase in the size of the flange in some specimens of *Abramites* is a homoplasy relative to similar condition of that structure in *Schizodon*.



**Figure 53.** Ventral portion of right pectoral girdle and fin of *Schizodon fasciatus*, FMNH 111351, 96.1 mm SL; medial view.

110. *Width of dorsal portion of supracleithrum*: (0) dorsal portion of supracleithrum narrow, lacking distinct flange on dorsal portion of bone running medial to posterodorsal portion of opercle or with flange weakly developed; (1) dorsal portion of supracleithrum broad, with distinct wide flange on dorsal portion of bone running medial to posterodorsal portion of opercle (Autapomorphy).

Members of the Anostomidae typically have a thin flange along the anterior margin of the supracleithrum that runs just medial to the extreme posterodorsal edge of the opercle (e.g. *Leporinus agassizi*, Fig. 14). The development of this flange of the supracleithrum in the Anostomidae varies considerably across the family, with some species (e.g. *Leporellus*, most species of *Leporinus*) possessing very thin flanges, and others (*Schizodon*) possessing distinctly wider flanges about twice as wide as the flange present in *Leporellus*. Variation in the degree of development of the flange is continuous from the condition in *Leporellus* through the condition in *Schizodon* and that full range of variation is coded as state 0 (flange weakly developed). Among the examined species in the Anostomidae, *Abramites hypselonotus* uniquely has a very well-developed flange of the supracleithrum which extends anteriorly medial to much of the posterodorsal margin of the opercle. This well-developed flange results in an

overall dorsally wider, comma-shaped morphology to the supracleithrum from left lateral view (state 1, Fig. 15). The width of this flange in *Abramites* is three or more times the width of that flange in *Leporellus* and distinctly wider than that in *Schizodon* which has the widest form of the flange among the species possessing state 0 for this character.

The examined outgroups with the exception of *Xenocharax* possess flanges of the supracleithrum with widths similar to, or smaller than, that of *Leporellus*. *Xenocharax spilurus* has a somewhat broader form of the bone that is reminiscent of the condition in *Schizodon*. All of the examined outgroups thus meet the definition of state 0 (flange absent or weakly developed) and the condition in *Abramites* is an autapomorphy in the current dataset. There is, however, another valid species of *Abramites* (*A. eques*) from trans-Andean Colombia (Vari & Williams, 1987), and the hypertrophy of the flange of the supracleithrum running medial to the opercle may prove to be a synapomorphy for *Abramites* once *A. eques* is examined osteologically.

#### PELVIC FIN

111. *Modal number of branched pelvic-fin rays*: (0) eight or fewer branched pelvic-fin rays; (1) nine branched pelvic-fin rays (CI = 0.750; RI = 0.857).



A count of one unbranched and eight branched pelvic-fin rays (state 0, nine total elements) is common among members of the Characiformes. A ninth branched pelvic-fin ray (state 1, ten total elements) is present in a subset of the Anostomidae consisting of *Leporinus jatuncochi*, *L. cf. fasciatus*, *L. fasciatus* and *L. tigrinus*. Although not represented among the cleared and stained material, examined material of *Leporinus falcipinnis* from the Rio Orinoco (FMNH 104000), which displays a colour pattern similar to that of *L. fasciatus*, also possesses a ninth branched pelvic-fin ray. Among the proximate examined outgroups, six to eight branched rays occur in *Caenotropus* (Vari *et al.*, 1995) and eight in *Chilodus* (Isbrücker & Nijssen, 1988; Vari & Ortega, 1997). Turning to the second outgroup, there are seven to nine branched pelvic-fin rays in the Prochilodontidae (Castro & Vari, 2004), with basal genera in the Curimatidae (*Curimatopsis* and *Potamorhina*) having six or seven and eight or nine branched pelvic-fin rays, respectively (Vari, 1982b, 1984). A range of six to eight branched pelvic-fin rays is general for all other genera in the Curimatidae with the exception of a subset of species within *Curimata* including *C. inornata* (Vari, 1989b) that have nine branched rays in some individuals. *Potamorhina latior* and *Curimata inornata* are therefore polymorphic for this character. Among more distant outgroups, *Parodon suborbitalis* (Pavanelli, 1999) and *Brycon falcatus* both possess eight branched pelvic-fin rays (state 0), while *Hemiodus ocellatus* and examined members of the Citharinidae and Distichodontidae possess nine branched rays (state 1).

In our final reconstruction, the plesiomorphic condition within the Anostomidae optimizes as the possession of eight or fewer branched pelvic-fin rays, with the possession of a modal count of nine branched pelvic-fin rays a synapomorphy for the group of *Leporinus* species cited above (clade 10). The possession of nine branched pelvic-fin rays in *Potamorhina latior*, a subset of *Curimata* and the examined members of the Citharinidae, Distichodontidae and Hemiodontidae in the outgroups is clearly homoplastic with respect to the similar condition in some species of *Leporinus* under the present concepts of relationships of these taxa (Vari, 1979, 1983, 1989a, b, and results therein).

#### ANAL FIN

112. *Modal number of branched anal-fin rays*: (0) seven or fewer branched anal-fin rays; (1) eight branched anal-fin rays; (2) nine or more branched anal-fin rays (CI = 0.500; RI = 0.444).

Nearly every member of the Anostomidae possesses eight branched anal-fin rays, preceded by one to three

(usually two) unbranched anal-fin rays. Species of *Abramites* have higher branched anal-fin ray counts. *Abramites hypselonotus* possesses 10–12, and *Abramites eques* from the Río Magdalena of Colombia possesses 13 or 14 branched anal-fin rays (Vari & Williams, 1987: 92). *Anostomoides atrianalis* reportedly possesses ten branched anal-fin rays (Santos & Zuanon, 2006: 67). *Schizodon scotorhabdotus* uniquely among the examined Anostomidae possesses only seven branched anal-fin rays.

The branched anal-fin ray count varies widely among the outgroups. Members of the nearest outgroup (family Chilodontidae) possess between seven and ten branched-anal fin rays (Isbrücker & Nijssen, 1988; Vari *et al.*, 1995; Vari & Ortega, 1997). Members of the Curimatidae (e.g. *Potamorhina latior*) possess as many as 12 or as few as seven (e.g. *Curimatella alburna*) rays (Vari, 1984, 1992). Distantly related members of the outgroups in the Characiformes have variable numbers of branched anal-fin rays, with seven branched rays most common in *Parodon suborbitalis* (Pavanelli, 1999), 9–10 rays present in *Hemiodus ocellatus* (Vari, 1982a), 10–13 rays present in *Xenocharax* (Vari, 2007), 10–12 in *Distichodus* (Daget, 1959), 28 or more in *Brycon meeki* (Weitzman, 1962) and 20–31 in the various species of *Citharinus* (Daget, 1962b).

The conditions in *Abramites hypselonotus* and *Schizodon scotorhabdotus* are autapomorphies within the Anostomidae in the current matrix, but the two species of *Abramites* clearly share a derived increased in the number of branched anal-fin rays; a feature that will probably optimize as a synapomorphy for the genus in a future study. The decreased number of rays in *S. scotorhabdotus* may be found to be a synapomorphy of a small group of species in that genus once more taxa are examined.

#### CAUDAL FIN

113. *Form of connection of primary rays of caudal fin*: (0) first four to six principal rays of upper lobe of caudal fin and last four to six rays of lower lobe of caudal fin distinctly separated from each other except for membranous interconnections in adults; rays not thickened or conjoined into rigid plate-like structure in adults; (1) first four to six principal rays of upper lobe of caudal fin and last four to six rays of lower lobe of caudal fin not separated but rather with margins in contact in adults; rays thickened and conjoined into rigid plate-like structure in adults (CI = 1.000; RI = 1.000).

Adults of the examined species of *Schizodon* and *Rhytiodus* possess a remarkable morphology of the caudal fin in which the dorsal four to six principal rays of the dorsal lobe of the fin and the ventral four



to six rays of the ventral lobe of the fin are thickened and conjoined into rigid, plate-like structures (see condition in *Schizodon scotorhabdotus*, Sidlauskas *et al.*, 2007: fig. 2) This condition appears to develop late in ontogeny given that the examined cleared and stained specimens of *Rhytiodus*, which are distinctly smaller than adults, have these caudal fin rays either separate (*R. argenteofuscus*, *R. microlepis*) or only partially conjoined (*R. lauzannei*). The specimens of *Schizodon fasciatus*, *S. nasutus* and *S. vittatus* and the smaller specimens of *S. knerii* demonstrate only a partial connectivity of the rays, with complete connectivity present in the cleared and stained specimens and dry skeletons of *S. scotorhabdotus* and the larger cleared and stained mature adults of *S. isognathus* and *S. knerii* (Sidlauskas *et al.*, 2007). The examination of large-size alcohol-preserved specimens of all of these species of *Rhytiodus* and *Schizodon* leaves no doubt that thickened and tightly connected caudal-fin rays are present in adults of all of the examined species. No other examined species in the Anostomidae or any outgroups possesses the distinct union of the caudal-fin rays comparable with that found in adults of *Schizodon* and *Rhytiodus*.

In his description of *Schizodon jacuiensis*, Bergmann (1988) noted that *S. jacuiensis* lacks the tight connection of the caudal-fin rays that is found in the other species of *Schizodon*. It is difficult to extract much information about the caudal-fin ray morphology from the photograph of the holotype of *S. jacuiensis* included in that publication, but that specimen is surely an adult given its size (234.4 mm SL) and the thickening and tight connection of the caudal-fin rays appears to be either absent or much less pronounced in *S. jacuiensis* contrary to the condition in its congeners. If that is the situation, two scenarios exist. The thickening and conjoining of the caudal-fin rays may represent a synapomorphy for *Rhytiodus* and for only part of *Schizodon*, implying that *Rhytiodus* may be derived from within *Schizodon*. Alternatively, the thickening and conjoining of the caudal-fin rays could represent a synapomorphy for *Schizodon* and *Rhytiodus* that was later lost or secondarily reduced in *S. jacuiensis* or a more encompassing lineage within *Schizodon*.

It is also noteworthy that *Schizodon isognathus* and *S. knerii* display a lesser degree of thickening of the caudal-fin rays than that occurring in some other congeners, although both species have greatly increased ramification of the caudal fin and demonstrate conjoined caudal-fin rays late in ontogeny (Sidlauskas *et al.*, 2007). The ontogenetic onset of the thickening of the caudal-fin rays into a conjoined plate also varies within the genus, with onset relatively early in ontogeny in *S. scotorhabdotus* and comparatively later in *S. isognathus* and *S. knerii*. A

comprehensive examination of all species of *Schizodon* may reveal that state 1 of this character subsumes two distinct conditions: the late onset of eventual moderate thickening and interconnection of the caudal-fin rays such as the condition present in *S. isognathus*, and the early onset of the eventual extensive thickening and tight interconnection of the caudal-fin rays that is typical of *S. scotorhabdotus*. Regardless of whether that is the case, state 1 is a synapomorphy for clade 15 in this reconstruction.

#### SCALES

114. *Squamation of caudal fin*: (0) lobes of caudal fin free of scales; (1) lobes of caudal fin covered with scales (CI = 1.000; RI = 1.000).

Among the examined members of the Anostomidae, only the species in *Leporellus* possess a dense covering of scales over the major portion of both caudal-fin lobes (state 1). In most other species in the family the last transverse scale row overlaps the bases of the caudal-fin rays, but the majority of the surface of the caudal fin is free of scales (state 0). The unscaled condition of the lobes of the caudal fin is found throughout the examined outgroups. Although not coded formally as outgroups in this study, we note that members of *Curimatella* in the Curimatidae possess scaled caudal fins (Vari, 1992: fig. 20).

A host of characters indicate that the Anostomidae and Curimatidae are not closest relatives (Vari, 1983, 1989a; and results herein) and furthermore *Curimatella* is distinctly nested within the phylogeny of the Curimatidae (Vari, 1989a). The evolution of scaled lobes of the caudal fin in *Leporellus* and *Curimatella* is judged to be homoplastic, with the presence of that feature in *Leporellus* a synapomorphy for that genus (clade 2).

115. *Number of lateral line scales*: (0) 64 or fewer scales in complete lateral-line series, including scales overlapping the hypural plate; (1) 76 or more scales in complete lateral-line series, including scales overlapping hypural plate (CI = 0.667; RI = 0.500).

The number of scales along the lateral line, which is a function of the relative size of the scales, varies considerably among the examined members of the Anostomidae. The range extends from as few as 32 scales in *Leporinus gomesi* to as many as 92 scales in *Rhytiodus microlepis* (Géry, 1987: 372). Much of this variation is impossible to parse into discrete character states, but within the Anostomidae there is a large break between the 76 and 89 lateral-line scales found in *Rhytiodus lauzannei* (state 1; Géry, 1987: 372) and the next most numerous lateral-line scale counts within the family [48–56 scales in *Rhytiodus argenteofuscus* (Géry, 1987: 372) and 49–58 in *Laemolyta*

*fernandezi* (Mautari & Menezes, 2006: 32)]. Examination of the proximate outgroups reveals that all species (with the exception of species in the curimatid genus *Potamorhina*) possess 64 or fewer scales in the lateral line (state 0). *Potamorhina*, by contrast, possess 85–110 lateral-line scales, but that genus is nested within the Curimatidae (Vari, 1989a), with that family, in turn, most closely related to the Prochilodontidae (Vari, 1983, 1989a). *Parodon suborbitalis* has a lateral-line series composed of relatively large and therefore fewer scales (state 0) while *Xenocharax spilurus* and *Hemiodus ocellatus* have much smaller and numerous scales [state 1; 63–75 in *Xenocharax spilurus* (Vari, 2007); 88–96 in *Hemiodus ocellatus* (Vari, 1982a)]. Species of *Distichodus* and *Citharinus* vary greatly in lateral-line scale counts (Daget, 1959, 1962b), but we cannot determine the original scale counts of *Distichodus* sp. and *Citharinus* sp. from the cleared and stained material at hand, and the remainders of the lots from which those specimens were prepared were unavailable. *Distichodus* sp. and *Citharinus* sp. were therefore coded as possessing missing data for this character and for pigmentation characters 116–123 below.

Under the reconstruction in this study *Rhytiodus* is deeply nested within the Anostomidae, and that family, in turn, is most closely related to the Chilodontidae (Vari, 1983). The increase in the number of lateral-line scales is judged to be a synapomorphy for *R. lauzannei* and *R. microlepis* (clade 17), and the small scales characteristic of *Potamorhina*, *Hemiodus* and *Xenocharax* are homoplastic with respect to the small scales in the two cited species of *Rhytiodus*.

#### PIGMENTATION

116. *Vertical bands encircling body*: (0) body without vertical bands of at least two scales width completely encircling body; (1) body with vertical bands of at least two scales width, at least some of which completely encircle body (CI = 0.375; RI = 0.600).

Several species in the Anostomidae possess a series of wide transverse bands encircling their bodies, although with those bands becoming much fainter on the abdominal regions. Such examined banded species include *Abramites hypselonotus* (Fig. 2), *Leporinus jatuncochi*, *L. cf. fasciatus*, *L. fasciatus*, *L. tigrinus* and *Synaptolaemus cingulatus* (Fig. 3). *Petulanos plicatus* possesses very thin, irregular, vertical bands that are only one scale wide (Winterbottom, 1980: fig. 15), a pigmentation pattern that is notably different from, and presumably non-homologous with, the pattern of wide bands seen in the six species cited above. *Petulanos plicatus* is consequently not included in state 1. *Leporinus pellegrinii* possesses a series of alternating thick and thin dark vertical bands (see character 117),

but these bands are incomplete ventrally and, thus, assigned to state 0. Colour pattern varies considerably among the examined outgroups but none possesses complete transverse bands encircling the body. Alcohol-preserved material was unavailable for *Citharinus* sp. and *Distichodus* sp., and those two taxa were coded as possessing missing data for characters 116–123, all dealing with pigmentation.

Our final phylogenetic reconstruction suggests that the banded pattern evolved independently in *Abramites*, *Synaptolaemus* and in clade 10 within *Leporinus*, consisting of *L. jatuncochi*, *L. cf. fasciatus*, *L. fasciatus* and *L. tigrinus*. Although skeletal material was not available for *Leporinus falcipinnis*, that taxon possesses the banded colour pattern and extra branched pelvic-fin ray (see character 111) that optimize as synapomorphies for clade 10. Consequently, it is likely that *L. falcipinnis* is also a member of that clade.

117. *Possession and form of dark vertical blotches on lateral surface of body*: (0) lateral surface of body without dark vertical blotches; (1) lateral surface of body with two to five dark, vertical blotches intersecting the lateral-line scale row and continuing dorsal and ventral to the lateral-line scale row (CI = 0.250; RI = 0.700).

Several species in the Anostomidae possess a series of two to five (usually three or four) dark vertical blotches along the lateral surface of body (e.g. *Schizodon scotorhabdotus*, Sidlauskas *et al.*, 2007: fig. 1). In general, the first blotch is located immediately posterior to the opercle, the second ventral to the dorsal fin, the third midway between the bases of the dorsal and adipose fins, and the fourth above the anal fin. This blotched colour pattern differs from the banding pattern described in character 116 in that the dark coloration of the blotches fades out both dorsally and ventrally and does not encircle the body. The dark coloration, furthermore, does not have the form of pigmentation patches with well-defined margins as is the case in the bands in character 116, state 1. The blotched colour pattern differs from the pattern of lateral-line spots described in character 118 in that the blotches extend significantly above and below the lateral-line scale row and frequently have indistinct margins, whereas the spots in state 1 of character 118 are mostly confined to the horizontal row of scales containing the lateral line and have well-defined margins. The blotched pattern is particularly noticeable in some species of *Schizodon* (e.g. *S. fasciatus*, *S. vittatus* and *S. scotorhabdotus*) but also appears, albeit indistinctly, in *Anostomoides laticeps*, *Laemolyta fernandezi* (Mautari & Menezes, 2006: figs 6, 8, 9), *L. orinocensis*, *L. proxima*, *Schizodon knerii* (Sidlauskas *et al.*, 2007: fig. 6B) and the species of

*Rhytiodus* (Fig. 1). We also include the pattern of alternating blotches and thin partial bands seen in *Leporinus pellegrinii* in state 1 [for an illustration of this colour pattern, see the photo of the very similar and possibly conspecific *L. maculatus* in Planquette *et al.* (1996: 149)]. Blotches are absent (state 0) in *Laemolyta garmani*, *L. taeniata*, *Schizodon nasutus*, *S. isognathus* and all examined species in the genera not discussed above, including all examined outgroups.

On the final phylogeny arrived at herein, possession of the blotches (state 1) optimizes as a synapomorphy for clade 12 containing *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon*, *Synaptolaemus* and *Leporinus pellegrinii*. Within clade 12, reversals to state 0 (blotches absent) are synapomorphies for clades 19 (*Schizodon isognathus* and *S. nasutus*) and 21 (*Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptolaemus*). State 1 (blotches present) evolves again as a synapomorphy for clade 24 (*Laemolyta orinocensis* and *L. proxima*).

118. *Presence or absence of lateral-line spots*: (0) lateral-line spots absent; (1) series of one or more dark spots with distinct margins present along lateral-line scale row, each spot approximately one to two scales in height (CI = 0.091; RI = 0.444).

Many species in the Anostomidae possess a series of spots along the lateral-line scale row. Species possessing the spots include *Petulanos* (Winterbottom, 1980: figs 11, 15, 16), *Gnathodolus* (Winterbottom, 1980: fig. 18), *Hypomasticus megalepis*, *H. mormyrops*, *H. pachycheilus*, *Leporinus aripuanaensis*, *L. cf. moralesi*, *L. cf. niceforoi*, *L. cf. ecuadorensis*, *L. friderici* (Fig. 4), *L. gomesi*, *L. ortomaculatus*, *Pseudanos gracilis*, *P. irinae*, *P. trimaculatus* and *Sartor elongatus*. Most of these species possess no more than four distinct, well-separated, round spots, but *Leporinus cf. moralesi* has approximately eight spots partially conjoined to form an irregular lateral stripe. The spots are squarish in *Hypomasticus pachycheilus* and *Leporinus gomesi* contrary to the round spots present in the other species cited above. We considered the differences in spot shape between these last three species and those with the round form common in many anostomids insufficient to merit the creation of additional character states and included all forms of spots in state 1.

Among the outgroups, *Hemiodus ocellatus* and *Brycon falcatus* each possess a single distinct lateral-line spot (state 1), while the remainder of the examined outgroups lack such spots. Although not coded formally, *Caenotropus labyrinthicus* in the proximate outgroup family Chilodontidae frequently displays a single distinct lateral spot just posterior to the opercle

(Vari *et al.*, 1995: figs 17–19). *Ichthyoelephas humeralis* (Prochilodontidae) has a single very dark lateral-line spot (see Castro & Vari, 2004: fig. 29), but in this species the melanophores lie in a fleshy layer above the scale, as opposed to the condition in the Anostomidae and *Caenotropus* in which the melanophores lie beneath the scale layer, and is judged on positional differences *a priori* to be non-homologous with the lateral spots in the Anostomidae. Various other taxa throughout the Characiformes also possess lateral-line spots, and there is little purpose in cataloguing all that variation here.

In the final hypothesis of relationships arrived at herein, the presence of the spots along the lateral line optimizes as a synapomorphy for clade 3 that is reversed four times within clade 8. One reversal occurs in *Leporinus agassizi*, another in clade 9 (*Abramites* and *Leporinus striatus*), another in clade 10 (*Leporinus fasciatus*, *L. cf. fasciatus*, *L. jatuncochi* and *L. tigrinus*) and the last in clade 12 (*Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Leporinus pellegrinii*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon* and *Synaptolaemus*). Various potential resolutions of the polytomy within clade 8 would indicate that some of the above losses of lateral-line spots are not independent. Within clade 12, spots evolve again as a synapomorphy for clade 26 linking *Pseudanos gracilis*, *P. trimaculatus* and *P. irinae*. Under ACCTRAN another gain of spots is a synapomorphy for clade 29 (*Gnathodolus*, *Petulanos*, *Sartor*, *Synaptolaemus*) with a reversal in *Synaptolaemus cingulatus*. Under DELTRAN lateral-line spots are independently evolved synapomorphies for *Petulanos* and clade 32 containing *Gnathodolus* and *Sartor*.

119. *Presence or absence of dark spots above and below lateral line*: (0) no large dark spots on lateral surface of body, or if large dark spots present then all centred along lateral-line scale row; (1) lateral surface of body of adults with large dark spots located above and below lateral-line scale row (CI = 0.250; RI = 0.000).

Some of the species in the Anostomidae that possess a series of spots along the lateral-line scale row (see character 118) also have distinct spots above and below the lateral line (state 0). Many species of *Leporinus* display this colour pattern as juveniles (e.g. *L. friderici*), but the only species in the dataset that demonstrate this pattern as adults are *Hypomasticus megalepis*, *H. pachycheilus*, *Leporinus gomesi* and *L. ortomaculatus*. None of the examined outgroups possesses spots above and below the lateral line, although in the proximate outgroup family Curimatidae, *Curimata vittata* (not formally coded) does possess a few spots on the dorsal portion of the body



as juveniles, with certain individuals of the species retaining one or more such spots as adults (Vari, 1989b: figs 18, 19). This condition differs considerably from the pigmentation pattern in the species of *Hypomasticus* and *Leporinus* cited above.

None of the four cited species with spots above and below the lateral line are sister species in the arrived at phylogeny and this character is completely homoplastic on the final phylogeny. A pattern of spots above and below the lateral line may serve as a synapomorphy for small groups of *Leporinus* species once additional taxa are added to a future phylogenetic analysis.

120. *Presence or absence of complete dark stripe along lateral-line scale row*: (0) complete stripe along lateral line absent; (1) complete stripe of approximately height of one scale or greater running along lateral line from opercle to caudal peduncle in majority of examined specimens (CI = 0.091; RI = 0.474).

Many species in the Anostomidae possess a dark lateral stripe running along the lateral-line scale row from the opercle to the caudal peduncle. In some species this stripe is dark [*Anostomus anostomus* (Winterbottom, 1980: fig. 3), *A. ternetzi* (Winterbottom, 1980: fig. 17), *Hypomasticus despaxi*, *L. striatus*, *Pseudanos winterbottomi* (Sidlauskas & Santos, 2005: fig. 1), *Schizodon isognathus*, and all examined species of *Laemolyta*]. Other species have the stripe varying in intensity among examined individuals or being occasionally absent (*Rhytiodus argenteofuscus*, *Schizodon nasutus*, *S. knerii* and *S. scotorhabdotus*). Although typically present, the stripe is particularly faint in *Anostomoides laticeps* and *Leporellus*. Nonetheless, in all of these species the stripe, when present, is continuous from the opercle to the caudal peduncle and all are coded as state 1. *Leporinus agassizi* and *Schizodon vittatus* have incomplete lateral stripes that always fall short of the opercle anteriorly, and these three species are coded as state 0. The remaining examined species in the Anostomidae consistently lack any indication of a lateral stripe. The lateral stripe in the examined specimens of *Rhytiodus argenteofuscus* is rather prominent in smaller individuals, but very faint in larger specimens. We should note that the only fully adult specimens of this species that we examined had long been in preservative with much of their dark pigmentation faded or absent. Santos (1980: fig. 13), illustrated a 270-mm SL *Rhytiodus argenteofuscus* that he identified as an adult and which has a definite midlateral stripe. Consequently, the species is coded as state 1 (stripe present).

Among the examined outgroups, *Caenotropus maculosus* and *Chilodus punctatus* in the immediate outgroup have complete lateral stripes (state 1; Isbrücker

& Nijssen, 1988: fig. 1; Vari *et al.*, 1995: figs 12–17). *Caenotropus mestomorgmatos* possesses a very thin, but complete lateral stripe (Vari *et al.*, 1995: figs 9, 10), which is coded as 0 due its narrowness. *Parodon suborbitalis* also possesses a distinct lateral stripe. The remaining members of the outgroups are all coded as 0, although some other members of the Curimatidae do possess thin, deep-lying lateral stripes of varying degrees of completeness that, nonetheless, fail to meet the criteria for state 1.

According to the final phylogeny, optimization for this character at the base of the Anostomidae is unclear. Either state 1 is a synapomorphy for clade 2 (*Leporellus*) or state 0 is a synapomorphy for clade 3, containing the remaining species in the Anostomidae. Within clade 3, state 0 is the plesiomorphic condition, with a lateral stripe (state 1) acquired independently in *Hypomasticus despaxi*, *Leporinus striatus* and clade 13. Within clade 13, clades 17 (*Rhytiodus lauzannei* and *R. microlepis*), 20 (*Schizodon fasciatus* and *S. vittatus*), 26 (*Pseudanos gracilis*, *P. trimaculatus* and *P. irinae*) and 29 (*Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*) have secondarily lost the lateral stripe.

121. *Presence or absence of longitudinal stripes located dorsal and ventral to lateral-line scale row*: (0) longitudinal stripes absent or only single stripe present along lateral-line scale row; (1) one or more longitudinal stripes present dorsal and ventral to lateral-line scale row (CI = 0.333; RI = 0.333).

Four of the examined species in the Anostomidae, *Anostomus anostomus* (Winterbottom, 1980: fig. 1), *A. ternetzi* (Winterbottom, 1980: fig. 17), *Hypomasticus despaxi* and *Leporinus striatus*, possess prominent dark stripes located dorsal and ventral to the lateral-line scale row. The remaining species in the Anostomidae as well as all examined outgroups lack these stripes, with the possible exception of *Parodon suborbitalis*, which has stripes above but not below the lateral line. Because it lacks stripes ventral to the lateral line, *Parodon suborbitalis* does not meet the definition of state 1 above and the species is coded as possessing state 0.

Winterbottom's (1980: 55–56) hypothesis that the densely striped pattern is a synapomorphy for *Anostomus anostomus*, *A. brevior* (Winterbottom, 1980: fig. 10) and *A. ternetzi* is corroborated by the final phylogeny, in which the presence of longitudinal stripes dorsal and ventral to the lateral line is a synapomorphy for clade 28, our concept of *Anostomus*. Based on their considerable separation in the final phylogenetic hypothesis arrived at herein, the stripes in *Anostomus* are derived independently from the similar conditions in *Hypomasticus despaxi* and *Leporinus striatus*.



122. *Presence or absence of small dark spots positioned at centres of scales*: (0) centres of scales same colour as, or lighter than, scale margins; no series of small dark spots along centre of each scale row; (1) most scales with small, dark spot lying under scale creating overall appearance of row of such spots along centre of each scale row; (2) small number of scales with small dark spot on lateral surface of scale, creating impression of rows of spots along centre of each scale row, but with such pigmentation limited to small patches of scales (CI = 0.286; RI = 0.375)

As noted by Winterbottom (1980: 54), some species in the Anostomidae possess a small dark spot lying beneath each scale, thereby creating the appearance of a row of small spots running down the centre of each scale row. *Pseudanos gracilis*, *P. irinae* (Winterbottom, 1980: fig. 21) and *P. winterbottomi* show the pattern most clearly (see Sidlauskas & Santos, 2005: fig. 1 for condition in *P. winterbottomi*), but the rows of spots also appear in the Anostomidae in *Leporellus vittatus* and *Anostomus anostomus*. The dark stripes present along the flanks of *A. anostomus* partially mask the small spots at the scale centres. All of these species are coded as state 1. The scale centres of *Pseudanos trimaculatus* are much lighter in colour than the scale edges and that species is assigned state 0. A few scales on some examined individuals of *Hypomasticus pachycheilus* possess dark spots on the scales, but in none of the examined specimens of that species do these spots form distinct rows over most of the body. *Hypomasticus pachycheilus* is coded as lacking the spots (state 0). *Leporinus gomesi* has a unique pigment pattern in which the external surfaces of some scales possess a dark patch of melanophores. Scales with this pigmentation are arranged into patches and give the impression of dark lines along the scale centres, but with the dark pigmentation limited to these patches of scales and not continuous along the scale row. Furthermore, the pigmentation on the scale centres of *L. gomesi* lies lateral to the rest of the body pigmentation and superficial to the scale itself. In *Pseudanos irinae*, *P. gracilis*, *P. winterbottomi*, *Anostomus anostomus* and *Leporellus vittatus* the dark pigmentation at the scale centres lies beneath the scales. The condition in *Leporinus gomesi* is sufficiently distinct that we code it as the autapomorphic character state 2.

