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The family Alestidae (Ostariophysi, Characiformes): a phylogenetic analysis of a trans-Atlantic clade

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The overall most parsimonious hypothesis of relationships based on 200 characters indicates that the Alestidae is the closest relative of *Chalceus*, a genus previously assigned to the Neotropical Characidae. *Chalceus* is shifted into the Alestidae, which becomes the only trans-Atlantic family level group within the Characiformes. Various previously proposed suprageneric assemblages within the Alestidae (e.g. Petersiini) failed to delimit monophyletic groups under the intrafamilial phylogenetic analysis. The evaluation of fossil alestids within the context of the phylogeny indicates that the ancestors of *Alestes*, *Arnoldichthys*, *Brycinus*, *Bryconaethiops* and *Hydrocynus* evolved prior to the early Eocene (Cuisian of Upper Ypresian), 49–54.8 million years ago, with the fossil *Alestoides* most closely related to *Alestes*. The phylogenetic information further indicates a minimum age of 90–112 million years for the Alestidae. Contrary to previous hypotheses, the fossil African *Sindacharax* was found to be most similar to the clade including the alestid genus *Bryconaethiops* rather than most closely related to the South American subfamily Serrasalminae. Evaluation of the fossil *Mahengecharax carrolli* fails to support its hypothesized placement as the sister group to all Recent members of the Alestidae. Two separate episodes of miniaturization and one episode of gigantism occurred within the evolution of the Alestidae. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **145**, 1–144. No claim to original US government works.

ADDITIONAL KEYWORDS: African Characidae – *Chalceus* – fossil evidence – gigantism – miniaturization – phylogeny – *Sindacharax*.

INTRODUCTION

The Characiformes, one of the major lineages of ostariophysan fishes, is widely distributed through freshwaters of major portions of the Americas and Africa. New World characiforms occur from the southern boundary regions of the United States to the central portions of Chile and Argentina. Characiforms inhabit freshwater ecosystems across broad regions of sub-Saharan Africa with the exception of the southern portions of the continent and the Horn of Africa, with the ranges of several characiform species extending through the Sahara Desert along the length of the Nile River basin. Phylogenetic studies