All examined members of the closest outgroup to the Anostomidae, the Chilodontidae, possess dark spots on each scale which are arranged into rows (Isbrücker & Nijssen, 1988; Vari *et al.*, 1995; Vari & Ortega, 1997). *Caenotropus labyrinthicus*, *C. mestomorgmatos* and *Chilodus punctatus* are all coded as state 1. The other examined outgroups lack a small spot of pigmentation on each scale and are assigned state 0 for this character.

Under this phylogenetic reconstruction, this character is ambiguously optimized and necessitates six transitions between states 0 and 1. Under ACCTRAN, the spots are a synapomorphy for the clade containing the Anostomidae and Chilodontidae that is lost in clade 3, which contains all genera in the Anostomidae except *Leporellus*. The spots then recur as a synapomorphy for clade 25 (*Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*) that is reversed in *Pseudanos trimaculatus*, *Anostomus ternetzi* and clade 29, containing *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*. Under DELTRAN, the spots evolve independently in the Chilodontidae, *Leporellus*, *Anostomus anostomus*, *Pseudanos winterbottomi*, *P. gracilis* and *P. irinae*.

123. *Striping of caudal fin*: (0) caudal fin without wide, dark stripes extending across much of each lobe; (1) caudal fin with wide dark stripes extending across much of each lobe; stripe(s) of dorsal lobe run from anterodorsal to posteroventral; stripe(s) of ventral lobe run from anteroventral to posterodorsal (CI = 0.500; RI = 0.500).

Species of *Leporellus* uniquely within the Anostomidae possess one or more wide dark stripes extending across most of the caudal-fin lobes (see Géry, 1977: 153). A similar pattern also occurs in the species of *Semaprochilodus* within the outgroup family Prochilodontidae (see Castro & Vari, 2004: figs 62, 67, 68). Some examined specimens of *Rhytiodus argenteofuscus* have the longest principal ray of both caudal-fin lobes darkly pigmented; in other specimens of this species the caudal-fin lobes are hyaline. It is unclear whether the variation in the pigmentation of the caudal fin lobes in *Rhytiodus argenteofuscus* reflects regional or ontogenetic variation within a single species, the presence of multiple cryptic species, or variation in preservation quality. Regardless of the cause of that variation, the orientation of the bars of dark pigmentation on the caudal fin of *Rhytiodus argenteofuscus* runs perpendicular to the alignment of the bars present in *Leporellus* and the two conditions are clearly non-homologous. Several outgroup species have various pigmentation patterns on the caudal fin (e.g. a crescent-shaped mark in *Brycon falcatus*), but none of these other than the species of *Semaprochilodus* has markings resembling those in *Leporellus*. Under the final reconstruction arrived at herein, the presence of dark stripes extending across the lobes of the caudal fin is a synapomorphy for *Leporellus* (clade 2).

#### UNUTILIZED CHARACTERS

In the course of the analysis, we revisited various characters proposed by previous researchers as infor-

mative as to phylogenetic relationships among the examined outgroups, within the Anostomidae, or within Winterbottom's (1980) concept of the Anostominae, the clade formed by *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus* in this study. The reanalysis based on more extensive series of specimens and a more encompassing group of taxa of the Anostomidae raised questions about the utility of some of these features or the feasibility of using them in this study for various reasons. Such characters and the perceived problems with their utilization are discussed below. Characters are numbered sequentially with a leading 'U' and follow the sequence of discussion of body systems in the preceding sections.

*U1. Degree of curvature of anterior tip of mesethmoid*

Winterbottom (1980) cited a hooked morphology of the anterior tip of the mesethmoid as a synapomorphy for *Petulanos intermedius*, *P. plicatus* and *P. spiloclistron*. We found that several other anostomids possess a much more pronounced hook in this region (state 1 of character 15), and that the slightly ventrally inclined morphology of the mesethmoid in *Petulanos* fits well within our definition of character state 0 for character 15 (mesethmoid anteriorly or anteroventrally aligned and without strong hook).

*U2. Presence or absence of lateral mesethmoid wings*

Vari (1979: 277) cited the lack of a lateral triangular 'wing' or process on the supraethmoid (= mesethmoid) as a synapomorphy uniting the outgroup families Citharinidae and Distichodontidae. Vari also noted that this process is also 'lacking in many characoids with an elongate skull'. Although we do not dispute the lack of such a process in the Distichodontidae and Citharinidae, neither did we observe such a process among the taxa included in this study [with the possible exceptions of *Parodon* and *Brycon*, see Weitzman (1962: fig. 2)]. The lateral processes of the mesethmoid observed in *Hypomasticus* that insert into a premaxillary fossa (see character 16) are more anteriorly placed than the processes in *Brycon* and *Parodon*, and the overall morphologies of the mesethmoid and premaxilla in these genera are very different. We do not consider the processes in *Hypomasticus* to be homologous with the conditions in *Brycon* and *Parodon*. As such this character is not informative relative to the relationships among the examined outgroups or within the Anostomidae and it was excluded from analysis.

*U3. Presence or absence of mesethmoid spine*

Vari (1979: 277–278) cited the absence of a simple supraethmoid (= mesethmoid) spine as a synapomorphy for the Distichodontidae and Citharinidae. We

found alternative states within this character objectively difficult to define, as some members of the Distichodontidae (e.g. *Distichodus niloticus*, Vari, 1979: fig. 6C) possess a distinct anteromedial point on this bone (albeit, as part of an unusual trifurcate morphology of the anterior margin of the mesethmoid) while other have blunt anterior margins. There is considerable variation in the width and morphology of the mesethmoid among the other outgroup families and distinct character states are consequently difficult to define across that spectrum. All examined anostomids appear to possess an anteriorly tapered or pointed mesethmoid (Fig. 28, for example) and this character is not informative within the Anostomidae. This character may be informative among the outgroups, but given the difficulties in coding it, we elected to exclude it from this analysis.

*U4. Degree of development of wing of lateral ethmoid*

Winterbottom (1980: 51–52) considered a 'very well-developed lateral ethmoid' to be a synapomorphy of the species of *Pseudanos*. Leaving aside the difficulty in defining degree of development in this region, we were unable to quantify the development of the lateral ethmoid in *Pseudanos* as any more or less developed than is the form of that bone typical of other members of the Anostomidae. Winterbottom's discussion of this character is linked to his discussion of the presence or absence of a notch in the anterior edge of the lateral ethmoid. Character 25 above encodes that variation.

*U5. Presence or absence of groove in posterior surface of supraoccipital to receive neural complex of Weberian apparatus*

Winterbottom (1980: 52) cited an absence of a vertical groove in the supraoccipital that accommodates the anterior portion of the neural complex of the Weberian apparatus in other anostomids as a synapomorphy for *Pseudanos*. Re-examination of Winterbottom's *Pseudanos* specimens and other material of the genus revealed a shallow groove in this region. The character is therefore invariant across the family.

*U6. Breadth of supraoccipital sulcus*

According to Winterbottom (1980: 52), the species of *Pseudanos* have a narrower supraoccipital sulcus than do other members of the Anostomidae. He also indicated the presence of a bony rim to the sulcus in *Pseudanos* that is absent in other anostomids. When we considered the full spectrum of variation across the family, we were unable to identify unequivocally a difference in the rim of the sulcus in *Pseudanos* with respect to other anostomids and were unable to parse

variation in the breadth of the sulcus into discrete states.

*U7. Presence or absence of exoccipital–intercalar ridge*

Winterbottom (1980: 52) cited the presence of a distinct ridge of bone on the exoccipital between the vagus foramen and the intercalar as a synapomorphy for *Anostomus* (including *Petulanos*), *Synaptolaemus*, *Gnathodolus* and *Sartor*. The ridge is particularly well developed in *Synaptolaemus*, clearly present in *Gnathodolus* and *Sartor*, and clearly absent in many basal genera such as *Leporellus*, *Leporinus* and *Anostomoides*. We had difficulty, however, in unequivocally confirming the presence of the ridge in the species of *Anostomus* and *Petulanos* and were unable to delimit consistently the presence or absence of the ridge in *Pseudanos*. In light of the difficulty in coding the feature objectively, we elected to exclude it from our analysis.

*U8. Angle of pterosphenoid–orbitosphenoid joint*

According to Winterbottom (1980: 52), the joint between the orbitosphenoid and pterosphenoid is more anteriorly aligned in *Anostomus*, *Gnathodolus*, *Sartor* and *Synaptolaemus* than in other anostomids. He admitted that the character is 'difficult to quantify', and in our examination of material from across the family we found it impossible to recognize discrete states in the angle between those bones. Thus, we deferred from utilizing the character.

*U9. Degree of development of ventral flange of parasphenoid*

Winterbottom (1980: 52) cited the increased development of the ventral flange of the parasphenoid as a synapomorphy for *Anostomus* (including *Petulanos*), *Gnathodolus*, *Pseudanos*, *Sartor* and *Synaptolaemus*. Examination of additional material from across the Anostomidae revealed that the degree of development of this flange actually varies considerably and continuously across the family, with the extent of the flange apparently increasing late in ontogeny. Winterbottom (1980: 55) also suggested that the very great development of the flanges on the vomer and parasphenoid are jointly a synapomorphy for *Gnathodolus* and *Sartor*. We agree that these species have very strong development of the flanges, but those structures in *Synaptolaemus* are scarcely less developed and a complete continuous series of progressively less-developed flanges is found elsewhere in the family. In light of the difficulty in recognizing discrete states and the possible ontogenetic changes in the degree of development of the flanges, we refrained from coding this character.

*U10. Shape of premaxilla*

Mautari & Menezes (2006: 29) considered a wide premaxilla with a recurved upper premaxillary margin and with a fold on its medial ventral margin prolonged as a rounded process to diagnose *Laemolyta*. These authors did not define an alternative character state for this feature and wide premaxillae with prolonged medial folds occur commonly throughout the Anostomidae. In the absence of a clear standard of comparison and based on our examination of a broader diversity of anostomids, we consider the condition of the premaxilla in *Laemolyta* to be fundamentally equivalent to the condition of this bone in all other members of the family.

*U11. Form of lower jaw*

Vari (1983: 10) discussed the foreshortening of the lower jaw in the Anostomidae plus Chilodontidae and again in the Prochilodontidae relative to the Curimatidae and generalized characiform condition (e.g. *Brycon meeki*, Weitzman, 1962) as a homoplasy. Although indeed foreshortened, the overall morphology of the dentary in the Prochilodontidae is significantly modified relative to all other characiforms (see Castro & Vari, 2004) and is not considered to be homologous with the foreshortening typical of many anostomids and chilodontids under present concepts of relationships among these taxa. Furthermore, the elongation and form of the lower jaw varies extensively within the Anostomidae and that variation is encoded within the present data matrix (see in particular characters 57–59). In order to incorporate better the variation in lower jaw shape within the Anostomidae, in our analysis we did not use Vari's (1983) character as originally conceived.

*U12. Presence or absence of protuberance on anteroventral margin of ectopterygoid*

Mautari & Menezes (2006: 29) proposed that the presence of a rounded protuberance on the anteroventral margin of the ectopterygoid is a diagnostic character for the species of *Laemolyta*. We do not dispute the presence of the protuberance, but consider the condition in various other anostomids, including *Schizodon nasutus* and *Anostomoides laticeps*, to be indistinguishable from the condition present in *Laemolyta* (compare Mautari & Menezes, 2006: fig. 2 with fig. 42). Furthermore, the degree of anterior development of the ventral portion of the ectopterygoid exhibits continuous variation throughout the remainder of the family. Therefore, we do not utilize the protuberance of the ectopterygoid as a synapomorphy for *Laemolyta*.

*U13. Shape of mesopterygoid*

Mautari & Menezes (2006: 29) cited an elongated mesopterygoid with a small ventrally directed process



on its lateral surface as a diagnostic character of *Laemolyta*. We are uncertain as to the relative metric used to judge the length of this bone. Although the mesopterygoid in *Laemolyta* is relatively elongate, there is a degree of intrageneric variability in that feature when measured against the posterior limit of the metapterygoid–quadrate fenestra. Furthermore, if we use that landmark for defining the relative length of the mesopterygoid we find that other anostomids would also fit the criterion of an elongate mesopterygoid. As such the relative length of that bone *per se* is not unique to the members of *Laemolyta*. We are uncertain as to the identity of the cited ventral process on the lateral surface of the mesopterygoid. Possibly these authors were referring to the small ventral process on the medial surface of the bone, which is a reduction of the larger ventrally directed process plesiomorphically present in the family (see character 75). We found the reduced medial process to be also present in *Synaptolaemus* and *Anostomus anostomus* and thus not diagnostic for *Laemolyta*.

*U14. Proximity or contact of the palatine and quadrate*

The palatine and quadrate of members of the Anostomidae are typically separated by portions of the ectopterygoid and mesopterygoid to various degrees. Winterbottom (1980: 50–54) proposed that a reduction in the separation between these bones was a synapomorphy for *Anostomus* (including *Petulanos*), *Pseudanos*, *Gnathodolus*, *Sartor* and *Synaptolaemus*, with actual contact between the quadrate and palatine a synapomorphy uniting *Pseudanos irinae* and *P. trimaculatus*. We agree with Winterbottom that the bones are in close proximity in all these species, but the same is true of other anostomids including members of *Laemolyta* and *Anostomoides*. We were unable to identify an obvious break in the continuum in the degree of proximity of these bones across the family. In our material of *Pseudanos irinae* and *P. trimaculatus*, the palatine and quadrate are in close proximity but are not in contact, probably indicating intraspecific variation within those species.

*U15. Presence or absence of autogenous ossification in cartilaginous fourth infrapharyngobranchial*

In their study of *Abramites*, Vari & Williams (1987) hypothesized that an autogenous ossification in the cartilaginous fourth infrapharyngobranchial might be a synapomorphy for the two recognized species of *Abramites* in light of the absence of that structure in the examined outgroup genera in the Anostomidae. In the more inclusive examination of cleared and stained anostomids in this study we discovered that the character has a much broader distribution, being found not only in *Abramites*, but also in *Leporinus striatus*,

*Anostomus anostomus*, *Schizodon fasciatus*, one side of a specimen of *Anostomus ternetzi*, both sides of one of two examined specimens of *Leporinus ortomaculatus*, and both sides of one of two examined specimens of *Laemolyta orinocensis*. Given the variability in the presence of the ossification within genera, species or even a single specimen, we did not include the character in the phylogenetic data matrix.

*U16. Presence or absence of posterior process on lateral-most branchiostegal ray*

Winterbottom (1980: 51) reported that a posterior process is present on the ‘last’ (lateral-most) branchiostegal ray in all anostomids except *Gnathodolus*, *Sartor* and *Synaptolaemus*. We find instead that the presence, absence and degree of development of the process vary considerably intraspecifically and appear to be correlated with ontogeny. As the age and size of our examined specimens was not standardized, we excluded this variation from analysis.

*U17. Angle of joint between anterior and posterior ceratohyals*

Winterbottom (1980: 51) cited an increased angle between the anterior and posterior ceratohyals (the epihyal and ceratohyal of that study) as a synapomorphy for the species of *Anostomus* (including *Petulanos*), a clade that was not recovered in this analysis. Although the species in *Anostomus* and *Petulanos* undeniably possess a distinctly inclined joint between those bones, similar angles relative to the long axis of the hyoid bar occur in species of other anostomid genera (*Leporellus*, many species of *Leporinus*, *Synaptolaemus*). Although some other taxa possess an essentially vertical joint between these bones (e.g. *Schizodon*, *Abramites*), a continuum exists between the deeply inclined and vertical endpoints rendering it impossible to parse that variation into discrete states across the Anostomidae. Two related characters (97 and 98, dealing with the length of the dorsal margin of the anterior ceratohyal and the presence of a ventral process on that bone) were discovered to be informative at more restricted levels within the Anostomidae.

*U18. Width of dorsal portion of neural complex*

Winterbottom (1980: 52) indicated that the dorsal portion of the neural complex within the Weberian apparatus is wider in *Pseudanos* than in other examined anostomids. We had difficulty determining how Winterbottom measured the bone, but found no objective difference in our taxonomic sample between the width of the neural complex in *Pseudanos* and that of the other anostomids, some of which Winterbottom (1980) indicated possessed a rod-like morphology of the bone. *Rhytidodus* and *Abramites*, alternatively, do



possess distinct morphologies of the neural complex (see character 104).

*U19. Form of extrascapular canal*

In the typical characiform condition, as in *Brycon meeki* (Weitzman, 1962: 42, fig. 9) and *Xenocharax* (Daget, 1960: fig. 7), the extrascapular has a tripartite sensory canal with one canal leading posteroventrally to the canal running within the posttemporal, one communicating dorsally with the canal system of the parietal, and one leading anteroventrally to the canal system of the pterotic. Vari (1983: 36) indicated that possession of a quadripartite extrascapular canal system is a synapomorphy for members of the Anostomidae. Indeed, other than for one side of the single examined specimen of *Petulanos intermedius* and one specimen of *Hypomasticus mormyrops*, the extrascapular in all anostomids has an additional posteriorly directed canal branch extending over the posttemporal and apparently continuing into the soft tissue of the surface of the body in the region dorso-lateral to the Weberian apparatus. This results in an overall shape to the canal system resembling the Greek capital letter Π. Similar conditions were, however, observed in *Curimatopsis microlepis*, *Brycon falcatus* and *Distichodus* sp., while quadripartite canal systems with different geometries were observed in the examined members of the Prochilodontidae and in *Hemiodus ocellatus*. As such, a quadripartite canal of the extrascapular appears to have a broad, albeit irregular, distribution across the Characiformes and as such is questionably synapomorphic for the Anostomidae. As the character is essentially invariant within the Anostomidae, neither was it informative as to phylogenetic relationships within the family, and the character was not formally coded and included in analysis.

*U20. Form of joint of mesocoracoid with scapula and coracoid*

Winterbottom (1980: 53) reported that the mesocoracoid in *Pseudanos* is joined equally to the scapula and coracoid, whereas it is joined primarily to the coracoid in all other anostomids. In all our examined material, including that of *Pseudanos*, the mesocoracoid is joined primarily to the coracoid (Fig. 53). There may be a polymorphism within *Pseudanos* not revealed by our specimens. Such a polymorphism, if present, would not be appropriate to utilize in the analysis.

*U21. Form of pelvic bone*

Vari (1979: 311) indicated that a bifurcate anterior process of the pelvic bone is a synapomorphy uniting the Citharinidae and Distichodontidae. He also acknowledged that 'a somewhat bifurcate pelvic bone also occurs in various Neotropical characoid groups'

(Vari, 1979: 311), although he considered the Neotropical groups to have less extreme bifurcation. We discovered considerable variation in the extent of bifurcation of this bone among the species utilized herein and could not objectively define distinct character states for the extent of the bifurcation. As such, we excluded this character.

*U22. Presence or absence of foramen in hypural 1*

Winterbottom (1980: 53) cited the presence of a foramen in hypural one as a synapomorphy of *Petulanos plicatus*, *P. intermedius* and *P. spiloclistron*. Such an opening is, however, only variably present in our material of *Petulanos* (*P. spiloclistron* not examined) and irregularly occurs in some specimens of other species (e.g. *Leporinus fasciatus*, *Laemolyta garmani*). In light of the considerable intraspecific variation in the presence versus absence of such a foramen, we excluded this character from the analysis.

*U23. Presence or absence of enlarged lamina of bone on anterior face of neural spine of preural centrum 2*

Winterbottom (1980: 55, fig. 67) noted that the species of *Anostomus* (including *Petulanos*, a clade not recovered in this study) had a distinctive broad lamina on the anterior face of the neural spine of the second preural centrum. Our comparative studies confirm the presence of that process in the species of *Anostomus* and *Petulanos*, but also found the extent of the lamina to vary intra- and interspecifically, with a broad lamina also present outside of *Anostomus* and *Petulanos* in various other members of the family (e.g. *Rhytiodus microlepis*, *Leporellus vittatus* and *Hypomasticus pachycheilus*). In light of the broader distribution of the feature beyond *Anostomus* and its intraspecific variation, we deferred from utilizing this character in the phylogenetic reconstruction.

*U24. Location of olfactory lobe*

Vari (1979: 322–323) discussed an anterior shift of the olfactory bulb relative to the typical characiform condition as a synapomorphy for the Distichodontidae plus Citharinidae, albeit with convergent occurrence in *Salminus*, the Parodontidae and 'some African characids' (= members of the Alestidae *sensu* Zanata & Vari, 2005). We do not dispute that conclusion, but formal evaluation of this character would have required an additional set of dissections that were unnecessary to meet the stated goals of this study and which would necessitate materials unavailable at this time. As such, we did not include the character.

*U25. Musculature*

Vari's (1983) monograph on the relationships of the Anostomidae, Chilodontidae, Curimatidae and

Prochilodontidae included several characters drawn from the musculature of the head. For example, he cited the longitudinally expanded attachment of the hyohyoidei abductores on the urohyal as a synapomorphy for the four family assemblage (Vari, 1983: 47), and the absence of the  $A\omega$  portion of the adductor mandibulae as a synapomorphy for the Anostomidae (Vari, 1983: 51). We do not dispute any of these characters, but evaluating them in this study would have required a parallel set of specimens for muscular dissections. Many of the species examined herein are rare (e.g. *Sartor elongatus*, known only from the type series) and additional specimens of others of the examined species were not consistently available. As a consequence, we were unable to include Vari's (1983) muscular characters in the present analysis.

## DISCUSSION

Overall, this study obtained excellent phylogenetic resolution and the final hypothesis of relationships presented in Figure 5 represents a major advance in the understanding of the evolutionary history of the Anostomidae. With over 120 morphological characters discovered to vary informatively within the Anostomidae and with many nodes in the final phylogeny possessing Bremer support values of three or higher, this analysis demonstrated that, contrary to the arguments of Scotland, Olmstead & Bennett (2003), many informative morphological characters remain unmined and a robust phylogenetic hypothesis can still be formulated on morphological grounds. There is every reason to believe that is also the situation with many other groups of South American freshwater fishes that have not been the subject of a morphology-based phylogenetic analysis, and indeed, many other groups of fishes worldwide.

The list of synapomorphic character state transitions obtained by mapping character states onto the final phylogeny (Appendix 4) revealed that major shifts in jaw position within the Anostomidae occurred nine times. Jaw position for the family is plesiomorphically subterminal (*Leporellus*, *Hypomasticus*), rather than the terminal position more common in characiforms. The superterminal or superior jaws possessed by taxa such as *Gnathodolus* and *Sartor* were revealed to be derived products of many successive morphological shifts in the oral jaws, the anterior portions of the suspensorium and neurocranium and undoubtedly the associated soft tissue systems. The reconstructed transitions in jaw evolution are elaborated upon in a subsequent section.

Much of the discovered morphological variation within the Anostomidae was in the suspensorium (24 characters), oral jaws and associated soft tissues (20 characters), oral dentition (14 characters), and ante-

rior portions of the neurocranium (16 characters) and was largely associated with the nine major shifts in jaw morphology. Other highly variable systems included the infraorbitals (14 characters) and integument (scales and pigmentation, ten characters). Some portions of anatomy were found to be apparently more morphologically conservative within the Anostomidae, including the fins and fin girdles (six characters), Weberian apparatus (six characters) and hyoid arch (three characters). Although the pharyngeal arches and associated dentition and musculature are highly modified in the Anostomidae and its sister clade, the Chilodontidae, relative to other characiforms (see discussion in Vari, 1983: 18–21), those systems are relatively invariant within the Anostomidae (only six characters discovered herein).

The distribution of morphological variation among anatomical systems in the Anostomidae differed strikingly from the distribution of variation in the close outgroups. For example, the Chilodontidae have experienced numerous morphological shifts within the pectoral girdle (Vari *et al.*, 1995), and much of the phylogenetic resolution within the Curimatidae resulted from informative variation in the pharyngeal arches (Vari, 1989a), a system that is nearly invariant within the Anostomidae except for shifts in the degree of development of, and dentition on, the dentigerous tooth-plates. The diverse patterns of phylogenetically informative body systems exemplify the difficulty, or indeed, impossibility of predicting where the greatest concentration of phylogenetically informative characters will lie *a priori*. Morphological phylogenetic analyses should clearly investigate as many anatomical systems as possible.

While homoplasy certainly existed in the dataset (CI for each most parsimonious tree = 0.425) and contributed to the lack of resolution at certain levels, particularly within *Leporinus*, most of the similarity in the dataset could be interpreted as synapomorphy (RI for each most parsimonious tree = 0.805). Characters with high levels of homoplasy (CI < 0.400) occurred in all major anatomical systems, but so did characters that optimized perfectly (CI = 1.000). Nevertheless, some systems interestingly demonstrated greater levels of homoplasy than did others. Many of the characters with high levels of homoplasy within the Anostomidae dealt with tooth morphology and cusping (characters 32, 36, 39), infraorbital morphology (characters 3, 5, 8, 9, 12), presence or absence of elements in the basibranchial series (character 92), branchiostegal series (character 100) or the bones surrounding the Weberian ossicles (character 105) and pigmentation (characters 116, 118, 119, 120, 121, 122). Alternatively, characters involving the neurocranium, suspensorium, oral jaws and opercular series tended to have much lower levels of homoplasy within the

Anostomidae. Despite the commonality of homoplasy, only character 119 (presence or absence of spots above and below the lateral line) had a retention index of 0; every other character indexed some synapomorphy or defined an autapomorphy likely to be a synapomorphy of a small group of species in a future analysis involving increased taxon sampling. Several characters with low CIs had RIs over 0.900 (characters 10, 65, 74), demonstrating that even highly homoplastic characters can be informative about relationships and should be retained in analysis.

#### PHYLOGENETIC RECONSTRUCTION AND SUPPORT

The support for each of the 32 resolved nodes within the Anostomidae (numbered in Fig. 7) is discussed below. The list of synapomorphies diagnosing each node appears in Appendix 4. Reconstructed relationships among the outgroup taxa in this study cannot be taken as well-supported phylogenetic hypotheses. Taxon sampling outside of the Anostomidae was of necessity sparser than within, no effort was made to collect new characters informative about relationships among and within the outgroups, and in the interest of space efficiency, many characters from the literature informative about relationships among species within particular outgroup families were excluded from this analysis. At least one reconstructed outgroup relationship in this study (the apparent clade containing *Curimatopsis* and *Curimata* to the exclusion of *Potamorhina* in the majority rule consensus) is clearly misleading and contradicts the extensive analysis of Vari (1989a), who listed 13 synapomorphies supporting a clade containing *Curimata*, *Potamorhina* and several genera not examined herein to the exclusion of *Curimatopsis*. Those 13 synapomorphies involved characters extraneous to, and not included in, this analysis.

The 17 unambiguous synapomorphies for the Anostomidae recovered by this study combined with the five additional muscular synapomorphies discovered by Vari (1983: 50–51), a bootstrap value of 100 and a Bremer value of 14 leave no doubt that the Anostomidae is monophyletic. Interestingly, seven of the character states listed as synapomorphies for the Anostomidae also occurred in the Prochilodontidae (characters 51, 62, 65, 83, 84, 85 and 134). Vari's previous analysis (1983) concluded that the Anostomidae and Chilodontidae are sister taxa on the basis of 15 synapomorphies. The hypothesis that the Prochilodontidae and Curimatidae are sister taxa was supported originally by 11 synapomorphies (Vari, 1983). In a later paper, Vari (1989a) advanced four additional synapomorphies for this clade and Castro & Vari (2004: 59–60) identified an additional potential synapomorphy for the two-family clade. In light of

the large number of synapomorphies supporting the hypothesis of a sister-group relationship between the Prochilodontidae and Curimatidae, the seven shared derived characteristics of the Anostomidae and Prochilodontidae are considered homoplasies.

Many of the clades recovered in the final phylogenetic hypothesis corresponded to existing genus-level concepts within the Anostomidae. *Leporinus* and *Anostomus*, by contrast, were not found to be monophyletic as currently conceived (Fig. 5) and present nomenclatural issues that are addressed subsequently.

The monophyly of *Leporellus* (clade 2) was strongly supported (bootstrap value = 99, Bremer value = 7) on the basis of eight unambiguous synapomorphies, five of which did not occur homoplastically elsewhere in the Anostomidae. *Leporellus* was reconstructed as the most basal genus in the Anostomidae. Clade 3, containing the remainder of the genera, was also well supported (bootstrap value = 96, Bremer value = 6) with eight unambiguous synapomorphies not shared by *Leporellus*. These synapomorphies included the large antorbital with a horizontal process (character 1), the well-developed ventromedial plate of the mesethmoid (character 18), the ventrally positioned attachment of the primordial ligament on the maxilla (character 49), the narrow ventral portion of the maxilla (character 52), the infilling with a bony plate of the plesiomorphically widely separated posterodorsal and posterior processes of the quadrate (character 76), and the long symplectic (character 87).

Clade 4, which matched Borodin's concept (1929) of the subgenus *Hypomasticus* of *Leporinus* and is herein recognized as the genus *Hypomasticus*, was supported by four unambiguous synapomorphies and had moderate support (Bootstrap value = 80, Bremer value = 2). The synapomorphies that were present at that node (characters 16, 46, 55, 56) were very distinctive, particularly the trough-like ascending process of the anguloarticular possessed by all four species (character 56). A few synapomorphies supported the division of the four species of *Hypomasticus* into two sister-species pairs (clades 5 and 6, two unambiguous synapomorphies each). The evidence linking *Hypomasticus despaxi* and *H. megalepis* (clade 5) was the fusion of the fourth and fifth infraorbitals (character 9) and the reduction from four to three teeth on the premaxilla (character 31), modifications that occurred homoplastically in other anostomids. *Hypomasticus mormyrops* and *H. pachycheilus* (clade 6) have notched second dentary teeth (character 40), possess a block-like form of the ascending process of the premaxilla not seen in any other species (character 47) and have the most strongly downturned mouths of any anostomids.

The basal position of *Hypomasticus* relative to the species traditionally assigned to *Leporinus* and herein



retained in that genus, along with the remaining genera in the Anostomidae (clade 7), was supported by five unambiguous synapomorphies (bootstrap value = 74, Bremer value = 3). Many of the changes occurring at the base of clade 7, including modifications to the maxilla (character 48), ectopterygoid (character 72) and mesethmoid (character 19), contributed to a shift in mouth position from subterminal (*Leporellus*, *Hypomasticus*) to terminal (basal members of clade 7).

Clade 8 contained *Abramites* and the examined species of *Leporinus* except for *L. gomesi* in a large polytomy along with a clade consisting of *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon* and *Synaptolaemus*. Clade 8 received bootstrap support below 50% and a Bremer value of only 1; thus, the implied basal position of *Leporinus gomesi* within *Leporinus* is poorly supported. The source of the polytomy within clade 8, specifically the general lack of a resolution of relationships among the species of *Leporinus*, was not an absence of morphological variation within the genus, but rather the lack of congruence among the characters that did vary within *Leporinus*. For example, four characters optimized as changing states at the branch subtending clade 8, but all four were immediately reversed in one or more of the lineages within clade 8 (but never the same set of lineages). Two of these four synapomorphies for clade 8 deal with the cusping of the premaxillary dentition (characters 32, 33), one involves the number of rows of upper pharyngeal teeth (character 94), and the fourth deals with the presence or absence of a process on the lateral ethmoid directed at the mesethmoid (character 27). Most of the characters that varied within *Leporinus* in clade 8 involved the number of teeth (characters 31 and 36), details of tooth cusping (characters 32, 33, 34) and modifications of the infraorbital series (characters 5, 8, 9). All of the above characters were clearly evolutionarily labile at this level of the phylogeny. Conversely, the bones of the neurocranium, suspensorium and gill arches (excluding the pharyngeal dentition) of members of *Leporinus* were either nearly invariant or exhibited continuous variation that proved impossible to parse into discrete character states. The problem with character state discrimination due to continuous variation is likely to be exacerbated by future increased taxon sampling in this region of the phylogeny. Although additional morphological examination may yield more informative characters within *Leporinus*, morphological signal at this level of the phylogeny appears to be lacking generally. Erection of a robust phylogenetic hypothesis for the bulk of the species of *Leporinus* may require a molecular dataset.

Within clade 8, *Abramites hypselonotus* clustered with *Leporinus striatus* (clade 9) on the basis of nine synapomorphies. *Abramites* is a very distinctive taxon, and if the list of 13 unambiguous character state changes optimizing to the branch subtending *Abramites* is any indication (Appendix 4), *A. hypselonotus* has experienced a high rate of morphological evolution relative to the species of *Leporinus*. That high rate of morphological evolution may explain the low support for its placement as sister to *Leporinus striatus* (Bremer value = 2) relative to the large number of synapomorphies implied by that placement. Many of the apomorphic morphologies possessed by *Abramites* also evolved in a variety of species of other anostomoid genera including *Anostomoides*, *Anostomus*, *Gnathodolus*, *Leporellus*, *Pseudanos*, *Synaptolaemus*, *Leporinus striatus*, *L. cf. ecuadorensis*, *L. cf. moralesi*, *L. jatuncochi* and *L. agassizi* in various combinations. Thus, trees only a few steps longer than the most parsimonious trees include *Abramites* in a variety of placements. Nevertheless, the bulk of the evidence suggests that *Abramites* fits within the grade occupied by the species in the present concept of *Leporinus*.

Three non-homoplastic autapomorphies for *Abramites hypselonotus* were discovered, the neural complex in the form of an equilateral triangle (character 104), the dorsally widened supracleithrum (character 110) and the increased number of anal-fin rays (character 112). These three characters combined with the very deep and compressed body typical of the genus (not coded) suggest that *A. hypselonotus* and *A. eques*, the latter minimally possessing the deep body and high anal-fin ray count present in the former (Vari & Williams, 1987), will form a clade.

The situation in the four species of *Leporinus* in clade 10 (perhaps three, if *Leporinus fasciatus* and *L. cf. fasciatus* are conspecific; see comments in Material and Methods) is less problematic. The placement of this clade within the phylogeny was unclear, but the clade itself was diagnosed by three unambiguous synapomorphies: the possession of nine branched pelvic-fin rays (character 111, a uniquely derived morphology within the Anostomidae), the possession of a banded colour pattern (character 116) and the loss of lateral line spots (character 118). *Leporinus jatuncochi* and *L. tigrinus* clustered (clade 11) on the basis of one unambiguous synapomorphy, a reduction from four to three teeth on the premaxilla.

Clade 12 united one species of *Leporinus* (*L. pellegrinii*) with the remainder of the genera in the Anostomidae (*Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon*, *Synaptolaemus*), although support for this clade was low (Bremer value = 1). There were three unambiguous synapomorphies for the clade, one



dealing with elongation of the cartilage bridging the ventral portion of the metapterygoid–quadrate fenestra (character 80, although note that the same state is also found in three of the four members of clade 11) and two pigmentation characters (117 and 118). The placement of *Leporinus pellegrinii* in clade 12 depends critically upon our *a priori* decision to include the pigmentation pattern of alternating wide and narrow bars in that species in the same character state as the blotched colour pattern found in most species of *Anostomoides*, *Schizodon*, *Laemolyta* and *Rhytiodus* (see discussion of character 117). An alternative coding for that character (i.e. coding *Leporinus pellegrinii* for an autapomorphic character state) would cause clade 12 to collapse.

Resolution within clade 13 was higher than the resolution within clade 8 below the level of clade 13. Clade 13 also included ten of the 14 nominal genera in the Anostomidae but a much lower proportion of the overall species in the family. As a result, the intra-generic taxon sampling within clade 13 was much more complete (approximately 70% of species sampled) than was the taxon sampling in the more species-rich basal portions of the tree (approximately 25% of species sampled). Clade 13 received moderate support in the final reconstruction herein (bootstrap value = 63, Bremer value = 2).

*Anostomoides* in many respects represented a transitional taxon between *Leporinus* on the one hand and *Schizodon*, *Rhytiodus* and *Laemolyta* on the other. *Anostomoides* retained many of the plesiomorphic morphologies also possessed by *Leporellus* and *Leporinus*, including a triangular dentary with the teeth set in line with the joint of the quadrate and anguloarticular (character 58) and a long lateral flange of the quadrate (character 77). *Anostomoides* also possesses several derived morphologies that characterize clade 13, including the ventral repositioning of the retroarticular within the lower jaw (character 65), the vertical elongation of the fourth infraorbital (character 10, although ambiguously optimized due to the inability to code *L. pellegrinii* for that character), the possession of a complete (although faint) pigmented stripe along the lateral line in most specimens (character 120) and the continuously convex posterodorsal margin of the opercle (character 90). The sole examined species of *Anostomoides* (*A. laticeps*) also possesses three distinct morphological attributes that may prove to be synapomorphies of the genus or a species pair within *Anostomoides* when the other two nominal species in that genus are examined osteologically. One of these, the presence of a fenestra in the wing of the lateral ethmoid (character 26), is highly distinctive and only occurs elsewhere in the Anostomidae in *Leporellus*, the species of which have a much smaller form of the fenestra in question.

Clade 14, which linked *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon* and *Synaptolaemus*, had low support (Bremer value = 1). In this clade the dentary teeth became increasingly multicuspid (characters 41, 42) and the structure of the lower jaw and teeth was modified such that the primary cutting edge of the tooth is the distal margin rather than the posterior lamina (character 58). This last character is unambiguously optimized and unreversed on the final phylogenetic hypothesis.

The union of *Rhytiodus* and *Schizodon* in clade 15 was very well supported (Bremer value = 5, bootstrap value = 98) by seven unambiguous synapomorphies: the division of the dentary teeth into anterior and posterior lobes (character 40), the evolution of a very wide bony shelf above the orbit and an overall wide form of the neurocranium (character 30), the evolution of a new pore in the sensory canal of the dentary (character 63), an increase in the number of rows of teeth on the fifth upper pharyngeal tooth-plate (character 94), the conjoining of the caudal-fin rays into a rigid plate in adults (character 113), the poorly developed or absent lamina located dorsal to the sensory canal of the second infraorbital (character 7), and the posterior lobes of the dentary teeth with one or more distinct cusps (character 44). Clade 15 was divided unequivocally into clades 16 and 18, corresponding to existing concepts of *Rhytiodus* and *Schizodon*, respectively.

The monophyly of *Rhytiodus* was supported by six unambiguous synapomorphies (bootstrap value = 92, Bremer value = 3), five of which occurred nowhere else in the Anostomidae. Among these are the thickening of the walls of the sensory canal of the first infraorbital and relocation of that canal lateral to the main lamina of bone (character 6), the distinct depression of the neurocranium (character 29), and a series of unusual modifications of components of the Weberian apparatus (characters 101, 102, 104). Members of *Rhytiodus* also have the most slender bodies of all the members of the Anostomidae (not coded, but see Fig. 1).

Within *Rhytiodus*, *R. lauzannei* and *R. microlepis* formed the well-supported clade 17 (bootstrap value = 99, Bremer value = 3). Clade 17 was supported by three unambiguous synapomorphies: a marked modification to the os suspensorium (character 103), a decrease in scale size (character 115) and the loss of the lateral stripe (character 17).

*Schizodon* (clade 18) was recovered as monophyletic (bootstrap value = 91, Bremer value = 3) on the basis of distinctive morphologies of the oral dentition (characters 33, 41, 42), the expanded width of the anguloarticular (character 55) and a torsion in the medial flange of the mesocoracoid (character 109). *Schizodon isog-*

*nathus* and *S. nasutus* formed clade 19 on the basis of six unambiguous synapomorphies: the horizontal alignment of the ventral process of the mesethmoid (character 17), the reduction from three to two cusps on the first and second teeth of the dentary (characters 41 and 42), the obtuse angle formed by the dentary and the anguloarticular (character 59), the anterodorsal inclination of the ectopterygoid (character 72) and the lack of vertical blotches on the body (character 117). *Schizodon fasciatus* and *S. vittatus* formed clade 20, supported by the possession of an elongate lateral process of the palatine (character 69) and a lack of a stripe along the lateral line (character 120). The relatively low Bremer support for clade 19 relative to the large number of synapomorphies results from three characters implying an alternative sister relationship between *S. isognathus* and *S. knerii* (characters 3, 7, 27). These conflicting hypotheses should be evaluated in a future morphological phylogenetic study including the other described species of *Schizodon*.

Clade 21 contained the species with the most strongly upturned jaws in the Anostomidae (*Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptolaemus*) and was supported by four unambiguous synapomorphies: the presence of a single pore on the ossified portion of the sensory canal of the second infraorbital (character 8), the reduction or elimination of the posterior lamina on the dentary teeth (character 38), the rotation of the premaxilla into a fully horizontal orientation (character 46) and the loss of dark vertical blotches on the sides of the body (character 117). The first and last of these synapomorphies are later reversed, but the synapomorphic states of characters 38 and 46 are maintained throughout clade 21.

As predicted by Winterbottom (1980: 2), *Laemolyta* (clade 22) was sister to the clade formed by the other six genera listed above, which formed clade 25. The monophyly of *Laemolyta* was supported by four unambiguous synapomorphies: the incisiform morphology of the first and second dentary teeth (characters 41–42) and also by the reduction of the posterior flange of the fifth infraorbital (character 11), a modification that occurs homoplastically in *Rhytidodus*, and the presence of an ossified first basibranchial (character 92), an element that appears to have been gained and lost several times in the evolution of the Anostomidae. A fifth character state (the incisiform margin of the third tooth of the dentary, character 43) clearly changed to state zero at the node subtending *Laemolyta*; it is listed as an ambiguous transition due to uncertainty in the ancestral state at the base of clade 21. The support for the monophyly of *Laemolyta* in the final reconstruction (bootstrap value = 81, Bremer value = 2) may be inflated by the decision to code the cusping of the three dentary teeth

closest to the symphysis in three separate multistate characters (41–43), all of which contain transitions that optimize as synapomorphies for this clade. These three characters were needed to recognize substantial informative variation among the dentary teeth in many other genera within the Anostomidae.

Within *Laemolyta*, the examined species were similar to each other except for details of squamation and body shape [mostly uncoded; see Mautari & Menezes (2006) for more information]. Clade 23, containing *L. orinocensis*, *L. proxima* and *L. taeniata*, is supported by an increase to four cusps on the premaxillary teeth (characters 32, 33), while clade 24 containing *L. orinocensis* and *L. proxima* is supported by the presence of indistinct dark blotches on the sides of the body (character 117). Neither of these clades is strongly supported.

Clade 25 (*Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*), which matches Winterbottom's (1980) concept of the subfamily Anostominae, was the best-supported clade within the Anostomidae, with a bootstrap value of 100 and a Bremer value of 13. Thirteen unambiguous and seven ambiguous synapomorphies were recovered for this clade. The unambiguous synapomorphies are: modifications to the infraorbital series (characters 4, 12 and 14), mesethmoid (character 17), vomer (character 21), lateral ethmoid (character 27), maxilla (character 50), palatine arch (characters 67, 72), metapterygoid (character 81), preopercle (character 85), and the bones surrounding the Weberian ossicles (characters 105, 106). Many of these synapomorphies occurred in the anterior portions of the skull (e.g. character 72, the posterodorsal incline of the ectopterygoid, and character 21, the presence of pentagonal raised area of the vomer medial to the articulations with the palatines). These were correlated with the shift of the mouth to a fully superior position more extreme than the supraterminal position of that opening found in *Laemolyta* (Mautari & Menezes, 2006: 29).

Within clade 25, there is a basal trichotomy involving *Pseudanos winterbottomi*, clade 26 containing the remaining species of *Pseudanos* (*P. irinae*, *P. gracilis* and *P. trimaculatus*), and clade 27, containing *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*. The lack of resolution at this level and the low support for clade 26 (Bremer value = 1) stems from significant conflicts among characters informative as to the relationships of the various species of *Pseudanos* to each other and to clade 27 (e.g. characters 25, 28, 53, 79, 100, 118, 120 and 122; see also Sidlauskas & Santos, 2005). The majority rule consensus (Fig. 6) implies that *Pseudanos* may be paraphyletic, with *P. winterbottomi* more closely related to *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus* than it is to the remaining species of

*Pseudanos* (clade 26). At present it is impossible to make a definitive statement.

Laying aside the difficulties related to the placement of *P. winterbottomi*, the monophyly of *Pseudanos trimaculatus*, *P. irinae* and *P. gracilis* [a group matching Winterbottom's (1980) concept of the genus] was supported by three unambiguous synapomorphies. These are the reduction from four to three branchiostegal rays (character 100), the presence of a series of dark spots along the lateral-line scale row (character 118), and the loss of a lateral stripe (character 120). We note that most of the original synapomorphies that Winterbottom (1980) described for this clade were found either to be symplesiomorphies with more basal anostomid genera or to be impossible to code unequivocally in the context of the greater range of variation found among the species examined in this study.

Clade 27, encompassing *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*, was well supported (bootstrap value = 86, Bremer value = 5). Seven unambiguous synapomorphies supported this clade: the repositioning of the antorbital (character 2), the narrow mesethmoid (character 19), the parallel and widely separated articular facets of the vomer with the palatine (character 22), the reduction or elimination of the anterodorsal process of the ectopterygoid (character 71), the repositioning ventrally of the joint between the interhyal, symplectic, hyomandibular and metapterygoid (character 89), the distinct concavity in the posterodorsal margin of the opercle (character 90), and the presence of an ossified first basibranchial (character 92). This clade was also recovered by Winterbottom (1980).

Structure within clade 27 was also well resolved. *Anostomus anostomus* and *A. ternetzi* formed clade 28 on the basis of the shared striped pigmentation pattern (character 121) and the closure of the frontal-parietal fontanel (character 28). *Anostomus* was sister to the well-supported clade 29 (bootstrap value = 90, Bremer value = 4) which contained *Gnathodolus*, *Petulanos*, *Sartor* and *Synaptolaemus*. Synapomorphies of clade 29 included the loss of all but one cusp on the first and second dentary teeth (characters 28 and 29), the increased width of the ventral portion of the maxilla (character 52), the termination of the lateral shelf of the quadrate anteriorly prior to reaching the articular condyle (character 78), the high urohyal (character 99) and the lack of a longitudinal stripe along the body (character 120). The coupling of *Petulanos intermedius* and *P. plicatus* with *Gnathodolus*, *Sartor* and *Synaptolaemus* contradicted Winterbottom's (1980) phylogeny, which hypothesized a clade containing *Petulanos* and *Anostomus* to the exclusion of *Gnathodolus*, *Sartor* and *Synaptolaemus*.

This analysis confirmed the monophyly of *Petulanos* (clade 28) containing *Petulanos intermedius*,

*P. plicatus* and the very similar *P. spiloclistron* (not examined herein). This clade of three species was also obtained, but not named, by Winterbottom (1980). Four unambiguous synapomorphies supported the monophyly of *Petulanos*. Most notable among these was the novel triangular form of the symplectic (character 80) first noted by Winterbottom (1980: 55). The poring patterns of the first and second infraorbitals (characters 5, 8) are also diagnostic for this clade, as is the reduction from three to two of the number of cusps on the symphyseal tooth of the premaxilla (character 32). The Bremer and bootstrap values (4 and 99, respectively) for this clade are high.

Clade 30, containing *Synaptolaemus*, *Sartor* and *Gnathodolus*, appeared as sister to *Petulanos* on the basis of five unambiguous synapomorphies. Two of these were evolutionary novelties within the Anostomidae (character 66: the presence of dermal papillae on the lower lip; and character 86: the triangular process on the ascending arm of the preopercle) and three were reversals (character 14: the sixth infraorbital not posteriorly expanded and entirely separate from the suprapreopercle; character 43: the distal margin of the main lobe of the third tooth of the dentary with only a single cusp; and character 51: the untwisted maxilla)

Lastly, *Gnathodolus* and *Sartor* together formed clade 30 on the basis of four unambiguous synapomorphies: the curvature of the premaxillary teeth (character 35), the hyperelongation of the dentary teeth (character 37), the morphology of the dorsomedial portion of the maxilla (character 54), and the loss of the sensory canal segment in the dentary (character 61). As indicated in Appendix 4, *Synaptolaemus*, *Sartor* and *Gnathodolus* each have a large series of autapomorphies that may be found to be synapomorphies when the other two species of *Sartor* can be examined or if additional species of *Gnathodolus* and *Synaptolaemus* are discovered.

#### CHANGES TO CLASSIFICATION AND COMPARISONS WITH PREVIOUS CLASSIFICATIONS

Following a phylogenetic study, the primary nomenclatural goals should be: (1) to preserve as much nomenclatural stability as possible, especially in cases where additional taxon sampling may alter the phylogenetic reconstruction; and (2) to avoid naming paraphyletic and polyphyletic groups. As discussed below, the existence of two (possibly three) named grades within the Anostomidae in the final phylogeny makes it impossible to fulfil both of these goals. Two choices confronted us: either reducing 12 recognized genera to two (and thereby recognizing almost none of the internal phylogenetic structure in the family by way of genus names), or (2) retaining a genus that is probably



a grade while also preserving the other genus-group names that clearly apply to clades. We have chosen the latter option for the reasons discussed below.

*Leporellus* is well supported and should clearly be maintained. *Leporinus* as it has been recognized by recent authors, by contrast, is the major generic-level nomenclatural problem in the family. The traditional definition of the genus *Leporinus* appears to be a grade-level concept encompassing all of clade 3 except *Abramites* and the ten genera that form clade 13 (note comments regarding *Hypomasticus* below). Due to the basal position of *Leporinus* relative to all other named genera (except *Leporellus*), there is no universally satisfying solution to the quandary of how to reconcile the lack of resolution in the phylogeny with the need to erect stable and biologically meaningful taxon names. Clade 3 could be designated as a genus, in which case all anostomoid genera except *Leporellus* would enter the synonymy of *Anostomus*, the oldest genus name in the family. This action would necessitate major nomenclatural restructuring and necessitate replacement names for some species (e.g. *Schizodon fasciatus*, if placed in the same genus as *Leporinus fasciatus*). Another option would be to create a monophyletic *Leporinus* restricted to clade 10, which contains the type species of the genus, *L. fasciatus*. Such an action would leave the bulk of the species in *Leporinus* in nomenclatural limbo in the absence of the improved phylogenetic resolution and comprehensive taxon sampling necessary to sort them into monophyletic genera. We prefer to leave *Leporinus* largely unchanged in anticipation of a future more resolved phylogenetic hypothesis involving most, if not all, of the species in the genus. If the phylogeny of the species in *Leporinus* can be resolved (perhaps utilizing molecular data), the second option above (a restricted *Leporinus* coupled with the erection of new genera within the previous concept of that genus) becomes a workable solution.

One step in the direction of resolving the *Leporinus* morass can be taken now. The species in Borodin's (1929) nominal subgenus *Hypomasticus* of *Leporinus* form a clade in this reconstruction (clade 4) with a clear external diagnosis (the strongly subterminal mouth not in conjunction with the serrated teeth of *Schizodon*) and a phylogenetic position basal to the rest of *Leporinus*. We elevate *Hypomasticus* to a genus, an action that alleviates some of the paraphyly in the present concept of *Leporinus* and recognizes a clade that is at least as distinctive as many other named genera in the Anostomidae. In addition to the four species examined in this study that are assigned to *Hypomasticus*, radiographs of the holotype of *Leporinus thayeri* (MCZ 20364) and several specimens of *L. julii* (INPA 9508) demonstrate the characters delimiting *Hypomasticus*. A photograph of the holo-

type of *L. garmani* (MCZ 20420), which has had the jaw partially dissected, reveals the strongly downturned mouth and non-serrated teeth that characterize *Hypomasticus*. These three species are also assigned herein to *Hypomasticus*. Resolution of the placement of other *Leporinus* species with somewhat downturned mouths must await the availability of cleared and strained specimens.

*Myocharax* and *Leporinops* are also available as subgenera of *Leporinus*. *Myocharax*, represented in this study by *Leporinus jatuncochi*, is morphologically distinctive, but it clusters inside clade 10, which also includes the type species of *Leporinus* (*L. fasciatus*). *Myocharax* is likely to be placed into the synonymy of *Leporinus* in a phylogenetic analysis of all known members of *Leporinus*, a reality that argues against recognizing it as a genus. Relationships of *Leporinops* within *Leporinus* are uncertain, as *Leporinus* cf. *moralesi*, assignable to the subgenus *Leporinops*, appears as part of the large polytomy in clade 8. In light of this situation, we do not recognize *Leporinops* at the genus level.

*Abramites* clusters as sister to *Leporinus striatus*, further rendering the present concept of *Leporinus* paraphyletic. Several options present themselves, including synonymizing *Abramites* with *Leporinus* or placing *L. striatus* within *Abramites*. In a future phylogenetic analysis with better taxon sampling within *Leporinus* and the application of additional datasets (e.g. molecular information) we think it likely that other species will be discovered that group with *Abramites* and *Leporinus striatus*. The position of that clade within the present concept of *Leporinus* may also become apparent. When such information is available, we would support expanding *Abramites* to encompass a larger monophyletic group of species. Without knowing the eventual composition of that clade, it is premature to begin assigning additional species to *Abramites*, and we leave the limits of *Abramites* unchanged for the present.

*Anostomoides* appears as the sister taxon to the remainder of the genera in clade 13. Clade 15, which contains *Rhytiodus* and *Schizodon*, is clearly monophyletic, as are both *Rhytiodus* and *Schizodon* as currently defined (clades 16 and 18). Continued recognition of these clades creates no nomenclatural issues.

*Laemolyta* as currently defined is monophyletic in this reconstruction, albeit with the support for that monophyly essentially provided by the unusual morphology of the teeth on the dentary. Its phylogenetic position as sister to clade 25 is well supported and we leave *Laemolyta* unchanged.

*Pseudanos* is a problematic genus that may or may not be monophyletic due to uncertainty in the placement of *Pseudanos winterbottomi*. Without any clear indication on the question, we retain the present



composition of *Pseudanos*. Alternative solutions would either necessitate a new genus for *Pseudanos winterbottomi* or expand *Anostomus* to include *Petulanos*, *Pseudanos*, *Sartor*, *Gnathodolus* and *Synaptolaemus*. Such a broadly encompassing *Anostomus* would be equivalent to the Anostominae of Winterbottom (1980). The expansion of *Anostomus* would formally recognize the best supported clade in the analysis (clade 25), but also would change the generic assignment of the 12 species currently in *Pseudanos*, *Petulanos*, *Synaptolaemus*, *Sartor* and *Gnathodolus*. As *Synaptolaemus*, *Sartor* and *Gnathodolus* are among the most distinctive genera in the family, we deem it inappropriate to pursue that option and expand *Anostomus*. Likewise, it is premature to erect a new monotypic genus for *Pseudanos winterbottomi*. At such time as the basal trichotomy in clade 25 can be resolved, perhaps with molecular data, the genus-level nomenclature in this portion of the anostomid tree should be reappraised.

*Anostomus* as defined prior to this study is paraphyletic. *Anostomus intermedius*, *A. plicatus* and presumably the very similar *A. spiloclistron* (not examined) are more closely related to *Gnathodolus*, *Sartor* and *Synaptolaemus* than to *A. anostomus* and *A. ternetzi*. The analysis herein revealed that *Anostomus* is divided between two clades (clades 28 and 30) that are well supported on the basis of several synapomorphies. These clades were also recovered in Winterbottom's (1980) analysis, albeit with different implied relationships to the other genera in the Anostomidae. *Anostomus anostomus* is the type species and we restrict *Anostomus* to the species in clade 28, plus *A. brevior* and *A. anostomus longus* (cited as *A. longus* by Garavello & Britski, 2003), which were not examined in this study, but are nearly identical to *A. anostomus* externally (Géry, 1961b; Winterbottom, 1980). We designate clade 30 as a new genus, *Petulanos*, including three species previously assigned to *Anostomus*: *Petulanos intermedius*, *P. plicatus* and *P. spiloclistron* with *P. plicatus* (the oldest name) as the type species. Recognition of clade 30 as a new genus permits the continued recognition of *Synaptolaemus*, *Sartor*, *Gnathodolus* and the newly restricted *Anostomus* (clade 28).

#### GENUS *PETULANOS* GEN. NOV.

*Type species*: *Anostomus plicatus* Eigenmann, 1912: 296, designated herein

*Diagnosis*: *Petulanos* may be distinguished from the other members of the Anostomidae with strongly upturned mouths (*Anostomus*, *Gnathodolus*, *Pseudanos*, *Sartor* and *Synaptolaemus*) by the following combination of external characters: a series of dark

spots greater than one scale wide along the lateral line, a series of dark bars across the dorsal surface of the body, four branchiostegal rays, a lack of dermal papillae on the lower lip, two cusps occurring on the symphyseal tooth of the premaxilla, the possession in adults of only a single cusp on the symphyseal and second tooth of the dentary, and the presence of three cusps on the third tooth of the dentary. Based on skeletal anatomy, *Petulanos* may be distinguished from all other members of the Anostomidae by the possession of a symplectic with a distinctive triangular ventral lamina. *Petulanos* further differs from all examined members of *Anostomus*, *Gnathodolus*, *Pseudanos*, *Sartor* and *Synaptolaemus* in possession of two intermediate pores along the ossified portion of the sensory canal of the second infraorbital (versus one), and from all members of the genera cited above except *Pseudanos gracilis* by possession of only one intermediate pore along the ossified portion of the sensory canal of the first infraorbital (versus two). It can be further distinguished from *Anostomus* and *Pseudanos* by a very wide ventral portion of the maxilla, a high urohyal with the angle between the dorsal and ventral margins greater than 45°, and the anterior termination of the lateral shelf of the quadrate at a point posterior of the articular condyle on that bone. *Petulanos* can be further distinguished from *Gnathodolus*, *Sartor* and *Synaptolaemus* by the posterior expansion of the sixth infraorbital and its contact or fusion with the suprapreopercle, the rotation of the anterolateral flange of the maxilla and the ventral portion of that bone relative to each other, and the lack of a triangular process on the ascending arm of the preopercle.

*Etymology*: Derived from the Latin *petulans* (impudent or petulant) and the first four letters of the generic name *Anostomus* from which *Petulanos* was separated; both in allusion to the characteristic upturned mouth that gives these fishes the appearance of a perpetual pout.

#### SUBFAMILIAL CLASSIFICATION IN ANOSTOMIDAE

The Anostomidae of the present study has in the past also been considered a subfamily Anostominae (e.g. Géry, 1961a). The Anostominae has also been utilized as a subfamily within the Anostomidae in several senses. Some authors (e.g. Géry, 1977; López, Menni & Miquelarena, 1987) recognized an Anostominae that included all of the Anostomidae with the exception of *Leporellus* that they placed in its own subfamily, the Leporellinae. Winterbottom (1980) alternatively recognized a more restrictive Anostominae consisting of the species in *Anostomus* (then including *Petulanos*), *Gnathodolus*, *Pseudanos*, *Sartor*

and *Synaptolaemus*. Interestingly, each of these subfamilial concepts delimits a monophyletic assemblage under the results of this study. The recognition of a Leporellinae and Anostominae *sensu* Géry (1977) and López *et al.* (1987) would highlight the basal dichotomy in the family, but would provide no sense of structure within the broadly encompassing Anostominae of those authors. Winterbottom's (1980) more restricted Anostominae highlights the clade of species with superior mouths, but within the context of our phylogenetic results would require the proposal of several other subfamilies in order to satisfy the requirement that all subfamilies in the Anostomidae be monophyletic (even leaving aside the issues presented by the lack of resolution within *Leporinus*). Such a course of action is premature in light of the issues we discuss above, and we consequently do not recognize any subfamilies within the Anostomidae at this time.

#### MAJOR SHIFTS IN JAW MORPHOLOGY

Nine major shifts in jaw morphology occurred during the evolution of the Anostomidae. Most of these represent stages of a transition from a plesiomorphically subterminal mouth to a terminal and then increasingly upturned mouth. One transition represents a return to a subterminal mouth. The nine transitions are scattered more or less evenly throughout the phylogeny of the family, suggesting that jaw diversification occurred throughout the history of the Anostomidae. In this light, the very highly modified, superior jaws possessed by some genera (*Gnathodolus*, *Sartor*) can be understood as the product of several progressive shifts away from a more plesiomorphic subterminal jaw morphology (e.g. *Leporellus*).

The first shifts in jaw morphology (transition 1) within the Anostomidae are synapomorphies of the whole clade. All anostomids have the anguloarticular–quadrate joint in a more anterior position relative to the ventral wing of the lateral ethmoid and the orbit than is typical of other characiforms. The repositioning of the joint of the lower jaw was represented in the data matrix by character 83, the elongation of the interopercular–mandibular ligament. This modification also reflects the elongation of the anterior portion of the quadrate (not explicitly coded). Other transitions associated with jaw architecture at the base of the Anostomidae are the positioning of the retroarticular in a deeply recessed pocket of the dentary (character 65), the evolution of spade- or chisel-like teeth on the dentary (character 37), the evolution of a well-developed triangular ascending process of the premaxilla (character 45), the thickening of the lateral ethmoid–ectopterygoid ligament and the relocation of the insertion of that

ligament to the ventral surface of the lateral ethmoid (character 24). This ligament, which binds the dorsal portion of the ectopterygoid to the neurocranium, appears to reduce or eliminate motion of the suspensorium relative to the neurocranium and may create the fixed component in a four-bar linkage (*sensu* Westneat, 2003, 2004, 2006). The single species in the Anostomidae to have lost this ligament (*Gnathodolus bidens*, character 23) possesses a highly modified sliding relationship between the suspensorium and anteroventral portion of the neurocranium that is much different from that found elsewhere in the family, or indeed anywhere in the Characiformes.

The stabilization of the suspensorium provided by the lateral ethmoid–ectopterygoid ligament may be important to the function of the anteriorly shifted jaws in the Anostomidae exclusive of *Gnathodolus*, and the linkages between cranial elements in the family should be examined and modelled and the functional implications analysed. The diversification in jaw orientation within the Anostomidae may also represent diversification of linkage geometry, mechanical advantage and feeding ecology, but this conjecture remains to be tested across the family (for studies that explicitly link jaw shape to function and ecology, see Westneat, 1995; Hulsey & Wainwright, 2002; Wainwright *et al.*, 2004).

The most basal members of the Anostomidae (*Leporellus*, Fig. 33) have slightly downturned mouths similar to that in *Caenotropus* in the closest outgroup, the Chilodontidae. The members of the next most derived genus in the Anostomidae (*Hypomasticus*) also have subterminal mouths, and the downturned mouth position appears to be the plesiomorphic condition for the Anostomidae. *Hypomasticus* and basal members of its sister taxon (*Leporinus* within clade 7) have, however, modified the plesiomorphic jaw morphology in different ways.

The species in *Hypomasticus* (formerly a subgenus of *Leporinus*) evolved a more exaggerated subterminal mouth position (transition 2; Fig. 34) characterized by a vertically orientated premaxilla (character 46) and a widened, trough-like morphology of the anguloarticular (characters 55 and 56). The apparent function of this trough was discussed in the character descriptions, but briefly, it appears to function in the manner of a pulley, altering the direction of the force vector applied by the adductor mandibulae to the maxilla.

In the sister group to *Hypomasticus* (clade 7), the mouth became fully terminal (transition 3) and the basal components of this clade have assumed the condition typical of *Leporinus* (Fig. 35). The anterior portion of the mesethmoid which attaches to the premaxilla shifted from ventrally hooked (Figs 16, 17) to straight (character 15; Fig. 18) and the process of

the mesethmoid connecting to the vomer became posteroventrally aligned (character 17; Fig. 18). The maxilla acquired a vertical or posterodorsal orientation (character 48; Fig. 35) and the ectopterygoid assumed a vertical orientation (character 72; Fig. 41) as the joint of the lower jaw with the quadrate became more anteriorly positioned than was the case in *Leporellus*, *Hypomasticus* and the proximate outgroup, the Chilodontidae.

The next major shift in jaw morphology (transition 4) occurred in clades 13 and 14, all members of which possess upturned mouths at some point in ontogeny. *Rhytiodus* and *Schizodon* have supraterminal mouths only as small juveniles and larvae and have terminal or subterminal mouths as adults. *Anostomoides* has only a slightly supraterminal mouth in the adult condition (juveniles of the genus not examined), while *Laemolyta*, *Pseudanos*, *Anostomus*, *Petulanos*, *Synaptolaemus*, *Sartor* and *Gnathodolus* have supraterminal or fully superior mouths apparently throughout ontogeny (small juveniles of *Synaptolaemus*, *Sartor* and *Gnathodolus* were not examined). Transition 4 involved a ventral shift in the position of the retroarticular in clade 13 (character 65; compare Figs 35, 36). In the slightly more derived clade 14, the functional edge of the lower teeth shifted from the posterior lamina to the distal margin of the tooth (compare Fig. 32A–C with Fig. 32E, F), and the orientation of the teeth in the dentary relative to that bone also changed (compare Fig. 35 with Figs 36, 38; see discussion of character 58). The shift in orientation may have changed the angle of force applied by the teeth. A biomechanical model [e.g. that of Westneat (2003), or a modification thereof] should be applied to test this conjecture and fully characterize the transition in jaw function in clades 13 and 14.

The jaw of *Schizodon nasutus* (Fig. 39) within clade 13 displays the most remarkable instance of convergence in the Anostomidae (transition 5). This species evolved a strongly subterminal mouth similar to, but independent of, the condition in *Hypomasticus* (Fig. 34). *Schizodon nasutus* also independently acquired three of the four skeletal morphologies that diagnose *Hypomasticus*: the transversely widened anguloarticular (character 55, also shared with all species of *Schizodon*), the trough-like ascending process of the anguloarticular (character 56) and the vertically aligned premaxilla (character 46). The convergence between *Hypomasticus* and *Schizodon nasutus* appears to be an excellent example of two lineages evolving the same solution to a comparable mechanical problem, effective functioning of ventrally rotated oral jaws. It has not, however, been demonstrated that the subterminal jaws of *Schizodon nasutus* and *Hypomasticus* are convergent functionally as well as morphologically.

The next major shift in jaw evolution in the Anostomidae (transition 6) occurred in clade 21, all the members of which have fully upturned jaws throughout ontogeny. Transition 6 is characterized by a fully horizontal orientation of the premaxilla (character 46; Figs 36, 37) and the reduction or elimination of the posterior lamina of the dentary teeth (compare Fig. 32E with 31E or 32F). The ontogenetic shift in mouth position in *Rhytiodus* and *Schizodon* (see discussion in Sidlauskas *et al.*, 2007), which together form the sister to clade 21, suggests that the strongly upturned mouths of the taxa in clade 21 may have resulted from heterochrony (paedomorphic fixation of the juvenile state in adults). The conjecture of heterochrony should be investigated further by comparison of ontogenetic series of skeletal preparations.

The six genera in clade 25 have the most strongly upturned jaws in the Anostomidae, and indeed proximate outgroup families, with the mouth opening completely on the dorsal surface of the head. Several morphological synapomorphies characterize this shift (transition 7). The ventral process of the mesethmoid runs vertically or nearly so (character 17), the ventral surface of the vomer developed a pentagonal raised area that contacts the restructured palatine (characters 21 and 67), and the ectopterygoid became almost totally posterodorsally inclined (character 66; Fig. 54) as the joint of the lower jaw with the quadrate moved ever more anteriorly. Somewhere near the base of this clade, a notch also developed in the lateral ethmoid to accommodate the now nearly horizontal alignment of the ectopterygoid–lateral ethmoid ligament (character 25; Fig. 26). The level at which this notch of the lateral ethmoid is a synapomorphy is uncertain due to the lack of resolution concerning *Pseudanos*.

The penultimate shift in jaw orientation in the Anostomidae occurred in the lineage leading to *Sartor* and *Gnathodolus* (transition 8). These two genera have the mouth so strongly upturned (backwards facing in *Sartor*) that the quadrate–anguloarticular joint is relocated to anterior of the opening of the mouth (Fig. 37). The maxilla also became plate-like with a distinctive medial process (character 54), the dentary teeth became elongate and recurved (character 37; Figs 31H, I, 37), and the premaxillary teeth became bowed (character 35; Fig. 29G, H).

The final major shift in jaw morphology in the family (transition 9) occurred in the derived genus *Gnathodolus*, in which the dentary was reduced to a slender cylinder bearing only a single tooth (characters 33 and 57; Fig. 31I), the ligamentous connection of the lateral ethmoid to the ectopterygoid that characterizes all other anostomids was lost (character 23), the palatine assumed the shape of an elongate hourglass (character 70) and the vomer developed a deep groove on each side into which the dorsal portions of



the mesopterygoid and metapterygoid fit (character 20, Fig. 22; see also Winterbottom, 1980: fig. 58). Functionality of the jaws in *Gnathodolus* appears to require that the dorsal portion of the suspensorium slide along grooves in the ventral portion of the neurocranium. That would be impossible if the lateral ethmoid–ectopterygoid ligament were retained. If so, the linkages within the skull of *Gnathodolus* may differ considerably from those found in other anostomids and may require construction of a new biomechanical model.

#### PHYLOGENETIC BIOGEOGRAPHY

All 14 genera in the Anostomidae comprising approximately 140 species are present in the vast cis-Andean mid-elevation and lowland portions of tropical and temperate South America. Anostomids inhabit myriad river systems from the Caribbean Sea versant drainages of northern Venezuela (Lasso *et al.*, 2004a) through the Río Orinoco (Lasso *et al.*, 2004b) and Río Amazonas (Garavello & Britski, 2003) basins south to the Río de La Plata system (Britski, Silimon & Lopes, 1999; López, Miquelarena & Menni, 2003; Menni, 2004). Anostomids are also diverse in the Atlantic versant rivers of the continent from the Guianas (Lowe-McConnell, 1964; Planquette *et al.*, 1996) south through the coastal rivers of eastern Brazil (Britski, Sato & Rosa, 1984; Malabarba, 1989). Many fewer anostomid genera and species inhabit the less extensive but topographically complex trans-Andean region of South America. Only six species in four genera are now recognized in the arch from the Lago Maracaibo basin of northwestern Venezuela (*Schizodon*, Vari & Raredon, 1991) through the Caribbean and Pacific slope rivers of northern and western Colombia (*Abramites*, *Leporellus*, *Leporinus*, Dahl, 1971; Mojica-C, 1999) to the Río Guayas basin of southeastern Ecuador (*Leporinus*, Eigenmann & Henn, 1916; Barriga, 1991).

Incomplete understanding of anostomid species diversity and geographical distribution at the species level preclude a fine-grained analysis of their phylogenetic biogeography. This problematic situation is exemplified by the continuing publications describing new species within the family and/or refining concepts of species limits and geographical ranges for previously described forms (e.g. Sidlauskas & Santos, 2005; Sidlauskas *et al.*, 2007). Although the phylogenetic reconstruction arrived at herein included only a subset of the species and yielded incomplete resolution, particularly within *Leporinus* (Fig. 5), it nevertheless allows estimates of minimum ages for several major intrafamilial cladogenic events.

An interesting pattern is apparent when the distribution of genera of the Anostomidae to the two sides

of the Andean Cordilleras is evaluated within the context of the arrived at phylogeny (Fig. 5). This analysis finds that those genera in the family with representatives on both sides of that mountain chain are all restricted to the somewhat more basal components of the phylogeny. These are *Abramites* with one species (*A. hypselonotus*) broadly distributed in cis-Andean regions and its congener (*A. eques*) endemic to the Río Magdalena system (Vari & Williams, 1987; Mojica, 1999), *Leporellus* with several nominal species occurring east of the Andes and one form identified as *L. vittatus* reported from the Río Magdalena basin (Dahl, 1971; Maldonado-Ocampo *et al.*, 2005), *Schizodon* with representatives broadly distributed east of the Andes (Sidlauskas *et al.*, 2007, and references therein) and one species, *S. corti*, endemic to the Lago Maracaibo basin of northern Venezuela (Vari & Raredon, 1991; Lasso *et al.*, 2004a) and finally *Leporinus*, a genus with over 90 recognized species (Garavello & Britski, 2003), only three of which are reported to occur in river systems to the west of the Cordilleras. These are *L. ecuadorensis* from the Río Guayas basin of Ecuador (Eigenmann & Henn, 1916; Barriga, 1991), *L. muyscorum* from the Río Magdalena, Río Atrato, Río Ranchería and Río Sinú basins of northern Colombia (Mojica-C, 1999; Mojica *et al.*, 2006), and *L. striatus*, reported from river systems of northern and western Colombia (Dahl, 1971; Mojica-C, 1999).

Although some species of the Anostomidae live in mid-level, upland river systems (e.g. *Leporellus* in the Río Magdalena system, Maldonado-Ocampo *et al.*, 2005), most occur in lower elevation settings and no members of the family are inhabitants of the precipitous drainage systems of the higher regions of the Andean Cordilleras. As such, the uplift of the Andean Cordilleras probably served as a vicariant event or sequential events dividing the ancestral components of *Abramites*, *Leporellus*, *Leporinus* and *Schizodon* into cis- and trans-Andean components.

*Schizodon* (clade 18) is the most deeply nested of the clades within the Anostomidae that includes cis- and trans-Andean components. *Schizodon corti*, an endemic to the trans-Andean Lago Maracaibo basin (Vari & Raredon, 1991; Lasso *et al.*, 2004a) and the sole member of the genus found in a trans-Andean drainage, was not incorporated into the phylogenetic analysis of this study. *Schizodon corti* shares, however, the externally obvious attributes of its congeners and it is reasonable to assume that *S. corti* is a component of clade 18. It follows directly that clades arising at progressively more inclusive nodes within the phylogeny of the Anostomidae below clade 18 (the ancestors of clades 1, 3, 7, 8, 12, 13, 14 and 15; Fig. 5) evolved prior to this isolation of components of that family to each side of the uplifting Cordilleras.



Furthermore, the ancestors of the three genera with members to the two sides of the Andes (*Abramites*, *Leporellus*, *Leporinus*) evolved prior to the uplift and the same applies to *Anostomoides* and *Hypomasticus*, genera limited to river basins east of the Andes. Given that clade 15 (containing *Schizodon* and *Rhytiodus*) is the sister to clade 21 (*Laemolyta*, *Pseudanos*, *Anostomus*, *Petulanos*, *Synaptolaemus*, *Gnathodolus*, and *Sartor*), stem members of clade 21 must also have evolved by the final uplift of the Cordilleras.

The specific geological event associated with final vicariance into cis- and trans-Andean components of the Anostomidae cannot be identified in so far as it is impossible to determine the degree of uplift that resulted in the ultimate division of that component of the ichthyofauna into eastern and western subunits. Nonetheless, the minimum age for such vicariance would be the closure of the north-flowing Maracaibo–Falcon outlet of the Río Orinoco. That closure occurred approximately 8 Mya during the final major uplift sequence of the northern portions of the Andean Cordilleras (Hoorn, 1993; Hoorn *et al.*, 1995; Lundberg *et al.*, 1998). Evidence from the phylogeny when correlated with geological information is, however, further informative in terms of older likely vicariance events for the Anostomidae.

*Schizodon corti*, which is endemic to the Lago Maracaibo basin, is the sole trans-Andean species of the Anostomidae in that basin (Lasso *et al.*, 2004a). The other trans-Andean species of the Anostomidae (species of *Abramites*, *Leporellus* and *Leporinus*) inhabit river systems that lie west of the central and western Andean Cordilleras in the portions of South America from the Río Guayas to the Río Ranchería. These mountain ranges underwent uplift prior to the closure of the Maracaibo–Falcon outlet with the resultant isolation of Lago Maracaibo from what is now the Río Orinoco basin. The most recent and thus pertinent of the major uplift events in that region that is relevant to the question of a minimum date for the division of the anostomid faunas east and west of the Central and Western Andean Cordilleras involved the Sierra de Perija, the mountain range between the Lago Maracaibo basin and the river systems that drain regions to the west of those uplands. This uplift event of that portion of the northeastern Andes took place approximately 11.8 Mya as evidenced by the westward shifts of the palaeocurrents within the present valley of the Río Magdalena system (Hoorn *et al.*, 1995; Lundberg *et al.*, 1998). The uplift of the Sierra de Perija 11.8 Mya provides a minimum age for the Anostomidae and for the ancestors of *Abramites*, *Leporellus*, *Hypomasticus* and *Leporinus* (clades 1, 2, 3, 7, 8, 9; Fig. 5). Although *Abramites* and *Leporinus* form a largely unresolved polytomy in our final phy-

logeny (Fig. 5), that lack of resolution does not bear on the hypothesis of the age of these genera as the phylogenetic hypothesis clusters all members of those genera at clade 8. As such the ancestor of the subunit of the Anostomidae at that level of the phylogeny also was present prior to 11.8 Mya.

When we consider the degree of morphological diversity present between the Anostomidae and its close relatives, the Chilodontidae, Curimatidae and Prochilodontidae, the latter two of which also have cis- and trans-Andean components (Vari, 1988; Castro & Vari, 2004) and the fact that a series of cladogenic events within the Anostomidae (the basal splits within clades 1, 3, 7 and 8) preceded the vicariant events of 11.8 Mya, it seems very likely that the origin of the family and its basal clades most likely significantly pre-dated that time. Evidence from the fossil record of the Anostomidae and its close relatives is informative on this question.

Fossils of the Anostomidae have been rarely cited in the literature. It is uncertain whether this situation represents the rarity of such material in deposits within South America that include remains of freshwater taxa or the fact that fossils of the family remain unrecognized among samples of fossil fishes from such strata. Two reports of fossil anostomids are that of Roberts (1975) for remains from the Cuenca basin of southern Ecuador at approximately 19 Mya (Roberts, 1975: 261), and the more recent citation by Lundberg (1997: 73) based on material from the La Venta formation in Colombia from between 13.5 and 11.5 million years old (Guerrero, 1997: 41). Both of these samples are limited to teeth identified as having originated with a species of *Leporinus* (jaw and pharyngeal teeth in the Ecuadorian samples and a single premaxillary tooth in the case of the La Venta material). The age of these deposits minimally confirms the existence of species of *Leporinus* at the time of the uplift of the Sierra de Perija 11.8 Mya, a minimum age for the genus independently postulated above on the basis of distributional data evaluated in a geological context. The oldest possible age for the fossils (19 Myr for the Cuenca material) would indicate that the family and clades including *Leporinus* significantly pre-date that time period.

Fossils of close relatives of the Anostomidae within the Characiformes are also very limited and only one is informative as to the minimum age of the more inclusive clade including that family plus its close relatives, the Chilodontidae, Curimatidae, and Prochilodontidae. Malabarba (1996) demonstrated that a fossil fish described by Travassos & Santos (1955) as *Curimata mosesi* from Oligocene deposits of the Tremembé basin of eastern Brazil was assignable to the curimatid genus *Cyphocharax*, a component of a terminal polytomy deeply nested within the phylog-

eny of the Curimatidae (Vari, 1989a). The deposits from which the specimens of *Cyphocharax mosesi* originated are at least 22.5 million years old (Mala-barba, 1998; Reis, 1998) and the ancestors of the clade formed by the Curimatidae along with the Prochilodontidae and of that clade plus the Anostomidae and Chilodontidae therefore pre-date that time. Although not directly informative as to the age of the Anostomidae, this older date of 22.5 Myr is, nonetheless, congruent with the likely diversification of the Anostomidae well in advance of the uplift episodes of the Andean Cordilleras cited above as pertinent to likely vicariance events within the family. That date also distinctly pre-dates the minimum age of 11.5–13.5 Myr for the Anostomidae indicated by the limited fossil evidence for that family. The numerous cladogenic events between the divergence of the anostomid–chilodontid clade and the ancestor of *Cyphocharax* in conjunction with the pronounced degree of morphological divergences in each of those lineages are presumably indicative of a lengthy intervening time period, but it is impossible to determine whether the approximately 10 Myr between those events would accommodate that level of divergence.

Although not directly informative on that issue, evidence does indicate that the Characiformes evolved long in advance of even the 22.5-Myr date. The Characiformes as a whole long pre-dates the earliest fossils assignable to the Anostomidae as evidenced by both Old World fossil characiforms of the genera *Alestes*, *Brycinus* and *Bryconaethiops* in the family Alestidae (Zanata & Vari, 2005) that extend back approximately 49–54.8 Myr. It is also noteworthy that several instances of trans-Atlantic relationships within the Characiformes (see summary in Zanata & Vari, 2005: 120) would extend the African–South American drift vicariance at several phylogenetic levels within the Characiformes back approximately 90–112 Mya. There was thus a lengthy time period to accommodate the accumulation of evolutionary novelties between the origin of the Characiformes and the earliest fossils known at the level of the clade formed by the Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae or of *Leporinus* in the Anostomidae.

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## APPENDIX 1

## MATERIAL EXAMINED

In the following list, the species name and author is followed by an institutional catalogue number, the number of specimens cleared and counterstained (C&S), the standard length in millimetres and abbreviated locality information. Data on external morphology was typically taken from alcohol-preserved specimens from the same lot as the C&S preparations. Specimens prepared as dry skeletons are indicated by (DS) and additional alcohol specimens by (A). Asterisks indicate type species for nominal genera or subgenera.

## ANOSTOMIDAE

- \**Abramites hypselonotus* (Günther), FMNH 97711, 1 specimen, 76.0 mm; Colombia, Amazonas, Amazon River 1.6 km upstream from Leticia. FMNH 106574, 1 specimen, 53.3 mm, Bolivia, Pando, Río Nareuda; 7 river km above mouth of Tahumanu. MCZ 59240, 1 specimen (A), 98.6 mm; Ecuador, Río Punino, above Coca. USNM 164036; 1 specimen, 100.5 mm; Ecuador, lower Río Bobonaza. USNM 261491; 1 specimen, 47.6 mm; Peru, Loreto, Río Ucayali, at Masisea. USNM 261479; 1 specimen, 57.5 mm; Peru, Ucayali, Río Ucayali, at Pucallpa.
- Anostomoides laticeps* (Eigenmann), INHS 53677, 1 specimen, 106.6 mm; Peru, Loreto, Río Nanay (Río Amazonas drainage), Pampa Chica. USNM 389692 1 specimen, 111.3 mm; Venezuela, Bolivar, Río Orinoco.
- \**Anostomus anostomus* (Linnaeus), FMNH 109876, 1 specimen, 74.8 mm; Venezuela, Bolivar, Entrerios, edge of Río Caura near mouth of Río Erebató. USNM 227340, 1 specimen, 57.7 mm SL; Suriname, Nickerie, Corantijn River, Camp Hydro, approximately 30 km N of Tiger Falls. USNM 225364, 1 specimen; Suriname, Nickerie, stream along S bank of Lucie River, approximately 6 km upstream of ferry crossing along road from Amotopo to Camp Geologie.
- Anostomus ternetzi* Fernández-Yépez, FMNH 109883, 4 specimens, 37.5–58.2 mm; Venezuela, Bolivar, Río Caura, beach at El Playon. USNM 233230, 1 specimen, 43.4 mm; Venezuela, Delta Amacuro, Río Orinoco, small caño near mouth of Caño Socoroco.
- \**Gnathodolus bidens* Myers, ANSP 159389, 1 specimen; 66.6 mm, Venezuela, Bolivar, caño (possibly Caño Curimo) entering Río Caura near confluence of Río Caura and Río Orinoco. USNM 231539, 1 specimen, 76.2 mm; aquarium material. USNM 389623, 1 specimen, approximately 71 mm (disassociated), Venezuela, Bolivar, Río Caura.
- Hypomasticus despaxi* Puyo, MCZ 56552, 1 specimen, 45.4 mm; French Guiana, Ouaycoarou Island at edge of Fleuve Oyapock. USNM 310720, 6 specimens (A); Brazil, Ouayearau Island at edge of Río Oiapoque, halfway between St. Georges and Petit Francois (Camopi).
- Hypomasticus megalepis* Günther, INHS 49387, 1 specimen, 68.4 mm; Guyana, Essequibo drainage, Potaro River, Tumatumari cataract. USNM 225397, 2 specimens, 80.3–95.1 mm; Suriname, creek entering Corantijn River from Surinamese shore, approximately 2 km downstream of Cow Falls. USNM 231541 1 specimen, 66.5 mm; no locality data.
- \**Hypomasticus mormyrops* Steindachner, FMNH 112963, 1 specimen, 100.0 mm, USNM 318140, 1 specimen, approximately 104 mm SL (disarticulated); Brazil, Minas Gerais, Rio Mucuri, Mairinque. MCZ 97556, 1 specimen, 98.9 mm; Brazil, Minas Gerais, Rio Mucuri approximately 9 km W of Presidente Pena.
- Hypomasticus pachycheilus* Britski, INPA 6706, 1 specimen, 87.3 mm; Brazil, Pará, Rio Jamanxim, tributary of Rio Tapajos, Isla Terra Preta.
- Laemolyta* species, USNM 179514; 2 specimens, 75.3–77.0 mm; Brazil, Amazonas, Rio Urubu.
- Laemolyta garmani* (Borodin), FMNH 92498, 1 specimen, 73.9 mm; Peru, Loreto, Iquitos, Río Nanay, Avcacocha.
- Laemolyta orinocensis* (Steindachner), INHS 35764, 1 specimen, 76.5 mm, Venezuela, Anzoategui, Río Orinoco drainage, Laguna Terecaya. INHS 35837, 1 specimen, 147.7 mm; Venezuela, Anzoategui, Río Orinoco drainage, Laguna Aguilera. USNM 270311, 1 specimen, 91.6 mm; Venezuela, Amazonas, Balnearia Pozo Azul, approximately 1 km E of Puerto Ayacucho.
- Laemolyta proxima* (Garman), INHS 73275, 1 specimen, 81.8 mm; Brazil, Amazonas, Lake Janauari, approximately 8 km SW of Manaus.
- \**Laemolyta taeniata* (Kner), FMNH 103866, 1 specimen, 72.9 mm, Venezuela, Amazonas, pool behind beach of Río Ventuari on S side of river approximately 12 km above mouth in Río Orinoco, Laguna Pavon. INHS 61513, 85.2 mm; Venezuela, Apure, Río Cinaruco – Río Orinoco drainage, Caño San Miguel. USNM 280708, 1 specimen; Peru, Loreto, caños entering Río Nanay, NE of Iquitos.
- \**Leporellus pictus* (Kner), USNM 243225, 1 specimen, 40.7 mm; Brazil, São Paulo, along margin of Río Paraná, near Jupai. USNM 302487, 1 specimen, 115 mm; Brazil, São Paulo, Rio Pardo, Barragem de Itaipava, Usina Amalia, near Santa Rosa de Viterbo.
- Leporellus vittatus* Valenciennes, INHS 56128, 1 specimen, 78.2 mm; Venezuela, Portuguesa, Río Apure – Río Orinoco drainage, Río Portuguesa,



- Hwy 5 Bridge. USNM 121406; 1 specimen, 112.5 mm; Venezuela, Estado Aragua, Río Guarico and tributaries, between San Sebastian and San Casimiro. USNM 261458; 1 specimen, 80.0 mm; Peru, Ucayali, Río Ucayali, at Masisea. USNM 389690; 1 specimen, 121.4 mm; Venezuela, Barinas, Falcon, Río das Palmas.
- Leporinus agassizi* Fowler, FMNH 102219; 2 specimens, 80.1–98.6 mm; Ecuador, Napo, Río Tiputini, near mouth in Río Napo and quebradas. USNM 280656; 1 specimen; Peru, Loreto, Río Nanay, approximately 20 km upstream of mouth.
- Leporinus aripuanaensis* Garavello & Santos, INPA 15371, 1 specimen, 81.6 mm; Brazil, Amazonas, Rio Uatumã.
- Leporinus cf. ecuadorensis*, FMNH 102198, 2 specimens, 96.7–110.8 mm; Ecuador, Napo, Río Tiputini, near mouth in Río Napo. FMNH 102160, 1 specimen, 62.8 mm; Ecuador, Napo, Río Napo, Laguna Anangucocha. FMNH 100354, 5 specimens, 20.9–31.8 mm; Ecuador, Napo, N bank tributary to Río Tarapuy just downstream from road bridge.
- Leporinus falcipinnis* Mahnert, Géry & Muller, FMNH 104000, 1 specimen (A), 204.9 mm; Venezuela, Amazonas, backwater of island in Rio Atabapo about 1 hr. above San Fernando de Atabapo.
- \**Leporinus fasciatus* (Bloch), USNM 103847, 1 specimen, 74.5 mm; aquarium material. USNM 225991, 1 specimen, 87.8 mm; Suriname, Nickerie, Corantijn River. USNM 233574, 2 specimens, 29.5–38.2 mm; Venezuela, Monagas, Laguna Guatero, near Barrancas. USNM 279272, 1 specimen, 56.8 mm; Venezuela, Bolivar, small caño connecting with Río Orinoco immediately S of El Burro.
- Leporinus cf. fasciatus* FMNH 103450, 1 specimen, 53.7 mm; Venezuela, Amazonas rocks and rapids in Río Orinoco at Isla Cupaven.
- Leporinus friderici* (Bloch), FMNH 116829, 1 specimen (A), 180.5 mm; Suriname, Rechter Coppename River. USNM 225409, 1 specimen, 58.6 mm; Suriname, Nickerie, Kamp Kreek, 100 m N of turnoff to Kamp Geologie.
- Leporinus cf. friderici*, INPA 21605, 1 specimen (DS), 167.3 mm; Brazil, Amazonas, purchased at Manaus fish market.
- Leporinus gomesi* Garvello & Santos, INPA 14264, 1 specimen, 83.6 mm; Brazil, Mato Grosso, Rio Aripuana, Igarapé da Chapada near airport about 5 km from Humbolt.
- Leporinus jatuncochi* Ovchynnyk, INHS 38940, 1 specimen, 81.4 mm; Peru, Loreto, Río Nanay-Río Amazonas drainage, purchased from aquarium dealer in Santa Clara.
- Leporinus cf. moralesi* UMMZ 216425, 1 specimen, 39.8 mm; Brazil, Bahia, Barreiras, dead arm of Rio Grande.
- Leporinus cf. niceforoi*, FMNH 102150, 1 specimen, 55.7 mm; Ecuador, Napo, Río Yasuni, 1–2 km downstream from confluence with Río Jatuncocha.
- Leporinus ortomaculatus* Britski & Garavello, FMNH 109896, 1 specimen, 45.9 mm; Venezuela, Bolivar, Río Tacoto. INPA 10553, 1 specimen, 88.6 mm; Brazil, Rio Mucajaí.
- Leporinus pellegrinii* Steindachner, INPA 15672, 1 specimen, 82.3 mm; Brazil, Rio Tocantins.
- Leporinus* species, USNM 191634; 1 specimen, 33.1 mm; Brazil, Goiás, Rio Araguaia, at Aruanã.
- Leporinus striatus* Kner, FMNH 108517, 1 specimen, 68.8 mm; Brazil, Mato Grosso do Sul, Rio Negro drainage, Rio do Peixe.
- Leporinus tigrinus* Borodin, INPA 1917, 1 specimen, 103.6 mm; Brazil, Pará, Rio Tocantins, Tucuruí.
- Petulanos intermedius* (Winterbottom), INPA 15184, 1 specimen, 65.1 mm; Brazil, Rondônia, Rio Jamari.
- \**Petulanos plicatus* (Eigenmann), USNM 225396; 2 specimens, 75.8–95.3 mm; Suriname, Nickerie, Matappi Creek.
- Pseudanos gracilis* (Kner), CAS-SU 68314, 1 specimen, ? mm (disassociated); Venezuela, Amazonas, Río Orinoco drainage, Río Atabapo, San Fernando de Atabapo. FMNH 103454, 2 specimens, 71.8–80.5 mm; Venezuela, Amazonas, rocks in Río Atabapo, Isla de Sapó, approximately 1.2 hr above San Fernando de Atabapo. USNM 270309, 1 specimen, 71.8 mm; Venezuela, Amazonas, Río Negro, Caño Chola where crossed by road from San Carlos de Río Negro to Solano.
- Pseudanos irinae* Winterbottom, CAS 38502, 1 specimen, paratype, ? mm (disassociated); CAS-SU 68313, 1 specimen, paratype, ? mm (disassociated); Venezuela, Amazonas, Río Orinoco drainage, Orinoco bifurcation, Tamatama rocks and lake.
- \**Pseudanos trimaculatus* (Kner), FMNH 102122, 2 specimens, 75.7–78.8 mm; Ecuador, Napo, Río Yasuni drainage, Río Jatuncocha about 2 km upstream from Laguna Jatuncocha. USNM 280706, 1 specimen, 59.4 mm; Peru, Loreto, Río Nanay, approximately 20 km upstream of mouth. USNM 280742, 1 specimen, 93.1 mm; Peru, Loreto, streams along road W of Iquitos.
- Pseudanos winterbottomi* Sidlauskas & Santos, FMNH 104020, 2 specimens, paratypes, 76.8–91.5 mm; Venezuela, Amazonas, Río Ventuari about 12 km above mouth in Río Orinoco, Laguna Pavon.
- \**Rhytidodus argenteofuscus* Kner, FMNH 102159, 1 specimen (A), 243.5 mm; Ecuador, Río Aguarico near military outpost Cuyabeno and confluence of Río Cuyabeno with Río Aguarico. INHS 66082, 1 specimen, 66.1 mm; INHS 66721, 1 specimen, 67.3 mm; INHS 67453, 1 specimen, 64.4 mm; Brazil, Amazonas, Lake Janauaca, 42 km SW of Manaus. USNM 229055, 1 specimen, 108 mm SL;

- Brazil, Amazonas, Paraná do Lago Janauaca, entrance to Lago do Castanho. USNM 305145, 1 specimen, 101.1 mm; Brazil, Amazonas, entrance to Lago Januari.
- Rhytiodus lauzannei* Géry, FMNH 96132, 1 specimen (A), 241.0 mm; Peru, purchased at Iquitos fish market, probably collected in Río Amazonas. INPA 21604, 1 specimen (DS), 260 mm; Brazil, Amazonas, purchased at Manaus fish market. INHS 39321, 1 specimen, 117.5 mm; Peru, Loreto, Río Amazonas drainage, Río Yanashi, 112.3 km E of Iquitos. INHS 54744, 1 specimen, 111.5 mm; Peru, Loreto, Río Amazonas drainage, Río Marañon due S of Nauta, oxbow lake.
- \**Rhytiodus microlepis* Kner, FMNH 116468, 1 specimen (A), 285.0 mm; Brazil, Amazonas, Rio Amazonas, between tributaries Parana da Eva and Rio Madeira, between towns Novo Oriente and São Jose do Amajari. USNM 163850; 1 specimen, 131.7 mm; Peru, Loreto, Iquitos. USNM 229095, 1 specimen (A), 121.5 mm SL; Brazil, Amazonas, Ilha da Marchantaria. USNM 229146; 1 specimen, 28.0 mm; Brazil, Amazonas, Paraná de Janauaca, entrance into Lago do Castanho. USNM 389694, 1 specimen, 91 mm SL; Bolivia, Beni, Río Mamore. INHS 72856, 1 specimen, 86.6 mm; Brazil, Amazonas, Lake Janauaca, approximately 42 km SW of Manaus.
- Sartor elongatus* Santos & Jégu, INPA 1168, 1, paratype, 76.1 mm; Brazil, Pará, Rio Trombetas, Cachoeira Porteira.
- \**Schizodon fasciatus* Agassiz, FMNH 102211, 1 specimen (A), 225.8 mm, Ecuador, Napo, Quebrada Zancudocoha, about 1 km upstream from mouth in Río Aguatico. FMNH 111351, 1 specimen, 96.1 mm; Peru, Loreto, tributary to Río Samira just below ranger's station, approximately 50 km from mouth in Río Marañon. INPA 21606, 1 specimen (DS), 283 mm; Brazil, Amazonas, purchased in Manaus fish market. USNM 179507; 1 specimen, 49.3 mm; Brazil, Amazonas, Rio Urubu. USNM 280739; 2 specimens, 86.2–103.5 mm; Peru, Ucayali, Distrito Coronel Portillo, Yarinacocha.
- Schizodon isognathus* Kner, ANSP 53825, 1 specimen (A), 234.1 mm, Brazil, Mato Grosso, Descalvados; FMNH 59508, 5 specimens (A), 106.4–201.7 mm SL, Brazil, San Luis de Cáceres, Mato Grosso. MZUSP 88603, 1 specimen, 176.0 mm, Brazil, Mato Grosso, Santo Antônio do Leverger, Rio Cuiabá. UMMZ 206792, 2 specimens (A), 235.8–240.8 mm SL, Paraguay, Río Apa, ca 0.5 km upstream (E) of bridge between Brazil and Paraguay in Bella Vista.
- Schizodon knerii* Steindachner, ANSP 171828, 1 specimen (A), 142.5 mm, Brazil, Bahia, Rio Tatu (Bahia do Coco), tributary of Rio Itaguari/Rio Carinhanha, 7.0 km S of Cocos. ANSP 171830, 1 specimen, 124.6 mm; Brazil, Minas Gerais, Rio Salinas, tributary of Rio Verde Grande, 51.0 km WSW from Monte Azul on road to Jaíba. ANSP 171831, 3 specimens (A), 175.7–200.9 mm, Brazil, Rio Verde Grande, on road from Montes Claros to Janauba. MZUSP 88602, 2 specimens, 127.2–179.9 mm; Brazil, Minas Gerais, Três Marias, São Francisco, Rio São Francisco.
- \**Schizodon nasutus* Kner, FMNH 112960, 1 specimen, 106.7 mm; Brazil, Rio Paraná, Ilha Solteira. USNM 181760, 4 specimens (A); Paraguay, Laguna, Río Tebicuary, near Florida. USNM 302488, 1 specimen (A); Brazil, São Paulo, near Santa Rosa De Viterbo, Itaipava dam, Usina Amali, Rio Pardo, main channel of river, just below fish ladder. USNM 326944, 1 specimen, 111 mm; Brazil, Mato Grosso, Rio Paraná, Ilha Solteira.
- Schizodon scotorhabdotus* Sidlauskas, Garavello & Jellen, ANSP 165480, 1, paratype (A), 226.0 mm; Venezuela, Apure, Río Capanaparo, backwater lagoon (mouth of Caño Las Varitas) near San Fernando de Apure-Puerto Paez highway. ANSP 182897, 1, paratype (DS), 224 mm, Venezuela, Delta Amacuro, Río Orinoco on N shore at Isla Portuguesa, approximately 217 km from sea buoy, in Caño Anabata. FMNH 104024, 1 paratype, 92.4 mm; Venezuela, Guarico, Río Aguaro N of Cabruta. USNM 256961, 5 specimens, 19.0–20.5 mm; Venezuela, Apure, Río Apure, near San Fernando de Apure. MBUCV-V-32950, 1, holotype (A), 132.0 mm, Venezuela, Guárico, Río Aguaro, Río Aguaro N of Cabruta on cattle ranch on E side of Río Guarico. MBUCV-V-32970, 1 paratype (DS), 271 mm, Venezuela, Guarico, Río Orinoco basin, Río Guárico system, Río Orituco near Calabozo. USNM 258267, 3 specimens, 2 paratypes, 82.8–94.9 mm; Venezuela, Apure, marshes W of San Fernando de Apure.
- Schizodon vittatus* (Valenciennes), INPA 1543, 1 specimen, 108.5 mm; Brazil, Rio Tocantins, Icaingui. USNM 124401, 2 specimens (A); Peru, Río Ampiyacu. USNM 175914, 1 specimen (A); Peru, Tuye Caño.
- \**Synaptolaemus cingulatus* Myers and Fernández-Yépez, AMNH 91095, 1 specimen (A), 78 mm SL; Venezuela, Bolivar, Río Paraguay at Carapo Rapids, just upriver of mouth of Río Carapo. FMNH 103445, 1 specimen, 64.3 mm; Venezuela, Amazonas, rocks and rapids in Río Orinoco, Isla Cupaven. USNM 302356, 1 specimen, 32.5 mm; Brazil, Pará, Rio Trombetas. USNM 279336, 1 specimen, 88.8 mm; Venezuela, Bolivar, small caño off Río La Paragua, at La Paragua. USNM 302358, 1 specimen, 32.3 mm; Brazil, Rio Tapajós, São Luis. USNM 389693, 1 specimen, 99 mm; Venezuela, Bolivar, Río Caroni.

## CHARACIDAE

- Brycon argenteus* Meek and Hildebrand, USNM 293136, 1 specimen, 100 mm; Panama, Comaraca Kuna Yala, Quebrada Sigdi at Pingandi.
- Brycon falcatus* Müller and Troschel, USNM 226161, 2 specimens, 71.3–78.3 mm; Suriname, Nickerie, Corantijn River at km 180, side channel of main river along Surinamese shore.

## CHILODONTIDAE

- Caenotropus maculosus* (Eigenmann), USNM 231545, 2 specimens, 46.5–48.2 mm; Guyana. USNM 231546, 1 specimen, 108.0 mm; Suriname, Saracama River. USNM 389691, 1 specimen, 66.5 mm; Guyana, Tumatumari.
- Caenotropus mestomorgmatos* Vari, Castro & Raredon, INHS 43988, 2 specimens, 65.9–69.6 mm; Peru, Loreto, Río Amazonas drainage, Río Nanay, Pampa Chica, 4.54 km W of Iquitos.
- Caenotropus labyrinthicus* (Kner), FMNH 100377, 3 specimens, 45.6–57.9 mm; Venezuela, Monagas, Cocos between Puerto Ordaz & Barrancas, 300 km from sea buoy. USNM 231543, 1 specimen, 64.8 mm; Brazil, Amazonas, Rio Negro, São Gabriel do Cachoeira. USNM 231544, 1 specimen; Venezuela, Amazonas, upper Río Negro.
- Chilodus gracilis* Isbrücker and Nijssen, USNM 232358; 5 specimens, 27.7–29.6 mm; Brazil, Pará, Rio Inhangapi, 40 km E of Belém.
- Chilodus punctatus* Müller and Troschel, FMNH 100351, 7 specimens, 22.4–58.7 mm; Ecuador, Napo, Río Cuyabeno-Río Aguarico drainage, Laguna Avacocha. FMNH 102061, 1 specimen, 58.1 mm; Ecuador, Napo, Río Yasuni, Río Jatuncocha, about 2 km upstream from Laguna Jatuncocha. USNM 280444, 2 specimens, 55.0–63.5 mm; Peru, Loreto, Quebrada Corrientillo at road from Iquitos to Río Nanay. USNM 231542, 14 specimens, 45.7–58.7 mm; Peru, Loreto, Río Nanay.

## CITHARINIDAE

- Citharinus citharus* (St. Hilaire), USNM 52146, 1 specimen, 218.7 mm (only gill arches C and S); Sudan, junction of Nile and Atbara Rivers.
- Citharinus* sp., USNM 231554, 2 specimens 56.3–64.5 mm; Burkina Faso, Upper Volta, Black Volta River.

## CURIMATIDAE

- Curimata cyprinoides* (Linnaeus), USNM 225619, 1 specimen, 79.2 mm; Suriname, Nickerie, Makilik-abore Kreek.

- Curimata inornata* Vari, USNM 268597, 1 paratype, 115.7 mm; Brazil, Pará, Rio Tapajos, São Luis.
- Curimata vittata* (Kner), FMNH 101490, 3 specimens, 40.0–49.4 mm; Ecuador, Napo, Río Aguarico drainage, Laguna Grande de Cuyabeno and Río Cuyabeno. USNM 231434, 1 specimen, 53.7 mm; Brazil, Amazonas, Rio Negro.
- Curimatella alburna* (Müller & Troschel), FMNH 101529, 1 specimen, 62.7 mm; Ecuador, Napo, laguna open to Río Lagartococha, about 25 km upstream from mouth in Río Aguarico.
- Curimatella dorsalis* (Eigenmann & Eigenmann), USNM 243235, 2 specimens, 51.5–53.7 mm; Brazil, Amazonas, Rio Solimões, upriver of Coari.
- Curimatopsis macrolepis* (Steindachner), FMNH 100352, 5 specimens, 25.4–41.5 mm; Ecuador, Napo, Río Yasuni, Quebrada to Río Jatuncocha, approximately 2 km upstream from Laguna Jatuncocha. USNM 190285, 1 specimen, 34.7 mm; Peru, Loreto, Iquitos.
- Curimatopsis microlepis* Eigenmann & Eigenmann, USNM 268867, 1 specimen, 75.8 mm; Brazil, Amazonas, Rio Solimões, lago near Beruri.
- Cyphocharax abramoides* (Kner), USNM 267953, 1 specimen, 100.3 mm; Brazil, Pará, Rio Xingu, Belo Monte.
- Potamorhina laticeps* (Valenciennes), USNM 121325, 1 specimen, 129.3 mm; Venezuela, Zulia, Lago Maracaibo basin.
- Potamorhina latior* (Spix & Agassiz), FMNH 106591, 1 specimen, 82.5 mm; Bolivia, Pando, Lago de la Anguilla, Tahuamanu. USNM 228691, 1 specimen, 97.6 mm; Brazil, Amazonas, near Manaus.
- Psectrogaster curviventris* Eigenmann & Kennedy, FMNH 108026, 2 specimens, 43.6–48.0 mm; Paraguay, Alto Paraguay, Riacho Coeyu, tributary of Río Paraguay.
- Pseudocurimata patiae* (Eigenmann), USNM 287597, 1 specimen, 89.5 mm, Colombia, Narino, Río Patia.
- Steindachnerina conspersa* (Holmberg), USNM 252224, 1 specimen, 83.2 mm; Paraguay, Presidente Hayes, off Trans-Chaco Highway at km 50.

## DISTICHODONTIDAE

- Distichodus* sp., USNM 175436, 1 specimen, 62.5 mm; Congo, Stanley Pool.
- Paradistichodus dimidiatus* Pellegrin, USNM 231556, 2 specimens, 45.6–46.3 mm; Ghana, Dayi River at Gbefi.
- Xenocharax spilurus* Günther, USNM 227693, 1 specimen, 89.3 mm; Gabon, Allonha II, Lac Ezanga.

## HEMIODONTIDAE

- Hemiodus ocellatus* (Vari), USNM 225593, 1 paratype, 99.6 mm; Suriname, Nickerie District, Corantijn River.



*Hemiodus quadrimaculatus* Pellegrin, FMNH 116862, 2 specimens, 55.3–68.2 mm; Suriname, Morocco Sula.

## PARODONTIDAE

*Parodon suborbitalis* Valenciennes, USNM 231552, 2 specimens, 55.0–58.1 mm; Colombia, Río Salado.

*Parodon guyanensis* Géry, FMNH 116878, 2 specimens, 59.1–63.4 mm; Suriname, Sula Calliandra.

## PROCHILODONTIDAE

*Ichthyoelephas humeralis* (Günther), FMNH 80715, 1 specimen, 107.6 mm; Ecuador, Río Guayas basin, Río Palenque at Centro Científico Río Palenque. USNM 290374, 2 specimens, 130.4–133.6 mm; Ecuador, Quevedo fish market.

*Prochilodus costatus* Valenciennes, USNM 357391, 1 specimen, 103.5 mm; Brazil, Rio Jetuitae basin.

*Prochilodus magdalenae* Steindachner, USNM 79231, 2 specimens, 91.9–103.4 mm; Colombia, Calamar.

*Prochilodus mariae* Eigenmann, USNM 270243, 2 specimens, 92.6–97.1 mm; Venezuela, Bolivar, Río Orinoco. FMNH 103683, 1 specimen, 105.4 mm; Venezuela, Guarico, lagoon about 4 km from E side of Río Aguaro, N of Cabruta.

*Prochilodus nigricans* Agassiz, USNM 280609, 1 specimen, 78.5 mm; Peru, Ucayali, District Coronel Portillo, Yarinacocha.

*Prochilodus reticulatus* Valenciennes, USNM 121326, 3 specimens, 110.7–113.1 mm; Venezuela, Lago Maracaibo basin.

*Prochilodus rubrotaeniatus* Jardine, USNM 225419, 2 specimens, 89.0–100.4 mm; Suriname, Nickerie, Corantijn River.

*Prochilodus vimboides* Kner, MCZ 20169, 2 specimens, 93.4 and ? mm (disassociated); Brazil, Rio de Janeiro, Rio Paraiba. USNM 345752, 1 specimen, 114.8 mm; Brazil, Minas Gerais, Rio Jequitai basin.

*Semaprochilodus insignis* (Jardine), USNM 290148, 1 specimen, 102.5 mm; Brazil, Amazonas, vicinity of Manaus.

*Semaprochilodus kneri* (Pellegrin), USNM 279325, 1 specimen, 99.3 mm; Venezuela, Amazonas, Río Orinoco, near Puerto Ayacucho. FMNH 85634, 1 specimen, 86.3 mm; Venezuela, Amazonas, ponds 0.3 km S of Puerto Nuevo, towards Puerto Ayacucho.

*Semaprochilodus taeniurus* (Valenciennes), USNM 289798, 1 specimen, 78.2 mm; Brazil, Amazonas, near Manaus.



APPENDIX 2  
OUTGROUP CHARACTERS

**Table A1.** Characters informative as to outgroup relationships

No.	Character title and states	CI	RI	Citation and character number
124	<i>Presence or absence of trifurcate articular complex at anterior margin of mesethmoid:</i> (0) absent; (1) present.	0.500	0.750	Vari (1979: no. 10)
125	<i>Form of border of third posttemporal fossa:</i> (0) border formed by multiple bones; (1) bordered formed solely by epioccipital.	0.333	0.500	Vari (1983: no. 17)
126	<i>Depth and width of fossa for scaphium:</i> (0) fossa shallow and narrow, not connecting as in state 1; (1) fossa deep and wide, resulting in interconnections of fossa with lateral occipital foramen laterally and interior of cranium anteriorly.	1.000	1.000	Vari (1983: no. 14)
127	<i>Development of lateral margin of exoccipital lateral to foramen magnum:</i> (0) weakly developed posteriorly, not as in state 1; (1) well developed posteriorly, forming common aperture for foramen magnum, cavum sinus imparis, and paired fossae for scaphium and cover laterally for anterolateral surface of scaphium.	1.000	1.000	Vari (1983: no. 15)
128	<i>Presence or absence of reduced teeth not in direct contact with the jaws:</i> (0) absent; (1) present.	0.500	0.750	Vari (1983: no. H5)
129	<i>Presence or absence throughout ontogeny of dentition implanted on the maxilla:</i> (0) present; (1) absent.	0.500	0.750	Castro & Vari (2004)
130	<i>Presence or absence of premaxillary articular fossa:</i> (0) absent; (1) present.	0.500	0.667	Vari (1979: no. 7)
131	<i>Presence or absence of dentary replacement tooth trench:</i> (0) present; (1) absent.	0.333	0.667	Vari (1983: no. H3)
132	<i>Presence or absence of well-developed lateral shelf on quadrate.</i> (0) absent; (1) present.	0.333	0.714	Vari (1983: no. H1)
133	<i>Presence or absence of hyomandibular process that extends over posterodorsal region of metapterygoid:</i> (0) absent; (1) present.	0.500	0.889	Vari (1983: no. 57)
134	<i>Subdivision of anterior portion of preopercular laterosensory canal into two or more ossified tubes:</i> (0) not subdivided; (1) subdivided.	0.500	0.909	Vari (1983: no. H2)
135	<i>Presence or absence of distinct, posteroventrally aligned flange on lateral surface of opercle or further derived condition of that process:</i> (0) absent; (1) present.	0.500	0.800	Vari (1983: no. 13)
136	<i>Length of hyoid arch:</i> (0) moderately elongate; (1) foreshortened.	1.000	1.000	Vari (1983: no. 53)
137	<i>Angle of articulation between ventral portions of anterior and posterior ceratohyals:</i> (0) approximately vertical; (1) distinctly oblique.	0.500	0.889	Vari (1983: no. 54)
138	<i>Form of posterolateral portion of third infrapharyngobranchial:</i> (0) without flange; (1) with distinct dorsal flange.	1.000	1.000	Vari (1989a: no. 15)
139	<i>Form of posterior region of third infrapharyngobranchial:</i> (0) transversely moderately wide; (1) transversely very wide.	0.500	0.889	Vari (1983: no. 49)
140	<i>Form of uncinat process of third epibranchial:</i> (0) laterally aligned; (1) anteriorly aligned and overlying line of articulation between third infrapharyngobranchial and third epibranchial.	0.500	0.833	Vari (1989a: no. 13)
141	<i>Subdivision of anterior articular surface of the third epibranchial:</i> (0) not subdivided, medial portion not as in state 1; (1) subdivided, with medial portion of the articulation in form of medially directed ossified process extending along matching groove in anterodorsal portion of fourth infrapharyngobranchial.	1.000	1.000	Vari (1989a: no. 14)
142	<i>Form of anterior process of fourth epibranchial:</i> (0) rod-like to somewhat transversely expanded, but not simultaneously transversely and vertically expanded; (1) very well developed and transversely and vertically expanded.	1.000	1.000	Modified from Vari (1983: no. 51)

Table A1. *Continued*

No.	Character title and states	CI	RI	Citation and character number
143	<i>Alignment of dorsal process of fourth epibranchial</i> : (0) dorsally directed, not as in state 1; (1) orientated anteriorly with extension over dorsal surface of fourth infrapharyngobranchial.	1.000	1.000	Modified from Vari (1983: no. 5)
144	<i>Form of dorsal process of fourth epibranchial</i> : (0) thin; (1) thick.	1.000	1.000	Modified from Vari (1983: no. 50)
145	<i>Form of cartilaginous fifth epibranchial</i> : (0) small and not connected to fourth epibranchial; (1) anterodorsally elongate, attached to posterodorsal margin of fourth epibranchial, encircling fifth efferent branchial artery.	1.000	1.000	Vari (1983: no. 6)
146	<i>Form of complex formed by fourth infrapharyngobranchial and fourth upper pharyngeal tooth-plate</i> : (0) unconstricted, not as in state 1; (1) constricted, resulting in convex lateral margin to those conjoined elements.	1.000	1.000	Vari (1989a: no. 12)
147	<i>Form of fourth upper pharyngeal tooth-plate</i> : (0) flat; (1) curved and wrapping around fourth infrapharyngobranchial.	1.000	1.000	Vari (1983: no. 8)
148	<i>Alignment and contact of fourth and fifth upper pharyngeal tooth-plates</i> : (0) fourth upper pharyngeal tooth-plate aligned with and contacting fifth upper pharyngeal tooth-plate; (1) fourth upper pharyngeal tooth-plate angled and contacting fourth epibranchial.	1.000	1.000	Vari (1983: no. 47)
149	<i>Contact of fourth and fifth upper pharyngeal tooth-plate</i> : (0) in direct contact; (1) not in direct contact.	1.000	1.000	Vari (1983: no. 1)
150	<i>Vertical thickness of fifth upper pharyngeal tooth-plate</i> : (0) thin; (1) thick across wide area.	1.000	1.000	Vari (1983: no. 48)
151	<i>Presence or absence of dentition on fourth upper pharyngeal tooth-plate</i> : (0) present; (1) absent.	0.500	0.750	Vari (1983: no. 2)
152	<i>Size of dentition on fifth upper pharyngeal tooth-plate and plate of fifth ceratobranchial</i> . (0) absent or small and delicate; (1) large and robust.	1.000	1.000	Modified from Vari (1983: no. 45)
153	<i>Presence or absence of anteromedially directed process on fourth ceratobranchial's ventral surface</i> : (0) absent; (1) present.	0.500	0.800	Vari (1983: no. 12)
154	<i>Presence or absence of large sac-like, muscular epibranchial organ that extends dorsal to medial elements of dorsal portion of gill arches</i> : (0) absent; (1) present, See discussion in Vari (1983: 21–24) with regard to condition in Chilodontidae and Citharinidae.	1.000	1.000	Vari (1983: no. 7)
155	<i>Presence or absence of ventral elaborations of second and third vertebrae</i> : (0) absent; (1) present.	1.000	1.000	Modified from Vari (1979: no. 1)
156	<i>Fusion of postcleithra 2 and 3</i> : (0) unfused; (1) fused.	1.000	1.000	Vari (1979: no. 3)
157	<i>Presence or absence of two or more intercostal ligaments that join three or more anterior full pleural ribs</i> : (0) absent; (1) present.	1.000	1.000	Vari (1983: no. 58)
158	<i>Fusion of hypurals 1 and 2</i> : (0) unfused; (1) fused.	1.000	1.000	Vari (1979: no. 5)

These 35 characters were drawn from pre-existing phylogenetic studies and coded for the taxa examined herein. Although they are uninformative as to relationships within the Anostomidae, they were incorporated in the analysis to provide phylogenetic structure among the outgroup species. For each character, its number in the data matrix, its title, its alternative character states, its consistency and retention indices (CI and RI, respectively) on the final phylogenetic hypothesis herein and the citation for the original publication including the original character number are given. Characters that Vari (1983) enumerated as homoplasies include the capital letter 'H' in the citation for the original character number.

APPENDIX 3  
CHARACTER MATRIX

**Table A2.** Phylogenetic character matrix. Missing data or characters inapplicable to particular taxa are indicated by '?'. Character numbers correspond to those in the text and in Appendix 2. Polymorphisms are indicated by letters as follows: 0&1 = 'A', 1&2 = 'B', 2&3 = 'C', 0&1&2 = 'D', 4&5&6 = 'E'

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Abramites hypselonotus</i>	1	1	0	0	2	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0
<i>Anostomoides laticeps</i>	1	1	0	0	2	0	1	2	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	0	0
<i>Anostomus anostomus</i>	1	0	0	1	2	0	1	1	0	1	0	1	0	1	1	0	0	1	1	0	1	2	1	0	1	0	0	1	0	0
<i>Anostomus ternetzi</i>	1	0	0	1	2	0	1	1	0	1	0	1	1	1	1	0	0	1	1	0	1	2	1	0	1	0	0	1	0	0
<i>Gnathodolus bidens</i>	1	0	1	1	2	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	1	?	0	?	1	0	0	0	0	0
<i>Hypomasticus despaxi</i>	1	0	1	0	1	0	1	2	1	?	0	1	1	0	0	1	2	1	1	0	0	1	1	0	0	0	0	0	0	0
<i>Hypomasticus megalepis</i>	1	0	1	0	1	0	1	2	1	?	0	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
<i>Hypomasticus mormyrops</i>	1	0	1	0	1	0	1	2	0	0	1	A	0	0	1	2	1	1	0	0	1	1	0	0	0	0	0	0	0	0
<i>Hypomasticus pachycheilus</i>	1	0	0	0	2	0	1	1	0	0	0	1	0	0	1	2	1	1	0	0	1	1	0	0	0	0	0	0	0	0
<i>Laemolyta garmani</i>	1	1	0	0	2	0	1	1	0	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0
<i>Laemolyta orinocensis</i>	1	1	0	0	2	0	1	1	A	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Laemolyta proxima</i>	1	1	0	0	2	0	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0
<i>Laemolyta taeniata</i>	1	1	0	0	2	0	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0
<i>Leporellus pictus</i>	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
<i>Leporellus vittatus</i>	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
<i>Leporinus agassizi</i>	1	1	0	0	1	0	1	2	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Leporinus aripuanaensis</i>	1	1	0	0	1	0	1	2	1	?	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0
<i>Leporinus cf. ecuadorensis</i>	1	1	0	0	2	0	1	2	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus fasciatus</i>	1	1	0	0	1	0	1	2	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus cf. fasciatus</i>	1	1	0	0	1	0	1	2	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus friderici</i>	1	1	0	0	1	0	1	2	0	0	0	?	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus gomesi</i>	1	1	1	0	1	0	1	2	0	0	0	A	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Leporinus jatuncochi</i>	1	1	0	0	1	0	1	2	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus cf. moralesi</i>	1	1	0	0	B	0	1	2	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Leporinus cf. niceforoi</i>	1	1	0	0	1	0	1	2	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus ortomaculatus</i>	1	1	0	0	1	0	1	2	1	?	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus pellegrinii</i>	1	1	0	0	1	0	1	2	1	?	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Leporinus striatulus</i>	1	1	0	0	2	0	1	1	1	0	0	A	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0
<i>Leporinus tigrinus</i>	1	1	0	0	1	0	1	3	1	?	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0
<i>Petulanos intermedius</i>	1	1	0	0	1	0	1	2	0	1	0	1	1	1	1	0	0	1	1	0	1	2	1	0	1	0	0	0	0	0
<i>Petulanos plicatus</i>	1	1	0	0	1	1	0	1	2	0	1	1	1	1	1	0	0	1	1	0	1	2	1	0	1	0	0	0	0	0
<i>Pseudanans gracilis</i>	1	1	0	1	1	0	1	1	0	1	0	1	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0

Table A2. Continued

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Pseudanos irinae</i>	1	1	?	1	?	0	1	1	0	1	?	1	?	1	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0
<i>Pseudanos trimaculatus</i>	1	1	0	1	2	0	1	1	0	1	0	1	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0
<i>Pseudanos winterboftomi</i>	1	1	0	1	2	0	1	1	0	1	0	1	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0
<i>Rhytioidus argenteofuscus</i>	1	1	0	0	C	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	1	1
<i>Rhytioidus lauzannei</i>	1	1	0	0	3	1	0	C	0	1	0	1	0	1	0	1	1	1	0	0	0	1	1	0	0	0	1	0	1	1
<i>Rhytioidus microlepis</i>	1	1	0	0	3	1	0	2	0	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	1	0	1	1
<i>Sartor elongatus</i>	1	0	0	1	2	0	1	1	0	1	0	1	1	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0
<i>Schizodon fasciatus</i>	1	1	0	0	1	0	2	0	2	0	0	1	0	1	0	1	1	1	0	0	1	1	0	0	0	1	0	0	1	1
<i>Schizodon isognathus</i>	1	1	1	0	1	0	1	C	0	1	0	0	1	0	1	0	2	?	0	0	0	1	1	0	0	0	0	0	0	1
<i>Schizodon knerii</i>	1	1	1	0	1	0	1	2	0	1	0	0	1	0	1	0	1	?	0	0	0	1	1	0	0	0	0	0	0	1
<i>Schizodon nasutus</i>	1	1	0	0	2	0	0	1	0	1	0	0	1	0	0	0	2	1	0	0	0	1	1	0	0	0	1	0	0	1
<i>Schizodon scotrhobdotus</i>	1	1	0	0	1	0	0	2	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	1	0	0	1
<i>Schizodon vittatus</i>	1	1	0	0	1	0	0	2	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	1	0	0	1
<i>Synaptolaemus cingulatus</i>	1	0	0	1	2	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	1	2	1	1	1	0	0	0	0	0
<i>Caenotropus maculosus</i>	0	0	0	0	1	0	1	2	0	0	1	0	0	0	0	1	?	0	1	0	0	1	1	2	0	0	0	0	0	0
<i>Caenotropus mestomorgmatos</i>	0	0	0	0	1	0	1	2	0	0	1	0	0	0	0	1	?	0	1	0	0	1	1	2	0	0	0	0	0	0
<i>Chilodus punctatus</i>	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1	1	2	0	0	0	0	0	0
<i>Curimatopsis microlepis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Curimata inornata</i>	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	?	0	0	0	0	1	0	?	?	0	0	0	0	0
<i>Potamorhina laticeps</i>	0	1	0	0	0	0	1	1	0	0	0	2	1	0	1	0	?	0	0	0	0	1	0	?	?	0	0	0	0	0
<i>Prochilodus rubrotaeniatus</i>	0	0	0	0	2	0	1	1	0	0	0	2	0	0	1	0	?	0	0	0	0	2	0	?	?	0	0	0	0	0
<i>Senapaprochilodus insignis</i>	0	1	0	0	1	0	1	3	0	0	0	0	1	0	1	0	?	0	0	0	0	2	0	?	?	0	0	0	0	0
<i>Brycon falcatus</i>	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	0	?	0	0	0	0	1	0	?	?	0	0	0	0	0
<i>Hemiodus ocellatus</i>	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	?	0	1	0	0	2	0	?	?	0	0	0	0	0
<i>Parodon suborbitalis</i>	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	?	0	1	0	0	2	0	?	?	0	0	1	0	0
<i>Citharinus sp.</i>	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	0	?	0	0	0	0	1	0	?	?	0	0	0	0	0
<i>Distichodus sp.</i>	0	0	0	0	2	0	1	2	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	?	?	0	0	1	0	0
<i>Xenocharax spilurus</i>	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	?	0	0	0	0	1	0	?	?	0	0	0	0	0



Table A2. Continued

Taxon	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Abramites hypselonotus</i>	3	2	2	0	0	4	0	0	1	1	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Anostomoides laticeps</i>	4	2	3	1	0	4	0	A	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Anostomus anostomus</i>	4	3	3	0	0	4	0	1	0	0	2	2	3	?	1	2	0	1	1	1	0	0	0	0	0	0	0	0	0	1
<i>Anostomus ternetzi</i>	4	3	3	0	0	4	0	1	0	0	2	2	3	?	1	2	0	1	1	1	1	1	1	1	0	0	0	1	0	1
<i>Gnathodolus bidens</i>	4	2	C	?	1	1	1	1	?	?	2	?	?	?	1	2	0	1	1	1	1	1	1	1	0	0	1	1	0	1
<i>Hypomasticus despaxi</i>	3	2	2	0	0	3	2	?	?	?	?	?	?	?	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Hypomasticus megalopsis</i>	3	1	2	0	0	4	0	0	0	1	1	1	1	?	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Hypomasticus mormyrops</i>	4	1	2	0	0	4	0	0	0	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Hypomasticus pachycheilus</i>	4	1	2	0	0	4	0	0	0	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Laemolyta garmani</i>	4	3	3	0	0	4	0	1	0	0	0	0	0	?	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0	1
<i>Laemolyta orinocensis</i>	4	4	4	0	0	4	0	1	0	0	0	0	0	?	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0	1
<i>Laemolyta proxima</i>	4	4	4	0	0	4	0	1	0	0	0	0	0	?	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0	1
<i>Laemolyta taeniata</i>	4	4	4	0	0	4	0	1	0	0	0	0	0	?	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0	1
<i>Leporellus pictus</i>	4	2	B	0	0	4	0	0	0	0	1	1	1	?	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Leporellus vittatus</i>	4	2	3	0	0	4	0	0	0	0	1	1	1	?	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Leporinus agassizi</i>	4	2	2	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus aripuanensis</i>	4	1	2	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus cf. ecuadorensis</i>	4	2	2	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus fasciatus</i>	4	2	3	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus cf. fasciatus</i>	4	2	3	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus friderici</i>	4	3	3	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus gomesi</i>	4	1	2	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus jatuncochi</i>	3	3	3	1	2	3	1	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus cf. moralesi</i>	3	3	3	1	0	4	0	0	0	0	1	2	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus cf. niceforoi</i>	4	3	3	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus ortomaculatus</i>	4	3	3	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus pellegrinii</i>	4	3	3	0	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus striatus</i>	4	3	2	0	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Leporinus tigrinus</i>	3	3	3	1	0	4	0	0	0	0	1	1	1	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Petulanos intermedius</i>	4	2	3	0	0	4	0	1	0	0	1	1	3	?	1	2	0	1	1	1	0	1	1	0	0	0	0	0	0	1
<i>Petulanos plicatus</i>	4	2	3	0	0	4	0	1	0	0	1	1	3	?	1	2	0	1	1	1	0	1	1	0	0	0	0	0	0	1



Table A2. Continued

Taxon	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	
<i>Abramites hypselonotus</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	
<i>Anostomoides laticeps</i>	1	1	0	0	1	0	1	1	0	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	0	1	0	1	1	1	
<i>Anostomus anostomus</i>	1	1	0	0	1	0	0	?	?	0	1	2	1	1	1	1	2	0	1	1	1	0	1	1	0	1	0	0	0	0	
<i>Anostomus ternetzi</i>	1	1	0	0	1	0	0	?	?	0	1	2	1	1	1	2	0	1	1	?	1	0	1	1	1	1	0	0	0	0	
<i>Gnathodolus bidens</i>	0	1	?	0	1	1	0	?	?	1	1	2	0	0	1	1	0	1	1	?	1	0	1	1	1	1	1	0	0	0	
<i>Hypomasticus despaxi</i>	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	
<i>Hypomasticus megalopsis</i>	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	
<i>Hypomasticus mormyrops</i>	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	
<i>Hypomasticus pachycheilus</i>	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	
<i>Laemolyta garmani</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	1	1
<i>Laemolyta orinocensis</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	1	1
<i>Laemolyta proxima</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	1	1
<i>Laemolyta taeniata</i>	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	1	1
<i>Leporellus pictus</i>	1	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
<i>Leporellus vittatus</i>	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
<i>Leporinus agassizi</i>	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus aripuanensis</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus cf. ecuadorensis</i>	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus fasciatus</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus cf. fasciatus</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus friderici</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus gomesi</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus jatuncochi</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus cf. moralesi</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus cf. niceforoi</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus ortomaculatus</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus pellegrinii</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus striatus</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Leporinus tigrinus</i>	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0
<i>Petulanos intermedius</i>	1	1	0	0	0	1	0	?	?	0	1	2	1	1	1	1	2	1	1	1	1	0	1	1	0	0	1	0	1	0	0
<i>Petulanos plicatus</i>	1	1	0	0	0	1	0	?	?	0	1	2	1	1	1	1	2	1	1	1	1	0	1	1	0	0	1	0	1	0	0

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Table A2. Continued

Taxon	Character																															
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90		
<i>Pseudanos gracilis</i>	1	1	0	0	1	0	0	1	0	0	0	2	1	0	1	1	2	0	0	1	1	0	0	1	1	1	0	1	0	1	1	A
<i>Pseudanos irinae</i>	?	?	?	?	?	0	0	?	?	0	0	2	1	0	1	1	2	0	0	1	1	1	0	1	1	1	0	?	0	1	1	
<i>Pseudanos trimaculatus</i>	1	1	0	0	1	0	0	?	?	0	0	2	1	0	1	1	2	0	0	1	1	0	1	1	1	1	0	1	0	1	1	
<i>Pseudanos winterbottomi</i>	1	1	0	0	1	0	0	?	?	0	0	2	1	0	1	1	2	0	1	1	1	0	1	1	1	1	0	1	0	1	1	
<i>Rhytioidus argenteofuscus</i>	1	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Rhytioidus lauzannei</i>	1	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Rhytioidus microlepis</i>	1	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Sartor elongatus</i>	0	1	?	0	1	1	0	?	?	0	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	
<i>Schizodon fasciatus</i>	1	1	1	0	1	0	1	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Schizodon isognathus</i>	1	1	1	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Schizodon knerii</i>	1	1	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Schizodon nasutus</i>	1	1	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Schizodon scotrhobdotus</i>	1	1	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1	
<i>Schizodon vittatus</i>	1	1	1	0	1	0	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	
<i>Synaptolaemus cingulatus</i>	1	1	0	0	1	1	0	?	?	0	1	2	1	0	1	1	2	1	1	1	1	0	1	1	1	1	1	1	1	0	0	
<i>Caenotropus maculosus</i>	1	0	0	0	1	0	?	?	?	0	0	0	0	0	0	0	1	0	?	?	0	0	0	0	0	2	0	0	0	1	1	
<i>Caenotropus mestomorgnatus</i>	1	0	0	0	1	0	?	?	?	0	0	0	0	0	0	0	1	0	?	?	0	0	0	0	0	2	0	0	0	0	0	
<i>Chilodus punctatus</i>	1	0	0	0	1	0	?	?	?	0	0	0	0	0	0	0	1	0	?	?	0	0	0	0	0	2	1	0	0	1	1	
<i>Curimatopsis microlepis</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	1	1	?	?	?	?	0	0	0	0	0	2	0	0	1	0	1	
<i>Curimata inornata</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	1	1	?	?	?	?	0	0	0	0	0	2	0	0	0	1	1	
<i>Potamorhina laticeps</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	1	1	?	?	?	?	0	0	0	0	0	2	0	0	0	1	1	
<i>Prochilodus rubrotaeniatus</i>	1	1	0	0	0	0	?	?	?	0	2	0	0	0	1	0	0	0	?	?	0	0	1	1	1	0	0	0	0	1	1	
<i>Semaprochilodus insignis</i>	1	1	0	0	0	0	?	?	?	0	2	0	0	0	1	0	0	0	?	?	0	0	1	1	0	0	0	0	1	1	1	
<i>Brycon falcatus</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	0	0	?	?	?	?	0	0	0	0	0	2	0	1	0	1	1	
<i>Hemiodus ocellatus</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	0	1	?	?	?	?	0	0	0	0	0	2	0	0	0	1	1	
<i>Parodon suborbitalis</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	1	0	?	?	?	?	?	?	?	?	0	2	0	0	0	1	0	
<i>Citharinus</i> sp.	1	0	0	2	1	0	?	?	?	0	2	0	0	0	?	1	?	?	?	?	?	?	?	?	0	2	0	0	0	1	1	
<i>Distichodus</i> sp.	1	?	?	2	1	0	?	?	?	0	2	0	0	0	0	1	2	?	?	?	?	?	?	?	0	2	0	1	0	1	1	
<i>Xenocharax spilurus</i>	1	0	0	2	1	0	?	?	?	0	2	0	0	0	0	0	?	?	?	?	?	?	?	?	0	2	0	1	0	1	0	



Table A2. Continued

Taxon	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120		
<i>Abramites hypselonotus</i>	1	0	0	2	2	1	0	0	0	0	0	0	0	2	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0		
<i>Anostomoides laticeps</i>	1	0	0	1	2	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Anostomus anostomus</i>	1	1	0	1	2	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Anostomus ternetzi</i>	1	1	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Gnathodolus bidens</i>	1	1	0	1	2	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Hypomasticus despaxi</i>	1	1	0	2	2	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	
<i>Hypomasticus megalopsis</i>	1	1	0	2	2	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	
<i>Hypomasticus mormyrops</i>	1	1	0	2	2	2	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	
<i>Hypomasticus pachycheilus</i>	1	1	0	2	2	2	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	
<i>Laemolyta garmani</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	
<i>Laemolyta orinocensis</i>	1	1	0	1	2	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	
<i>Laemolyta proxima</i>	1	1	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Laemolyta taeniata</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	
<i>Leporellus pictus</i>	1	1	0	1	2	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	
<i>Leporellus vittatus</i>	1	1	0	1	2	2	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	
<i>Leporinus agassizi</i>	1	1	0	1	2	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Leporinus aripuanensis</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Leporinus cf. ecuadorensis</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	A	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	
<i>Leporinus fasciatus</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	
<i>Leporinus cf. fasciatus</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	
<i>Leporinus friderici</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus gomesi</i>	1	1	0	2	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus jatuncochi</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus cf. moralesi</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus cf. niceforoi</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus ortomaculatus</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus pellegrinii</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus striatus</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Leporinus tigrinus</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Petulanos intermedius</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Petulanos plicatus</i>	1	1	0	1	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Table A2. Continued

Taxon	Character																														
	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	
<i>Pseudanos gracilis</i>	1	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Pseudanos irinae</i>	1	0	0	1	2	1	0	0	?	0	?	0	0	0	0	A	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Pseudanos trimaculatus</i>	1	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Pseudanos winterbottomi</i>	1	0	0	1	2	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Rhytioidus argenteofuscus</i>	1	0	0	2	3	2	0	0	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1
<i>Rhytioidus lauzannei</i>	1	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0
<i>Rhytioidus microlepis</i>	1	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0
<i>Sartor elongatus</i>	1	1	0	1	2	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Schizodon fasciatus</i>	1	0	0	2	3	2	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0
<i>Schizodon isognathus</i>	1	0	0	2	3	2	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1
<i>Schizodon knerii</i>	1	0	0	2	3	2	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1
<i>Schizodon nasutus</i>	1	1	0	2	3	2	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1
<i>Schizodon scotorhabdotus</i>	1	0	0	2	2	2	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1
<i>Schizodon vittatus</i>	1	0	0	2	3	2	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0
<i>Synaptolaemus cingulatus</i>	1	0	0	1	2	1	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0
<i>Caenotropus maculosus</i>	0	1	0	1	3	2	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Caenotropus mestomorgnatus</i>	0	1	0	1	3	2	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chilodus punctatus</i>	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1
<i>Curimatopsis microlepis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	0	0	0	0
<i>Curimata inornata</i>	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	A	D	0	0	0	0	0	0	0	0	0
<i>Potamorhina laticeps</i>	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	A	0	0	A	2	0	0	1	0	0	0	0	0	0
<i>Prochilodus rubrotaeniatus</i>	0	1	0	0	?	0	0	0	1	0	0	0	0	0	1	0	0	A	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Semaprochilodus insignis</i>	0	1	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Brycon falcatus</i>	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0
<i>Hemiodus ocellatus</i>	0	1	0	0	2	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	0	0	1	0	0	?	1	0	0
<i>Parodon suborbitalis</i>	0	1	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Citharinus</i> sp.	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	1	2	0	0	?	?	?	?	?	?	?
<i>Distichodus</i> sp.	0	1	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	1	2	0	0	?	?	?	?	?	?	?
<i>Xenocharax spilurus</i>	0	1	0	0	2	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	2	0	0	1	0	0	0	0	0	0

Table A2. Continued

Character	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	
<i>Abramites hypselonotus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1
<i>Anostomoides laticeps</i>	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Anostomus anostomus</i>	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Anostomus ternetzi</i>	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Gnathodolus bidens</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Hypomasticus despaxi</i>	1	?	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Hypomasticus megalepis</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Hypomasticus mormyrops</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Hypomasticus pachycheilus</i>	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Laemolyta garmani</i>	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Laemolyta orinocensis</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Laemolyta proxima</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Laemolyta taeniata</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporellus pictus</i>	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporellus vittatus</i>	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus agassizi</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus aripuanensis</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus cf. ecuadorensis</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus fasciatus</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus cf. fasciatus</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus friderici</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus gomesi</i>	0	2	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus jatuncochi</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus cf. moralesi</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus cf. niceforoi</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus ortomaculatus</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus pellegrinii</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus striatus</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Leporinus tigrinus</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Petulanos intermedius</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1
<i>Petulanos plicatus</i>	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1

Table A2. Continued

Taxon	Character																															
	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150		
<i>Pseudanos gracilis</i>	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Pseudanos irinae</i>	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Pseudanos trimaculatus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Pseudanos winterbottomi</i>	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Rhytioidus argenteofuscus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Rhytioidus lauzannei</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Rhytioidus microlepis</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Sartor elongatus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Schizodon fasciatus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1
<i>Schizodon isognathus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Schizodon knerii</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Schizodon nasutus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Schizodon</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>scotrhabdatus</i>																																
<i>Schizodon vittatus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Synaptolaemus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>cingulatus</i>																																
<i>Caenotropus maculosus</i>	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Caenotropus</i>	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>mestomorgnatus</i>																																
<i>Chilodus punctatus</i>	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	
<i>Curimatopsis microlepis</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	
<i>Curimata inornata</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	
<i>Potamorhina laticeps</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	
<i>Prochilodus</i>	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	
<i>rubrotaeniatus</i>																																
<i>Semaprochilodus</i>	0	0	1	0	0	1	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0	0	
<i>insignis</i>																																
<i>Brycon falcatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hemiodus ocellatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Parodon suborbitalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Citharinus</i> sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Distichodus</i> sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Xenocharax spilurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	



Table A2. Continued

Taxon	151	152	153	154	155	156	157	158
<i>Abramites hypselonotus</i>	1	1	0	0	0	0	1	0
<i>Anostomoides laticeps</i>	1	1	0	0	0	0	1	0
<i>Anostomus anostomus</i>	1	1	0	0	0	0	1	0
<i>Anostomus ternetzi</i>	1	1	0	0	0	0	1	0
<i>Gnathodolus bidens</i>	1	1	0	0	0	0	1	0
<i>Hypomasticus despaxi</i>	1	1	0	0	0	0	1	0
<i>Hypomasticus megalepis</i>	1	1	0	0	0	0	1	0
<i>Hypomasticus momyrops</i>	1	1	0	0	0	0	1	0
<i>Hypomasticus pachycheilus</i>	1	1	0	0	0	0	1	0
<i>Laemolyta garmani</i>	1	1	0	0	0	0	1	0
<i>Laemolyta orinocensis</i>	1	1	0	0	0	0	1	0
<i>Laemolyta proxima</i>	1	1	0	0	0	0	1	0
<i>Laemolyta taeniata</i>	1	1	0	0	0	0	1	0
<i>Leporellus pictus</i>	1	1	0	0	0	0	1	0
<i>Leporellus vittatus</i>	1	1	0	0	0	0	1	0
<i>Leporinus agassizi</i>	1	1	0	0	0	0	1	0
<i>Leporinus aripuanensis</i>	1	1	0	0	0	0	1	0
<i>Leporinus cf. ecuadorensis</i>	1	1	0	0	0	0	1	0
<i>Leporinus fasciatus</i>	1	1	0	0	0	0	1	0
<i>Leporinus cf. fasciatus</i>	1	1	0	0	0	0	1	0
<i>Leporinus friderici</i>	1	1	0	0	0	0	1	0
<i>Leporinus gomesi</i>	1	1	0	0	0	0	1	0
<i>Leporinus jatuncochi</i>	1	1	0	0	0	0	1	0
<i>Leporinus cf. moralesi</i>	1	1	0	0	0	0	1	0
<i>Leporinus cf. niceforoi</i>	1	1	0	0	0	0	1	0
<i>Leporinus ortomaculatus</i>	1	1	0	0	0	0	1	0
<i>Leporinus pellegrinii</i>	1	1	0	0	0	0	1	0
<i>Leporinus striatus</i>	1	1	0	0	0	0	1	0
<i>Leporinus tigrinus</i>	1	1	0	0	0	0	1	0
<i>Petulanos intermedius</i>	1	1	0	0	0	0	1	0
<i>Petulanos plicatus</i>	1	1	0	0	0	0	1	0

Table A2. Continued

Taxon	151	152	153	154	155	156	157	158
<i>Pseudanos gracilis</i>	1	1	0	0	0	0	1	0
<i>Pseudanos irinae</i>	1	1	0	0	0	0	1	0
<i>Pseudanos trimaculatus</i>	1	1	0	0	0	0	1	0
<i>Pseudanos winterbottomi</i>	1	1	0	0	0	0	1	0
<i>Rhytioidus argenteofuscus</i>	1	1	0	0	0	0	1	0
<i>Rhytioidus lauzannei</i>	1	1	0	0	0	0	1	0
<i>Rhytioidus microlepis</i>	1	1	0	0	0	0	1	0
<i>Sartor elongatus</i>	1	1	0	0	0	0	1	0
<i>Schizodon fasciatus</i>	1	1	0	0	0	0	1	0
<i>Schizodon isognathus</i>	1	1	0	0	0	0	1	0
<i>Schizodon knerii</i>	1	1	0	0	0	0	1	0
<i>Schizodon nasutus</i>	1	1	0	0	0	0	1	0
<i>Schizodon scotorhabdotus</i>	1	1	0	0	0	0	1	0
<i>Schizodon vittatus</i>	1	1	0	0	0	0	1	0
<i>Synaptolaemus cingulatus</i>	1	1	0	0	0	0	1	0
<i>Caenotropus maculosus</i>	1	1	0	0	0	0	1	0
<i>Caenotropus mestomorgmatos</i>	1	1	0	0	0	0	1	0
<i>Chilodus punctatus</i>	1	0	0	0	0	?	1	0
<i>Curimatopsis microlepis</i>	1	0	1	1	0	0	0	0
<i>Curimata inornata</i>	1	0	1	1	0	0	0	0
<i>Potamorhina laticeps</i>	1	0	1	1	0	0	0	0
<i>Prochilodus rubrotaeniatus</i>	1	0	1	1	0	0	0	0
<i>Semaprochilodus insignis</i>	1	0	1	1	0	0	0	0
<i>Brycon falcatus</i>	0	0	0	0	0	0	0	0
<i>Hemiodus ocellatus</i>	0	0	1	0	0	0	0	1
<i>Parodon suborbitalis</i>	0	0	0	0	0	0	0	0
<i>Citharinus</i> sp.	1	0	0	0	1	1	0	1
<i>Distichodus</i> sp.	0	0	0	0	1	1	0	1
<i>Xenocharax spilurus</i>	0	0	0	0	1	1	0	1

## APPENDIX 4

## SYNAPOMORPHY LIST

The 32 numbered clades in Figure 7 and in the list below appear in all of the most parsimonious trees recovered during phylogenetic analysis. Lists of the character state transitions that optimize at the branch subtending each numbered clade in the strict consensus phylogeny are given, with unambiguously optimized synapomorphies appearing first (indicated by bold arrows), followed by ambiguous optimizations (indicated by normal arrows). Transitions optimized as autapomorphies of nominal genera or subgenera represented by only one species in the analysis also appear below. Each synapomorphic character state transition is followed by a brief description of each synapomorphy. Finally, information appears on whether that state transition is a reversal of a previous character state change within the Anostomidae, whether other clades within the Anostomidae have acquired that character state independently, and whether additional state transitions in the character in question occur within the clade defined by the synapomorphy. Not all state changes in each character are necessarily listed below; such information appears in the individual character descriptions.

Because character optimizations were performed on a strict consensus phylogeny, caution must be exercised in interpreting some synapomorphies involving clades that contain basal polytomies (i.e. clades 8, 10, 18, 25 and 26). In some cases, alternative resolutions of the polytomies would shift the interpretation of the synapomorphies up or down one hierarchical level. For example, state 1 of character 79 (aspect ratio of metapterygoid–quadrate fenestra) is interpreted on the strict consensus as an ambiguous synapomorphy for clade 25 (ACCTRAN optimization) with a reversal to state 0 in clade 26. Were the basal polytomy in clade 25 resolved as in the majority-rule consensus (Fig. 6), state 1 of character 79 would optimize instead as an unambiguous synapomorphy for a clade containing *Pseudanos winterbottomi* and clade 27.

## Clade 1: Family Anostomidae

- Character 31, state 5 → 4; four teeth on premaxilla; further modified in clades 5, 9, 11 and *Leporinus cf. moralesi*
- Character 37, state 4 → 0; dentary teeth spade or chisel-shaped, tapering to pointed or blunt distal margin with or without additional cusping; further modified in *Hypomasticus despaxi*, *L. jatuncochi* and clade 32
- Character 38, state 1 → 0; dentary teeth with large, well-developed posterior lamina; reversed in clade 21
- Character 45, state 0 → 1; ascending process of premaxilla large, well-developed and distinctly triangular overall
- Character 50, state 1 → 0; anterolateral flange of maxilla merges with ventral portion of maxilla on lateral face of ventral portion; reversed in clade 25
- Character 51, state 1 → 0; anterolateral and ventral flanges of maxilla rotated relative to each other along main axis of bone with result that ventral portion of maxilla lies in parasagittal plane and anterolateral flange of bone lies in transverse plane; reversed in clade 31
- Character 62, state 0 → 1; dentary with short laterosensory canal segment, terminating at, or posterior to, approximate longitudinal midpoint of bone
- Character 65, state 1 → 0; retroarticular laterally situated in lower jaw and deeply recessed into pocket formed primarily by dentary and to lesser degree by anguloarticular; line drawn along ventral margin of retroarticular clearly bisects ventral portion of dentary; reversed in clade 13
- Character 73, state 0 → 1; distinct process on lateral surface of ectopterygoid present; reversed in *Gnathodolus*
- Character 83, state 0 → 1; interopercular–mandibular ligament elongate, interopercle notably separated from retroarticular
- Character 84, state 0 → 1; presence of large shelf on lateral surface of preopercle that serves as origin for portion of adductor mandibulae muscle
- Character 85, state 2 → 0; anterodorsal process of preopercle that extends between symplectic and quadrate well-developed with broad triangular or rhomboidal form; further modified in clade 25
- Character 90, state 1 → 0; posterodorsal margin of opercle with slight or pronounced concavity; reversed in clade 13 with subsequent transition back to state 0 in clade 27, polymorphic in *Pseudanos gracilis*
- Character 91, state 0 → 1; curved anterior process of third epibranchial that extends medially over dorsal surface of fourth infrapharyngobranchial present
- Character 106, state 0 → 1; supraneural dorsal to Weberian apparatus present; reversed in clades 9 and 13, subsequently reversed in clade 25 and again in *Sartor*, polymorphic in *Leporinus cf. ecuadorensis* and *Pseudanos irinae*.
- Character 107, state 0 → 1; presence of two or more intercostal ligaments uniting in total four or more of anterior full ribs
- Character 134, state 0 → 1; anterior portion of preopercular laterosensory canal subdivided into two or more ossified tubes
- Character 22, state 1 → 0 (ACCTRAN); articular facets of vomer with palatines angled toward each

other anteriorly; further modified in clades 5 and 13, reversed to state 0 in clade 21, further modified in clade 27, reversed to state 0 in clade 32

- Character 33, state 1 → 2 (ACCTTRAN); second and third teeth of premaxilla with two cusps; modified to state 3 in *Leporellus vittatus* and clade 8, state 2 occurring again in clade 9, *Leporinus agassizi*, *L. aripuanaensis* and *L. cf. ecuadorensis*, further modified in *Schizodon* and clade 23, polymorphic for states 2 and 3 in *Gnathodolus*
- Character 8, state 1 → 2 (DELTRAN); two intermediate pores along ossified portion of sensory canal of second infraorbital; reversed in *Hypomasticus pachycheilus*, *Rhytiodus argenteofuscus*, *Schizodon nasutus* and clade 21 with subsequent transition back to state 2 in *Petulanos*, transition to state 3 in *Leporinus tigrinus*, polymorphic for states 2 and 3 in *Rhytiodus lauzannei* and *Schizodon isognathus*
- Character 60, state 0 → 1 (DELTRAN, ambiguity due to inapplicability of character to Chilodontidae and Curimatidae); dentary replacement tooth trench large and with distinct ventral fenestra
- Character 108, state 0 → 1 (DELTRAN); ten branched dorsal-fin rays present
- Character 24, state ? → 0 (ambiguous due to inapplicability of character to outgroups other than Chilodontidae); lateral ethmoid–ectopterygoid ligament inserts on ventral surface of anterior wing of lateral ethmoid; further modified in *Synaptolaemus*

Vari (1983) also detailed five myological synapomorphies for the Anostomidae which are listed below. These were not reinvestigated due to lack of appropriate material for dissection for many pertinent taxa.

- Presence of triangular, autogenous section of levator arcus palatini that arises from posterodorsal portion of orbital cavity and inserts on anterodorsal margin of hyomandibular
- Subdivision of A1 portion of adductor mandibulae
- Posterior part of A2 portion of adductor mandibulae medial of levator arcus palatini large and with partial origin on hyomandibular
- A3 and A2 portions of the adductor mandibulae with anterior dorsal expansion resulting in contact of these muscles with each other dorsal to tendon that attaches to main body of A2
- Absence of A<sub>0</sub> portion of adductor mandibulae

#### Clade 2: *Leporellus*

- Character 17, state 1 → 0; ventral process of mesethmoid runs vertically or nearly so, anterior portion of vomer positioned directly ventral to ventral process of mesethmoid; acquired independently in *Abramites* and clade 25
- Character 26, state 0 → 1; presence of fenestra on portion of lateral wing of lateral ethmoid situated

dorsal to lateral ethmoid–ectopterygoid ligament; acquired independently in *Anostomoides*

- Character 32, state 1 → 2; symphyseal tooth of premaxilla with two cusps; acquired independently in, *Anostomoides*, *Gnathodolus*, *Petulanos*, *Hypomasticus despaxi*, *Leporinus agassizi*, *L. cf. ecuadorensis*, clade 9 and in either clade 10 with reversal in clade 11 or in *L. fasciatus* and *L. cf. fasciatus* (optimization ambiguous)
- Character 64, state 0 → 1; retroarticular elongate and cup-shaped, with its length in lateral view more than three times its height, with interopercular–mandibular ligament attaching in cup-shaped depression near anterior margin of bone
- Character 93, state 0 → 1; second basibranchial with prominent lateral flanges resulting in overall shape resembling violin
- Character 98, state 0 → 1; presence of inflection point in joint between anterior and posterior ceratohyals and corresponding process of anterior ceratohyal running ventral to posterior ceratohyal
- Character 114, state 0 → 1; lobes of caudal fin covered with scales
- Character 123, state 0 → 1; caudal fin with wide dark stripes extending across much of each lobe; stripe(s) of dorsal lobe run from anterodorsal to posteroventral; stripe(s) of ventral lobe run from anteroventral to posterodorsal
- Character 15, state 1 → 0 (DELTRAN); anterior portion of mesethmoid ventrally directed and with strong hook; acquired independently in *Hypomasticus*, *Leporinus jatuncochi* and *Schizodon nasutus*
- Character 22, state 1 → 0 (DELTRAN); articular facets of vomer with palatines angled toward each other anteriorly; state 0 acquired independently in clade 7 and *Sartor* (reversal after transition to state 2 in clade 27)
- Character 120, state 0 → 1 (DELTRAN); complete stripe of approximately height of one scale or greater running along lateral line from opercle to caudal peduncle in majority of examined specimens; acquired independently in *Leporinus striatus* and clade 13
- Character 122, state 0 → 1 (DELTRAN); most scales with small, dark spot lying under scale creating overall appearance of row of such spots along center of each scale row; acquired independently in *Anostomus anostomus*, *Pseudanos gracilis*, *P. irinae*, and *P. winterbottomi*.

Clade 3: *Abramites*, *Anostomoides*, *Anostomus*, *Gnathodolus*, *Hypomasticus*, *Laemolyta*, *Leporinus*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon*, *Synaptolaemus*

- Character 1, state 0 → 1; antorbital relatively large, with distinct horizontally directed flange running



ventral to nasal cavity; flat bony plate may join vertical and horizontal portions of antorbital to varying degrees

- Character 13, state 0 → 1; anteroventral portion of sixth infraorbital not greatly expanded and overlapping anteroventral process of sphenotic; reversed in *Abramites hypselonotus* and *Anostomus anostomus*, polymorphic in *Hypomasticus mormyrops* and *Leporinus striatus*
- Character 18, state 0 → 1; distinct ventromedial plate-like process of mesethmoid extends ventrally and posteriorly towards vomer; reversed in *Laemolyta proxima*
- Character 49, state 0 → 1; area of attachment of primordial ligament on medial surface of maxilla located within ventral one-half of longest axis of bone
- Character 52, state 1 → 0; ventral portion of maxilla narrow, only slightly expanded in axis transverse to long axis of bone; reversed in clade 29
- Character 76, state 0 → 1; posterodorsal and posterior processes of quadrate entirely or almost entirely joined by thin intervening plate of bone with length of unfused portion of posterodorsal process much less than twice width of process
- Character 87, state 0 → 1; symplectic long with posterior margin of bone situated proximate to ventral margin of hyomandibular
- Character 118, state 0 → 1; series of one or more dark spots with distinct margins present along lateral-line scale row, each spot approximately one to two scales in height; reversed in *Hypomasticus despaxi*, *Leporinus agassizi*, *L. pellegrinii* and clades 9, 10 and 12, acquired independently in clade 26 and in either clade 29 with reversal in *Synaptaelamus* or in *Petulanos* and clade 32 (optimization ambiguous)
- Character 3, state 0 → 1 (ACCTRAN); supraorbital with deeply concave, distinctly notched anterior or anterolateral margin; reversed in clade 8, acquired independently in *Schizodon knerii*, *S. isognathus* and *Gnathodolus bidens*
- Character 96, state 2 → 1 (ACCTRAN); one or two complete rows of teeth on tooth-plate of fifth ceratobranchial; reversed in clades 6 and 15, reacquired in clade 17
- Character 105, state 0 → 1 (ACCTRAN); presence of dorsal process of third vertebra overlapping neural complex laterally; reversed in *Hypomasticus despaxi*, *H. pachycheilus*, *Laemolyta proxima*, *Leporinus* cf. *moralesi*, *L. striatus*, *L. tigrinus*, *L. pellegrinii*, and clade 25
- Character 120, state 1 → 0 (ACCTRAN); complete stripe along lateral-line absent; reversed in *Hypomasticus despaxi*, *Leporinus striatus* and clade 13; lost independently in clades 17, 26 and 29

- Character 122, state 1 → 0 (ACCTRAN); centers of scales same colour as, or lighter than, scale margins; no series of small dark spots along center of each scale row; reversed in clade 25 with independent reacquisition in *Pseudanos trimaculatus* and clade 27, followed by another reversal in *Anostomus anostomus*
- Character 33, state 1 → 2 (DELTRAN); two cusps on each of second and third teeth of premaxilla; further modified to state 3 in *Leporinus frederici*, *L. cf. moralesi*, *L. cf. niceforoi*, *L. ortomaculatus* and clades 10 and 12, with subsequent modification to state 4 in *Schizodon* and clade 23
- Character 68, state 0 → 1 (DELTRAN, ambiguity due to inapplicability of character to outgroups); process of palatine with distinct lateral, anterolateral or anteroventral orientation
- Character 95, state 1 → 2 (DELTRAN); most teeth on fifth upper pharyngeal tooth-plate bicuspid but with occasional teeth unicuspid; further modified to state 3 in *Rhytiodus argenteofuscus* and *Schizodon*

#### Clade 4: *Hypomasticus*

- Character 16, state 0 → 1; mesethmoid with two distinct lateral processes that fit into concavities on medial surface of premaxilla
- Character 46, state 1 → 0; premaxilla with vertical or anterodorsal inclination
- Character 55, state 0 → 1; ascending process of anguloarticular very wide, forming pronounced vertical ridge perpendicular to dentary; acquired independently in *Schizodon*
- Character 56, state 0 → 1; dorsal portion of ascending process of anguloarticular in form of deep trough; acquired independently in *Schizodon nasutus*
- Character 17, state 1 → 2 (ACCTRAN); ventral process of mesethmoid posteroventrally aligned; reversed in *Hypomasticus megalepis*, acquired independently in clade 20
- Character 22, state 0 → 1 (ACCTRAN); articular facets of vomer with palatines parallel and widely separated; acquired independently in clade 13, reversed in clade 21 with further modification in clade 27 and subsequent reversal in clade 32.
- Character 15, state 1 → 0 (DELTRAN); anterior portion of mesethmoid ventrally directed and with strong hook; acquired independently in *Leporellus*, *Leporinus jatuncochi* and *Schizodon nasutus*

#### Clade 5: *Hypomasticus despaxi*, *H. megalepis*

- Character 9, state 0 → 1; fourth and fifth infraorbitals fused; acquired independently in *Leporinus aripuanaensis*, *L. ortomaculatus*, *L. tigrinus* and *L. pellegrinii*, polymorphic in *Laemolyta orinocensis*.

- Character 31, state 4 → 3; three teeth on premaxilla; acquired independently in *Leporinus* cf. *moralesi* and clades 9 and 11
- Character 3, state 0 → 1 (DELTRAN); supraorbital with deeply concave, distinctly notched anterior or anterolateral margin; acquired independently in *Hypomasticus mormyrops*, *Leporinus gomesi*, *Schizodon isognathus*, *S. knerii* and *Gnathodolus*
- Character 96, state 2 → 1 (DELTRAN); one or two complete rows of teeth present on tooth-plate of fifth ceratobranchial; acquired independently in clade 7

Clade 6: *Hypomasticus mormyrops*, *H. pachycheilus*

- Character 40, state 0 → 1; distinct distal notch divides posterior lamina of second or third tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites*, *Leporinus* cf. *moralesi*, and clade 15
- Character 47, state 0 → 1; premaxilla with large, block-like anterodorsal process that fits above lateral process of mesethmoid
- Character 96, state 1 → 2 (ACCTTRAN); three or more complete rows of teeth present on tooth-plate of fifth ceratobranchial; acquired independently in clade 15 with subsequent reversal in clade 17
- Character 17, state 1 → 2 (DELTRAN); ventral process of mesethmoid horizontally or slightly posterodorsally aligned, vomer situated directly posterior of ventral portion of mesethmoid; acquired independently in *Hypomasticus despaxi* and clade 19

Clade 7: *Abramites*, *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Leporinus*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon*, *Synaptolaemus*

- Character 2, state 0 → 1; anterior margin of antorbital positioned distinctly anterior of anterodorsal opening of sensory canal of first infraorbital; reversed in clade 27
- Character 19, state 1 → 0; mesethmoid wide, with maximum width along transverse axis greater than maximum length along longitudinal axis; acquired independently in *Hypomasticus megalepis*, reversed in clade 27
- Character 34, state 0 → 1; medial surface of second and third teeth of premaxilla elaborated, with raised ridge originating at anterior edge of tooth and extending across medial surface of each tooth; reversed in clades 9 and 12, reacquired in *Anostomoides*
- Character 48, state 0 → 1; maxilla having vertical or posterodorsal orientation, with dorsal tip of maxilla situated directly dorsal to, or distinctly posterior of, ventral margin of bone
- Character 72, state 0 → 1; ectopterygoid vertically orientated with vertical through anterodorsal limit

of ectopterygoid passing through ventral portion of ectopterygoid; reversed in *Leporinus* cf. *niceforoi* and clade 19, further modified in clade 27

- Character 15, state 0 → 1 (ACCTTRAN); anterior portion of mesethmoid ventrally directed and with strong hook; reversed in *Leporinus jatuncochi* and *Schizodon nasutus*
- Character 22, state 1 → 0 (DELTRAN); articular facets of vomer with palatines angled toward each other anteriorly; acquired independently in *Leporellus*, subsequent transitions to state 1 in *Anostomoides* and clade 15, subsequent transition to state 2 in clade 27 with reversal to state 0 in *Sartor*
- Character 96, state 2 → 1 (DELTRAN); one or two complete rows of teeth present on tooth-plate of fifth ceratobranchial; acquired independently in clade 5

Clade 8: *Abramites*, *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Rhytiodus*, *Petulanos*, *Pseudanos*, *Sartor*, *Schizodon*, *Synaptolaemus*, *Leporinus agassizi*, *L. aripuanaensis*, *L. cf. ecuadorensis*, *L. friderici*, *L. cf. moralesi*, *L. cf. niceforoi*, *L. ortomaculatus*, *L. pellegrinii*, *L. striatus*, *L. fasciatus*, *L. cf. fasciatus*, *L. jatuncochi*, *L. tigrinus*

- Character 27, state 0 → 1; process of lateral ethmoid directed towards posterolateral corner of mesethmoid present (although sometimes incomplete); reversed in *Leporinus agassizi*, *L. cf. moralesi*, *Schizodon knerii*, *S. isognathus* and clade 25
- Character 32, state 1 → 3; symphyseal tooth of premaxilla with three cusps; reversed in *Leporinus aripuanaensis*, further modified in clades 9, 23 and 30, *Anostomoides*, *Gnathodolus*, *Hypomasticus despaxi*, *Leporinus agassizi*, *L. cf. ecuadorensis*, either clade 10 with reversal in clade 11 or in *L. fasciatus* and *L. cf. fasciatus* (optimization ambiguous), and in either clade 15 with reversal in clade 17 or in *Rhytiodus argenteofuscus* and clade 18 (optimization ambiguous)
- Character 33, state 2 → 3; second and third teeth on premaxilla each with three cusps; reversed in *Leporinus agassizi*, *L. aripuanaensis*, *L. cf. ecuadorensis*, and clade 9, acquired independently in *Leporellus vittatus*, further modified in *Schizodon* and clade 23
- Character 94, state 2 → 1; one or two full rows of teeth present on fifth upper pharyngeal tooth-plate; reversed in *Abramites* and clade 15
- Character 3, state 1 → 0 (ACCTTRAN); supraorbital with smoothly convex, straight or slightly concave anteroventral margin; reversal, subsequent reversal in *Gnathodolus*, *Schizodon knerii* and *S. isognathus*.

Clade 9: *Abramites* and *Leporinus striatus*

- Character 5, state 1 → 2; two intermediate pores present along ossified portion of sensory canal of

first infraorbital; acquired independently in *Hypomasticus pachycheilus*, *Leporinus* cf. *ecuadorensis*, and either in clade 13 with reversal in *Schizodon*, reacquisition in *Schizodon nasutus*, and further modification in *Rhytiodus*, or in *Anostomoides*, *Rhytiodus argenteofuscus*, *Schizodon nasutus* and clade 21 (optimization ambiguous)

- Character 8, state 2 → 1; one intermediate pore along ossified portion of sensory canal of second infraorbital; acquired independently in *Hypomasticus pachycheilus*, *Rhytiodus argenteofuscus*, *Schizodon nasutus* and clade 21
- Character 25, state 0 → 1; wing of lateral ethmoid with distinct notch along anterior margin that accommodates passage of ligament running between wing of lateral ethmoid and ectopterygoid; acquired independently either by clade 25 with reversals in *Pseudanos irinae* and *P. trimaculatus*, or in *P. winterbottomi*, *P. gracilis* and clade 27
- Character 31, state 4 → 3; three teeth on premaxilla; acquired independently in *Leporinus* cf. *moralesi* and clades 5 and 11
- Character 32, state 3 → 2; symphyseal tooth of premaxilla with two cusps; state 2 acquired independently in clades 2, 9 and 30, *Anostomoides*, *Gnathodolus*, *Hypomasticus despaxi*, *Leporinus agassizi*, *L. cf. ecuadorensis*, and in either clade 10 with reversal in clade 11 or in *L. fasciatus* and *L. cf. fasciatus* (optimization ambiguous)
- Character 33, state 3 → 2; second and third teeth on premaxilla each with two cusps; reversal, also reversed in *Leporinus agassizi*, *L. aripuanaensis*, *L. cf. ecuadorensis*, acquired independently in clade 3, polymorphic for states 2 and 3 in *Gnathodolus*
- Character 34, state 1 → 0; medial surface of second and third teeth of premaxilla flat plane or curved hollow, without raised ridge; reversal, also reversed in clade 12
- Character 106, state 1 → 0; absence of supraneural dorsal to Weberian apparatus; reversal, also reversed in clade 13, subsequent reacquisition in clade 25 and another reversal in *Sartor*, polymorphic in *Leporinus* cf. *ecuadorensis* and *Pseudanos irinae*
- Character 118, state 1 → 0; lateral-line spots absent; reversal, also reversed in *Hypomasticus despaxi*, *Leporinus agassizi* and clades 10 and 12, subsequent reversal within clade 12 in clade 26 and in either *Petulanos* and clade 32 or in clade 29 with reversal in *Synaptolaemus*
- Character 13, state 1 → 0 (ACCTTRAN); anteroventral portion of sixth infraorbital expanded and overlaps anteroventral process of sphenotic; reversal, also reversed in *Anostomus anostomus*, polymorphic in *Hypomasticus mormyrops*

#### *Abramites hypselonotus*

- Character 10, state 0 → 1; fourth infraorbital much longer along vertical axis than fifth infraorbital; acquired independently in either clade 12 or clade 13 (ambiguity due to inability to code character in *Leporinus pellegrinii*), reversed in *Gnathodolus*
- Character 17, state 1 → 0; ventral process of mesethmoid runs vertically or nearly so, anterior portion of vomer positioned directly ventral to ventral process of mesethmoid, acquired independently in *Leporellus* and clade 25
- Character 28, state 0 → 1; frontal–parietal fontanel partially or completely closed; acquired independently in *Anostomus* and either clade 26 with reversal in *Pseudanos gracilis*, or in *P. irinae* and *P. trimaculatus* (optimization ambiguous)
- Character 39, state 0 → 1; distinct notch divides symphyseal tooth of dentary into anterior and posterior lobes; acquired independently in *Gnathodolus bidens* and either clade 15 with reversal in *Rhytiodus argenteofuscus* or in *Schizodon* and clade 17
- Character 40, state 0 → 1; distinct distal notch divides posterior lamina of second or third tooth of dentary into anterior and posterior lobes; acquired independently in *Leporinus* cf. *moralesi*, and clades 6 and 15
- Character 92, state 1 → 0; ossified first basibranchial absent; independently lost in *Leporinus* cf. *niceforoi* and clade 13, with subsequent state transitions within clade 13
- Character 94, state 1 → 2; three or more full rows of teeth present on fifth upper pharyngeal tooth-plate; reversal, also reversed in clade 15
- Character 100, state 4 → 3; three branchiostegal rays; acquired independently in *Anostomoides*, clade 26 and *Anostomus ternetzi*
- Character 104, state 0 → 2; neural complex in form of equilateral triangle with nearly horizontal dorsal margin
- Character 109, state 0 → 1; dorsomedial flange of mesocoracoid very strongly developed; acquired independently in *Schizodon*
- Character 110, state 0 → 1; dorsal portion of supracleithrum broad, with distinct wide flange on dorsal portion of bone running medial to postero-dorsal portion of opercle
- Character 112, state 1 → 2; nine or more branched anal-fin rays present
- Character 116, state 0 → 1; body with vertical bands of at least two scales width, at least some of which completely encircle body; acquired independently in *Synaptolaemus* and clade 10
- Character 13, state 1 → 0 (DELTRAN); anteroventral portion of sixth infraorbital expanded and over-



laps anteroventral process of sphenotic; reversal, also reversed in *Anostomus anostomus*, polymorphic in *Hypomasticus mormyrops* and *Leporinus striatus*

*Leporinus* cf. *moralesi* (member of *Leporinops* Géry, nominal subgenus of *Leporinus*)

- Character 27, state 1 → 0; absence of process of lateral ethmoid directed towards posterolateral corner of mesethmoid; reversal, also reversed in *Leporinus agassizi*, *Schizodon knerii*, *S. isognathus* and clade 25.
- Character 31, state 4 → 3; three teeth present on premaxilla; acquired independently in clades 5, 9 and 11
- Character 40, state 0 → 1; distinct distal notch divides posterior lamina of second or third tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites*, and clades 6 and 15
- Character 42, state 1 → 2; distal margin of main lobe of second tooth of dentary with two distinct cusps; acquired independently in clades 14 and 19 with subsequent modifications within clade 14
- Character 105, state 1 → 0; absence of dorsal process of third vertebra overlapping neural complex laterally; reversal, also reversed in *Laemolyta proxima*, *Leporinus striatus*, *L. tigrinus*, *L. pellegrinii*, clade 25, and possibly *Hypomasticus despaxi* and *H. pachycheilus* (ACCTRAN optimization only)

Clade 10: *Leporinus fasciatus*, *L. cf. fasciatus*, *L. jatuncochi*, *L. tigrinus*

- Character 111, state 0 → 1; nine branched pelvic-fin rays
- Character 116, state 0 → 1; body with dark vertical bands of at least two scales width, at least some of which completely encircle body; acquired independently in *Abramites* and *Synaptolaemus*
- Character 118, state 1 → 0; lateral-line spots absent; reversal, also reversed in *Hypomasticus despaxi*, *Leporinus agassizi* and clades 9 and 12, additional state changes within clade 12
- Character 32, state 3 → 2 (ACCTRAN); two cusps on symphyseal tooth of premaxilla; reversed in clade 11, state 2 acquired independently in clades 2, 9 and 30, *Anostomoides*, *Gnathodolus*, *Hypomasticus despaxi*, *Leporinus agassizi* and *L. cf. ecuadorensis*
- Character 80, state 0 → 1 (ACCTRAN); cartilage body spanning ventral section of metapterygoid–quadrate fenestra long and rod-like; acquired independently in clade 12

Clade 11: *Leporinus jatuncochi* and *L. tigrinus*

- Character 31, state 4 → 3; three teeth present on premaxilla; acquired independently in *Leporinus* cf. *moralesi* and clades 5 and 9
- Character 32, state 2 → 3 (ACCTRAN); symphyseal tooth of premaxilla with three cusps; reversal
- Character 80, state 0 → 1 (DELTRAN); cartilage body spanning ventral section of metapterygoid–quadrate fenestra long and rod-like; acquired independently in *Leporinus* cf. *fasciatus* and clade 12

*Leporinus jatuncochi* (member of *Myocharax* Fowler, nominal subgenus of *Leporinus*)

- Character 15, state 1 → 0; anterior portion of mesethmoid ventrally directed and with strong hook; under ACCTRAN reversal, also reversed in *Schizodon nasutus*, under DELTRAN, independently acquired in *Leporellus*, *Hypomasticus* and *Schizodon nasutus*
- Character 35, state 0 → 2; at least two teeth present on premaxilla with strong ventral bend followed by anterior-facing alignment, resulting in zigzag shape to tooth in lateral profile
- Character 36, state 4 → 3; dentary with three teeth; acquired independently in *Hypomasticus despaxi* and *Sartor elongatus*
- Character 37, state 0 → 1; dentary teeth elongate with symphyseal tooth extremely elongate and recurved, overall shape reminiscent of awl or very narrow chisel; acquired independently in clade 32

Clade 12: *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon*, *Synaptolaemus*, *Leporinus pellegrinii*

- Character 80, state 0 → 1; cartilage body spanning ventral section of metapterygoid–quadrate fenestra long and rod-like; reversed in *Schizodon vittatus*, acquired independently in either clade 10 with reversal in *Leporinus fasciatus*, or in both *L. cf. fasciatus* and clade 10 (optimization ambiguous)
- Character 117, state 0 → 1; lateral surface of body with two to five dark, vertical blotches intersecting the lateral-line scale row and continuing dorsal and ventral to the lateral-line scale row; reversed in clades 19 and 21, reacquired in clade 24
- Character 118, state 1 → 0; lateral-line spots absent; reversal, also reversed in *Hypomasticus despaxi*, *Leporinus agassizi* and clades 9 and 10, subsequent reversal within clade 12 in clade 26 and in either *Petulanos* and clade 32 or in clade 29 with reversal in *Synaptolaemus*
- Character 10, state 0 → 1 (ACCTRAN); fourth infraorbital much longer along vertical axis than fifth infraorbital; acquired independently in *Abramites*, reversed in *Gnathodolus*



- Character 34, state 1 → 0 (ACCTRAN); medial surface of second and third teeth of premaxilla flat plane or curved hollow, without raised ridge; reversal with subsequent transition to state 1 in *Anostomoides*, also reversed in clade 9

Clade 13: *Anostomoides*, *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Sartor*, *Schizodon*, *Synaptolaemus*

- Character 65, state 0 → 1; retroarticular ventrally situated in lower jaw and forms part of ventral margin of lower jaw, line drawn along ventral margin of retroarticular barely, if at all, intersects ventral portion of dentary, reversal
- Character 90, state 0 → 1; posterodorsal margin of opercle continuously convex or straight and completely lacking concavity; reversal, reversed in clade 27, polymorphic in *Pseudanos gracilis*
- Character 92, state 1 → 0; ossified first basibranchial absent; independently lost in *Abramites* and *Leporinus* cf. *niceforoi*, reversed within clade 13 in *Schizodon nasutus*, *Laemolyta* and clade 27, another transition to state 0 in *Synaptolaemus*
- Character 106, state 1 → 0; absence of supraneural dorsal to Weberian apparatus; reversal, also reversed in clade 9, subsequent reacquisition in clade 25 and another reversal in *Sartor*, polymorphic in *Leporinus* cf. *ecuadorensis* and *Pseudanos irinae*
- Character 120, state 0 → 1; complete stripe of approximately height of one scale or greater running along lateral line from opercle to caudal peduncle in majority of examined specimens; reversal, reversed independently in *Hypomasticus despaxi* and *Leporinus striatus*, subsequent transitions back to state 0 in clades 17, 20, 26 and 29
- Character 5, state 1 → 2 (ACCTRAN); two intermediate pores present along ossified portion of sensory canal of first infraorbital; acquired independently in *Hypomasticus pachycheilus*, *Leporinus* cf. *ecuadorensis*, and clade 9, reversed in *Schizodon* with subsequent transition to state 2 in *S. nasutus*, reversed in *Petulanos* and *Pseudanos gracilis*, transition to state 3 in *Rhytiodus*
- Character 22, state 0 → 1 (ACCTRAN); articular facets of vomer with palatines angled toward each other anteriorly; reversal, reversed to state 0 in clade 21 with subsequent transitions to state 2 in clade 27 and to state 0 in clade 32
- Character 75, state 0 → 1 (ACCTRAN); mesopterygoid lacking ventral process overlapping quadrate, or process, if present, not significantly overlapping ossified portion of medial surface of quadrate; reversed in clade 15
- Character 10, state 0 → 1 (DELTRAN); fourth infraorbital much longer along vertical axis than fifth infraorbital; acquired independently in either clade 12 or 13 (ambiguity due to inapplicability of this character to *Leporinus pellegrinii*)

#### *Anostomoides*

- Character 26, state 0 → 1; presence of fenestra on portion of lateral wing of lateral ethmoid situated dorsal to lateral ethmoid–ectopterygoid ligament; acquired independently in *Leporellus*
- Character 32, state 3 → 2; symphyseal tooth of premaxilla with two cusps; state 2 acquired independently in *Gnathodolus*, *Leporellus*, *Petulanos*, *Hypomasticus despaxi*, *Leporinus agassizi*, *L. cf. ecuadorensis*, clade 9, and in either clade 10 with reversal in clade 11 or in *L. fasciatus* and *L. cf. fasciatus* (optimization ambiguous)
- Character 100, state 4 → 3; three branchiostegal rays; acquired independently in *Abramites*, clade 26 and *Anostomus ternetzi*
- Character 34, state 0 → 1 (ACCTRAN); medial surface of second and third teeth of premaxilla elaborated, with raised ridge originating at anterior edge of tooth and extending across medial surface of tooth; reversal
- Character 5, state 1 → 2 (DELTRAN); two intermediate pores present along ossified portion of sensory canal of first infraorbital; acquired independently in *Hypomasticus pachycheilus*, *Leporinus* cf. *ecuadorensis*, clade 9 and clade 14
- Character 22, state 0 → 1 (DELTRAN); articular facets of vomer with palatines parallel and widely separated; acquired independently in clade 15
- Character 75, state 0 → 1 (DELTRAN); mesopterygoid lacking ventral process overlapping quadrate, or process, if present, small and not significantly overlapping ossified portion of medial surface of quadrate; acquired independently in clade 21

Clade 14: *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Rhytiodus*, *Schizodon*, *Sartor* and *Synaptolaemus*

- Character 41, state 1 → 2; distal margin of main (anterior) lobe of symphyseal tooth of dentary with two distinct cusps; reversed to state 1 in clade 29, transition to state 0 in *Laemolyta* and state 3 in *Schizodon*, additional transitions to state 2 in clade 19 and *Gnathodolus*
- Character 42, state 1 → 2; distal margin of main lobe of second tooth of dentary with two distinct cusps; acquired independently in *Leporinus* cf. *moralesi*; reversed to state 1 in clade 29, transition to state 0 in *Laemolyta* and state 3 in *Schizodon*, additional transition to state 2 in clade 19 within *Schizodon*, additional transition to state 3 in *Synaptolaemus*

- Character 58, state 0 → 1; dentary squarish or rhomboidal with notable bend midway along anteroventral margin; teeth and anterior margin of dentary inflected so that line drawn through long axis of symphyseal tooth of dentary passes distinctly anterior of joint of quadrate and anguloarticular
- Character 43, state 1 → 3 (ACCTRAN); distal margin of main lobe of third tooth of dentary with three distinct cusps; subsequent transitions to state 2 in clade 17 and state 0 in *Laemolyta*, reversed to state 1 in *Rhytidodus argenteofuscus* and clade 31
- Character 77, state 0 → 1 (ACCTRAN); lateral shelf of quadrate moderate in length, extending posteriorly past midpoint of symplectic but not beyond posterior limit of symplectic; reversed in *Schizodon*, modified to state 2 in clade 25 with subsequent modification to state 0 in *Gnathodolus*
- Character 34, state 1 → 0 (DELTRAN); medial surface of second and third teeth of premaxilla flat plane or curved hollow, without raised ridge originating at anterior edge of tooth and extending across medial surface of tooth; reversal, reversed independently in *Leporinus pellegrinii* and clade 9
- Character 113, state 0 → 1; first four to six principal rays of upper lobe of caudal fin and last four to six rays of lower lobe of caudal fin not distinctly separated but rather with margins in contact in adults; rays thickened and conjoined into rigid plate-like structure in adults
- Character 5, state 2 → 1 (ACCTRAN); one intermediate pore present along ossified portion of sensory canal of first infraorbital; reversal with subsequent transition to state 2 in *Schizodon nasutus*, also reversed in *Petulanos* and *Pseudanos gracilis*
- Character 32, state 3 → 4 (ACCTRAN); symphyseal tooth of premaxilla with four cusps; reversed in clade 17; acquired independently in clade 23
- Character 39, state 0 → 1 (ACCTRAN); distinct notch divides symphyseal tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites* and *Gnathodolus bidens*, reversed in *Rhytidodus argenteofuscus*
- Character 75, state 1 → 0 (ACCTRAN); mesopterygoid with well-developed ventral triangular process that significantly overlaps ossified portion of medial surface of quadrate; reversal
- Character 95, state 2 → 3 (ACCTRAN); at least some teeth on fifth upper pharyngeal tooth-plate tricuspid and other teeth bicuspid; reversed in *Schizodon scotorhabdotus* and clade 17

#### Clade 15: *Rhytidodus*, *Schizodon*

- Character 7, state 1 → 0; lamina located dorsal to sensory canal of second infraorbital absent or poorly developed with maximum height less than diameter of sensory canal; reversed in *Schizodon isognathus* and *S. knerii*
- Character 30, state 0 → 1; bony shelf above orbit formed by lateral ethmoid, frontal and sphenotic bones very wide, distance between lateral tips of contralateral sphenotics 80% or greater of length of neurocranium from anterior tip of mesethmoid to tip of supraoccipital spine
- Character 40, state 0 → 1; distinct distal notch divides posterior lamina of second or third tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites*, *Leporinus cf. moralesi* and clade 6
- Character 44, state 0 → 1; posterior lobes of dentary teeth with one or more distinct cusps
- Character 63, state 0 → 1; sensory canal segment of dentary with pore positioned along midlength of canal segment between posterior opening of canal proximate to anguloarticular and anterior limit of canal and occurring in posterior one-half of length of dentary; acquired independently in *Leporinus cf. ecuadorensis*
- Character 94, state 1 → 2; three or more full rows of teeth present on fifth upper pharyngeal tooth-plate; reversal, reversed independently in *Abramites*
- Character 96, state 1 → 2 (ACCTRAN); three or more complete rows of teeth on tooth-plate of fifth ceratobranchial; reversed in clade 17, acquired independently in clade 6
- Character 22, state 0 → 1 (DELTRAN); articular facets of vomer with palatines parallel and widely separated; state 1 acquired independently in *Anostomoides*

#### Clade 16: *Rhytidodus*

- Character 6, state 0 → 1; walls of sensory canal of first infraorbital thickened and laterosensory canal located lateral to main lamina of bone; canal fused only weakly along its medial surface to main lamina of first infraorbital
- Character 11, state 0 → 1; flange of fifth infraorbital poorly developed or entirely absent, with at least dorsal section of flange missing; acquired independently in *Laemolyta*
- Character 29, state 0 → 1; neurocranium distinctly depressed; depth of neurocranium at angle in parasphenoid about 30–32% of length of neurocranium from anterior tip of mesethmoid to tip of supraoccipital spine; mesethmoid and horizontal portions of vomer separated by narrow gap in lateral view
- Character 101, state 0 → 1; presence or absence of anteriorly directed process of fourth pleural rib within Weberian apparatus

- Character 102, state 0 → 1; fourth pleural rib with anteriorly directed distal hook
- Character 104, state 0 → 1; neural complex in form of elongate triangle with nearly horizontal dorsal margin
- Character 43, state 3 → 1 (ACCTTRAN); distal margin of main lobe of third tooth of dentary with only single cusp; subsequent transition to state 2 in clade 17
- Character 77, state 0 → 1 (DELTRAN); lateral shelf of quadrate moderate in length, extending posteriorly past midpoint of symplectic but not beyond posterior limit of symplectic; acquired independently in *Laemolyta*
- Character 5, state (1 or 2) → 3 (ancestral state reconstruction ambiguous under ACCTTRAN and DELTRAN); three intermediate pores present along ossified portion of sensory canal of first infraorbital

Clade 17: *Rhytiodus microlepis*, *R. lauzannei*

- Character 103, state 0 → 1; os suspensorium very well-developed ventrally with distinct posterior curvature around anterior portion of swim bladder
- Character 115, state 0 → 1; 76 or more scales including scales overlapping hypural plate present in complete lateral-line series
- Character 120, state 1 → 0; complete stripe along lateral-line absent; reversal, reversed independently in clades 20, 26 and 29
- Character 32, state 4 → 3 (ACCTTRAN); symphyseal tooth of premaxilla with three cusps; reversal
- Character 95, state 3 → 2 (ACCTTRAN); most teeth on fifth upper pharyngeal tooth-plate bicuspid but with occasional teeth unicuspid; reversal, reversed independently in *Schizodon scotorhabdotus*
- Character 96, state 2 → 1 (ACCTTRAN); one or two complete rows of teeth present on tooth-plate of fifth ceratobranchial; reversal
- Character 39, state 0 → 1 (DELTRAN); distinct notch divides symphyseal tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites*, *Gnathodolus* and *Schizodon*
- Character 43, state (1, 3) → 2 (ancestral state reconstruction ambiguous under ACCTTRAN and DELTRAN); distal margin of main lobe of third tooth of dentary with two distinct cusps

Clade 18: *Schizodon*

- Character 33, state 3 → 4; second and third teeth of premaxilla each with four cusps; acquired independently in clade 23
- Character 41, state 2 → 3; distal margin of main lobe of symphyseal tooth of dentary with three distinct cusps; reversed in clade 19
- Character 42, state 2 → 3; distal margin of main lobe of second tooth of dentary with three distinct cusps;

acquired independently in *Synaptolaemus*; reversed in clade 19

- Character 55, state 0 → 1; ascending process of anguloarticular very wide, forming pronounced vertical ridge perpendicular to dentary; acquired independently in *Hypomasticus*
- Character 109, state 0 → 1; dorsomedial flange of mesocoracoid very strongly developed; acquired independently in *Abramites*
- Character 77, state 1 → 0 (ACCTTRAN); lateral shelf of quadrate elongate, extending posteriorly past posterior margin of symplectic to terminate ventral to hyomandibular; reversal, reversed independently in *Gnathodolus*
- Character 32, state 3 → 4 (DELTRAN); symphyseal tooth of premaxilla with four cusps; acquired independently in *Rhytiodus argenteofuscus* and clade 23
- Character 39, state 0 → 1 (DELTRAN); distinct notch divides symphyseal tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites*, *Gnathodolus* and clade 17
- Character 43, state 1 → 3 (DELTRAN); distal margin of main lobe of third tooth of dentary with three distinct cusps; acquired independently in clade 25
- Character 95, state 2 → 3 (DELTRAN); at least some teeth on fifth upper pharyngeal tooth-plate tricuspid and other teeth bicuspid; reversed in *Schizodon scotorhabdotus*, acquired independently in *Rhytiodus argenteofuscus*
- Character 96, state 1 → 2 (DELTRAN); one or two complete rows of teeth on tooth-plate of fifth ceratobranchial; acquired independently in *Rhytiodus argenteofuscus*

Clade 19: *Schizodon isognathus*, *S. nasutus*

- Character 17, state 1 → 2; ventral process of mesethmoid horizontally or slightly posterodorsally aligned, vomer directly posterior of ventral portion of mesethmoid; acquired independently in either *Hypomasticus* with reversal in *Hypomasticus megalepis*, or in both *Hypomasticus despaxi* and clade 6 (optimization ambiguous)
- Character 41, state 3 → 2; distal margin of main (anterior) lobe of symphyseal tooth of dentary with two distinct cusps; reversal
- Character 42, state 3 → 2; distal margin of main lobe of second tooth of dentary with two distinct cusps; reversal
- Character 59, state 0 → 1; long axes of dentary and anguloarticular form distinctly obtuse angle; acquired independently in *Schizodon knerii*
- Character 72, state 1 → 0; ectopterygoid anterodorsally inclined, with vertical through anterodorsal limit of ectopterygoid passing anterior to anterior

limit of ventral portion of ectopterygoid; reversal, reversed independently in *Leporinus* cf. *niceforoi*

- Character 117, state 1 → 0; lateral surface of body without dark vertical blotches; reversal, also reversed in clade 21

Clade 20: *Schizodon fasciatus*, *S. vittatus*

- Character 69, state 0 → 1; process of palatine very long, length of process approximately two or more times width of process
- Character 120, state 1 → 0; complete stripe along lateral-line absent; reversal, reversed independently in clades 17, 26 and 29

Clade 21: *Anostomus*, *Gnathodolus*, *Laemolyta*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptaemus*

- Character 8, state 2 → 1; one intermediate pore present along ossified portion of sensory canal of second infraorbital; acquired independently in *Hypomasticus pachycheilus*, *Rhytiodus argenteofuscus*, *Schizodon nasutus* and clade 9
- Character 38, state 0 → 1; dentary teeth either with small, poorly developed posterior lamina or posterior lamina entirely absent
- Character 46, state 1 → 2; horizontally orientated premaxilla with premaxillary teeth directed anteriorly
- Character 117, state 1 → 0; lateral surface of body without dark vertical blotches; reversal with subsequent transition to state 1 in clade 24, reversed independently in clade 19
- Character 22, state 1 → 0 (ACCTTRAN); articular facets of vomer with palatines angled toward each other anteriorly; reversal, transition to state 2 in clade 27 with subsequent transition to state 0 in either clade 32 or *Sartor* (ambiguity due to inability to code *Gnathodolus* for this character)
- Character 5, state 1 → 2 (DELTRAN); two intermediate pores present along ossified portion of sensory canal of first infraorbital; acquired independently in *Anostomoides*, *Hypomasticus pachycheilus*, *Leporinus* cf. *ecuadorensis* and clade 9, reversed to state 1 in *Pseudanos gracilis* and *Petulanos*
- Character 75, state 0 → 1 (DELTRAN); mesopterygoid lacking ventral process overlapping quadrate, or process, if present, small and not significantly overlapping ossified portion of medial surface of quadrate; acquired independently in *Anostomoides*

Clade 22: *Laemolyta*

- Character 11, state 0 → 1; flange of fifth infraorbital posterior of sensory canal poorly developed or entirely absent, with at least dorsal section of flange missing; acquired independently in *Rhytiodus*
- Character 41, state 2 → 0; distal margin of main body of symphyseal tooth of dentary with straight incisiform margin and no apparent cusps

- Character 42, state 2 → 0; distal margin of main body of second tooth of dentary with straight incisiform margin and no apparent cusps
- Character 92, state 0 → 1; ossified first basibranchial present; reversal, also reversed within clade 13 in *Schizodon nasutus* and clade 27
- Character 43, state 3 → 0 (ACCTTRAN); distal margin of main body of third tooth of dentary with straight incisiform margin and no apparent cusps
- Character 43, state 1 → 0 (DELTRAN); distal margin of main body of third tooth of dentary with straight incisiform margin and no apparent cusps
- Character 77, state 0 → 1 (DELTRAN); lateral shelf of quadrate moderate in length, extending posteriorly past midpoint of symplectic but not beyond posterior limit of symplectic; acquired independently in *Rhytiodus*

Clade 23: *Laemolyta orinocensis*, *L. proxima*, *L. taeniata*

- Character 32, state 3 → 4; symphyseal tooth of premaxilla with four cusps; acquired independently in either clade 15 with reversal in clade 17, or in *Rhytiodus argenteofuscus* and clade 18 (optimization ambiguous)
- Character 33, state 3 → 4; second and third teeth of premaxilla each with four cusps; acquired independently in *Schizodon*

Clade 24: *Laemolyta orinocensis*, *L. proxima*

- Character 117, state 0 → 1; lateral surface of body with two to five dark, vertical blotches intersecting lateral-line scale row and continuing dorsal and ventral to lateral-line scale row; reversal

Clade 25: *Anostomus*, *Gnathodolus*, *Petulanos*, *Pseudanos*, *Sartor*, *Synaptaemus*

- Character 4, state 0 → 1; origin of sensory canal of first infraorbital situated directly dorsal to, or posterodorsal to, distal terminus of canal of first infraorbital where that canal contacts canal of second infraorbital
- Character 12, state 0 → 1; sensory canal of sixth infraorbital straight and lacking medial pore; acquired independently in *Hypomasticus despaxi* and *H. mormyrops*, reversed in *Synaptaemus* and *Gnathodolus* or in clade 31 with subsequent transition to state 1 in *Sartor* (optimization ambiguous), polymorphic in *Leporinus gomesi* and *L. striatus*
- Character 14, state 0 → 1; sixth infraorbital posteriorly expanded and fused with sixth infraorbital; reversed in clade 31
- Character 17, state 1 → 0; ventral process of mesethmoid runs vertically or nearly so, anterior portion of vomer positioned directly ventral to ventral process



of mesethmoid; acquired independently in *Leporellus* and *Abramites*

- Character 21, state 0 → 1; ventral surface of main body of vomer with pentagonal raised area in ventral view medial to articulations with left and right palatines
- Character 27, state 1 → 0; absence of process of lateral ethmoid directed towards posterolateral corner of mesethmoid; reversal, reversed independently in *Leporinus agassizi*, *L. cf. moralesi*, *Schizodon isognathus* and *S. knerii*.
- Character 50, state 0 → 1; anterolateral flange of maxilla merges with ventral portion of maxilla on anterior edge of ventral portion; reversal
- Character 67, state 1 → 0; palatine without distinct process extending away from main, rounded portion of bone cradled by dorsal portion of ectopterygoid
- Character 72, state 1 → 2; ectopterygoid posterodorsally inclined with vertical through anterodorsal limit of ectopterygoid passing distinctly posterior of ventral portion of ectopterygoid
- Character 81, state 0 → 1; metapterygoid with three distinct facets; vertical sheet dorsal to quadrate and symplectic, horizontal or medially curved portion that contacts mesopterygoid, and inclined plane proximate to hyomandibular that meets other facets along well defined margins
- Character 85, state 0 → 1; anterodorsal process of preopercle with thin, needle-like form
- Character 105, state 1 → 0; absence of dorsal process of third vertebra overlapping neural complex laterally; reversal, also reversed in *Laemolyta proxima*, *Leporinus cf. moralesi*, *striatus*, *L. tigrinus*, *L. pellegrii*, and possibly *Hypomasticus despaxi* and *H. pachycheilus* (ACCTRAN optimization only)
- Character 106, state 0 → 1; presence of supraneural dorsal to Weberian apparatus; reversal, subsequent transition to state 0 in *Sartor*, polymorphic in *Pseudanos irinae*
- Character 25, state 0 → 1 (ACCTRAN); wing of lateral ethmoid with distinct notch along anterior margin that accommodates passage of ligament running between wing of lateral ethmoid and ectopterygoid; acquired independently in clade 9, reversed in *Pseudanos irinae* and *P. trimaculatus*
- Character 53, state 0 → 1 (ACCTRAN); dorsal portion of maxilla in form of flat, medially-directed plate; reversal in *Anostomus* and *Pseudanos trimaculatus*
- Character 77, state 1 → 2 (ACCTRAN); lateral shelf of quadrate short, extending posteriorly to point short of midpoint of symplectic; subsequent transition to state 0 in *Gnathodolus*
- Character 79, state 0 → 1 (ACCTRAN); metapterygoid–quadrate fenestra longer along axis running parallel to quadrate-metapterygoid joint

than along axis perpendicular to that joint; reversed in clade 26

- Character 122, state 0 → 1 (ACCTRAN); most scales with small, dark spot lying under scale creating overall appearance of row of such spots along center of each scale row; reversed in *Pseudanos trimaculatus* and clade 27 with subsequent transition to state 1 in *Anostomus anostomus*
- Character 43, state 1 → 3 (DELTRAN); distal margin of main lobe of third tooth of dentary with three distinct cusps; reversed in clade 31, acquired independently in *Schizodon*
- Character 77, state 0 → 2 (DELTRAN); lateral shelf of quadrate short, extending posteriorly to point short of midpoint of symplectic; subsequent reversal to state 0 in *Gnathodolus*

Clade 26: *Pseudanos gracilis*, *P. irinae*, *P. trimaculatus*

- Character 100, state 4 → 3; three branchiostegal rays; acquired independently in *Abramites*, *Anostomoides*, and *Anostomus ternetzi*
- Character 118, state 0 → 1; series of one or more dark spots with distinct margins present along lateral-line scale row, each spot approximately one to two scales in height, reversal, also reversed in either clade 29 with subsequent reversal in *Synaptolaemus*, or in *Petulanos* and clade 32 (optimization ambiguous)
- Character 120, state 1 → 0; complete stripe along lateral-line absent; reversal, reversed independently in clades 17, 20 and 29
- Character 25, state 1 → 0 (ACCTRAN); wing of lateral ethmoid without distinct notch along anterior margin; reversal, reversed in *Pseudanos gracilis*
- Character 28, state 0 → 1 (ACCTRAN); frontal–parietal fontanel partially or completely closed; acquired independently in *Abramites* and *Anostomus*, reversed in *Pseudanos gracilis*
- Character 79, state 1 → 0 (ACCTRAN); metapterygoid–quadrate fenestra shorter along axis running parallel to quadrate-metapterygoid joint than along axis perpendicular to that joint; reversal

Clade 27: *Anostomus*, *Gnathodolus*, *Petulanos*, *Sartor*, *Synaptolaemus*

- Character 2, state 1 → 0; anterior margin of antorbital positioned just dorsal of, or dorsal and posterior of, anterodorsal opening of sensory canal of first infraorbital; reversal
- Character 19, state 0 → 1; mesethmoid narrow, with maximum width along transverse axis much less than maximum length along longitudinal axis; reversal
- Character 22, state 0 → 2; articular facets of vomer with palatines parallel and widely separated;

reversed in either clade 32 or *Sartor* (ambiguity due to inability to code *Gnathodolus* for this character)

- Character 71, state 0 → 1 very small anterodorsal process of ectopterygoid running ventral to palatine, or process absent
- Character 89, state 1 → 0; joint of interhyal, metapterygoid, symplectic and hyomandibular positioned at approximately same horizontal plane as anterior portion of lateral shelf of metapterygoid
- Character 90, state 1 → 0; posterodorsal margin of opercle with slight or pronounced concavity; reversal
- Character 92, state 0 → 1; ossified first basibranchial present; reversal with subsequent transition to state 0 in *Synaptolaemus*, also reversed within clade 13 in *Schizodon nasutus* and *Laemolyta*
- Character 74, state 0 → 1 (ACCTRAN); posteriorly directed dorsolateral process of mesopterygoid present; reversed in clade 31 with subsequent transition back to state 1 in *Sartor*
- Character 122, state 1 → 0 (ACCTRAN); centers of scales same colour as, or lighter than, scale margins, no series of small dark spots along center of each scale row; reversal with subsequent transition back to state 1 in *Anostomus anostomus*
- Character 25, state 0 → 1 (DELTRAN); wing of lateral ethmoid with distinct notch along anterior margin that accommodates passage of ligament running between wing of lateral ethmoid and ectopterygoid; state 1 acquired independently in *Pseudanos gracilis* and *P. winterbottomi*
- Character 79, state 0 → 1 (DELTRAN); metapterygoid–quadrate fenestra longer along axis running parallel to quadrate–metapterygoid joint than along axis perpendicular to that joint; state 1 acquired independently in *Pseudanos winterbottomi*

#### Clade 28: *Anostomus*

- Character 28, state 0 → 1; frontal–parietal fontanel partially or completely closed; acquired independently in *Abramites* and either clade 26 with reversal in *Pseudanos gracilis*, or in *P. irinae* and *P. trimaculatus* (optimization ambiguous).
- Character 121, state 0 → 1; one or more longitudinal stripes present dorsal and ventral to lateral-line scale row; acquired independently in *Hypomasticus despaxi* and *Leporinus striatus*
- Character 53, state 1 → 0 (ACCTRAN); dorsal portion of maxilla rod-like, with tapered or pointed tip; reversal, reversed independently in *Pseudanos trimaculatus*
- Character 74, state 0 → 1 (DELTRAN); presence of posteriorly directed dorsolateral process of mesopterygoid; acquired independently in *Petulanos* and *Sartor*

#### Clade 29: *Gnathodolus*, *Petulanos*, *Sartor*, *Synaptolaemus*

- Character 41, state 2 → 1; distal margin of main (anterior) lobe of symphyseal tooth of dentary with only single cusp; reversal with subsequent transition back to state 2 in *Gnathodolus*
- Character 42, state 2 → 1; distal margin of main lobe of second tooth of dentary with only single cusp; reversal, further modified to state 3 in *Synaptolaemus*
- Character 52, state 0 → 1; ventral portion of maxilla very wide, greatly expanded in direction transverse to long axis of bone; reversal
- Character 78, state 0 → 1; lateral shelf of quadrate terminates anteriorly prior to reaching articular condyle
- Character 99, state 0 → 1; urohyal high, dorsal and ventral margins meet at angle greater than 45°; reversed in *Gnathodolus*
- Character 120, state 1 → 0; complete stripe along lateral-line absent; reversal, reversed independently in clades 17, 20 and 26
- Character 118, state 0 → 1 (ACCTRAN); series of one or more dark spots with distinct margins present along lateral-line scale row, each spot approximately one to two scales in height, reversal with subsequent reversal in *Synaptolaemus*, also reversed in clade 26
- Character 53, state 0 → 1 (DELTRAN); dorsal portion of maxilla in form of flat, medially-directed plate; acquired independently in *Pseudanos gracilis* and *P. winterbottomi*

#### Clade 30: *Petulanos*

- Character 5, state 2 → 1; one intermediate pore present along ossified portion of sensory canal of first infraorbital; reversal, also reversed in *Pseudanos gracilis*, also reversed in *Schizodon* under ACCTRAN optimization
- Character 8, state 1 → 2; two intermediate pores present along ossified portion of sensory canal of second infraorbital; reversal
- Character 32, state 3 → 2; symphyseal tooth of premaxilla with two cusps; state 2 acquired independently in clade 9, *Anostomoides*, *Gnathodolus*, *Leporellus*, *Hypomasticus despaxi*, *Leporinus agassizi*, *L. cf. ecuadorensis*, and in either clade 10 with reversal in clade 11 or in *L. fasciatus* and *L. cf. fasciatus* (optimization ambiguous).
- Character 88, state 0 → 1; ventral lamina of symplectic broad and triangular
- Character 74, state 0 → 1 (DELTRAN); presence of posteriorly directed dorsolateral process of mesopterygoid; acquired independently in *Anostomus* and *Sartor*

- Character 118, state 0 → 1 (DELTRAN); series of one or more dark spots with distinct margins present along lateral-line scale row; reversal; reversed independently in clades 26 and 32

Clade 31: *Gnathodolus*, *Sartor*, *Synaptaemus*

- Character 14, state 1 → 0; sixth infraorbital not posteriorly expanded and entirely separate from suprapreopercle; reversal
- Character 43, state 3 → 1; distal margin of main lobe of third tooth of dentary with only single cusp; reversal, also reversed in *Rhytiodus* or only in *R. argenteofuscus* (optimization ambiguous)
- Character 51, state 0 → 1; anterolateral flange of maxilla and ventral portion of bone without rotation relative to each other, and both lying in parasagittal plane; reversal
- Character 66, state 0 → 1; dermal papillae present on lower lip
- Character 86, state 0 → 1; anterior margin of ascending arm of preopercle with distinct triangular process overlapping joint between interhyal, hyomandibular, metapterygoid and symplectic in lateral view
- Character 12, state 1 → 0 (ACCTTRAN); sensory canal of sixth infraorbital tripartite or with form of angled tube with medial pore situated at angle of tube; reversal with subsequent transition back to state 1 in *Sartor*
- Character 74, state 1 → 0 (ACCTTRAN); absence of posteriorly directed dorsolateral process of mesopterygoid; reversal with subsequent transition back to state 1 in *Sartor*

*Synaptaemus*

- Character 24, state 0 → 1; insertion of lateral ethmoid–ectopterygoid ligament on dorsal surface of anterior wing of lateral ethmoid
- Character 42, state 1 → 3; distal margin of main lobe of second tooth of dentary with three distinct cusps; acquired independently in *Schizodon*
- Character 92, state 1 → 0; ossified first basibranchial absent; reversal
- Character 116, state 0 → 1; body with vertical bands of at least two scales width, at least some of which completely encircle body; acquired independently in *Abramites* and clade 10
- Character 118, state 1 → 0 (ACCTTRAN); lateral-line spots absent; reversal
- Character 12, state 1 → 0 (DELTRAN); sensory canal of sixth infraorbital tripartite or with form of angled tube with medial pore situated at angle of tube; reversal, also reversed in *Gnathodolus*

Clade 32: *Gnathodolus*, *Sartor*

- Character 35, state 0 → 1; at least two of teeth present on premaxilla with distinct dorsal curvature distally; teeth appearing strongly ventrally bowed in lateral profile with distal tips of teeth positioned more dorsally than base of teeth
- Character 37, state 0 → 1; dentary teeth elongate with symphyseal tooth extremely elongate and recurved, overall shape reminiscent of awl or very narrow chisel; acquired independently in *Leporinus jatuncochi*
- Character 54, state 0 → 1; anterolateral and posterior portions of maxilla merge to form flat plate orientated perpendicular to process of maxilla that contacts cartilage of palatine
- Character 61, state 1 → 0; sensory canal of dentary greatly reduced or absent
- Character 22, state 2 → 0 (ACCTTRAN); articular facets of vomer with palatines angled toward each other anteriorly; reversal
- Character 36, state 4 → 1 (ACCTTRAN); dentary with one tooth present
- Character 118, state 0 → 1 (DELTRAN); series of one or more dark spots with distinct margins present along lateral-line scale row; reversal, reversed independently in *Petulanos* and clade 26

*Gnathodolus*

- Character 3, state 0 → 1; supraorbital with deeply concave, distinctly notched anterior or anterolateral margin; reversal, also reversed in *Schizodon isognathus* and *S. knerii*
- Character 10, state 1 → 0; vertical extent of fourth and fifth infraorbitals approximately equal or fifth infraorbital longer along vertical axis than fourth infraorbital; reversal
- Character 20, state 0 → 1; vomer with two deep grooves on ventral surface that receive dorsal surfaces of mesopterygoid, metapterygoid and palatine
- Character 23, state 1 → 0; absence of lateral ethmoid–ectopterygoid ligament
- Character 32, state 3 → 2; symphyseal tooth of premaxilla with two cusps; state 2 acquired independently in *Anostomoides*, *Gnathodolus*, *Leporellus*, *Petulanos*, *Hypomasticus despaxi*, *Leporinus agassizi*, *L. cf. ecuadorensis*, clade 9, and in either clade 10 with reversal in clade 11 or in *L. fasciatus* and *L. cf. fasciatus* (optimization ambiguous)
- Character 39, state 0 → 1; distinct notch divides symphyseal tooth of dentary into anterior and posterior lobes; acquired independently in *Abramites* and either clade 15 with reversal in *Rhytiodus argenteofuscus* or in *Schizodon* and clade 17 (optimization ambiguous)

- Character 41, state 1 → 2; distal margin of main (anterior) lobe of symphyseal tooth of dentary with two distinct cusps; reversal
- Character 57, state 0 → 1; dentary extraordinarily elongate, distance from joint with anguloarticular to tip of dentary three times or more height of dentary just anterior to ascending process of anguloarticular
- Character 70, state 0 → 1; palatine in shape of dorsoventrally elongate hourglass, with triangular dorsal and ventral portions connected by thin thread of bone
- Character 73, state 1 → 0; absence of distinct process on posterolateral surface of the ectopterygoid; reversal
- Character 77, state 2 → 0; lateral shelf of quadrate elongate, extending posteriorly past posterior margin of symplectic to terminate ventral to hyomandibular; reversal
- Character 12, state 1 → 0 (DELTRAN); sensory canal of sixth infraorbital tripartite or with form of angled tube with medial pore situated at angle of tube; reversal, also reversed in *Synaptolaemus*
- Character 36, state 4 → 1 (DELTRAN); one tooth present on dentary
- Character 99, state 1 → 0; urohyal low, dorsal and ventral margins meet at angle equal to or less than 45°; reversal
- Character 106, state 1 → 0; absence of supraneural dorsal to Weberian apparatus; reversal
- Character 12, state 0 → 1 (ACCTRAN); canal of sixth infraorbital straight and lacking medial pore; reversal
- Character 36, state 1 → 3 (ACCTRAN); three teeth present on dentary, acquired independently in *Hypomasticus despaxi* and *Leporinus jatuncochi*
- Character 74, state 0 → 1 (ACCTRAN); presence of posteriorly directed dorsolateral process of mesopterygoid; reversal
- Character 22, state 2 → 0 (DELTRAN); articular facets of vomer with palatines angled toward each other anteriorly; reversal
- Character 36, state 4 → 3 (DELTRAN); three teeth present on dentary; acquired independently in *Hypomasticus despaxi* and *Leporinus jatuncochi*
- Character 74, state 0 → 1 (DELTRAN); presence of posteriorly directed dorsolateral process of mesopterygoid; acquired independently in *Anostomus* and *Petulanos*

#### *Sartor*

- Character 82, state 0 → 1; lateral surface of metapterygoid with well-developed lateral shelf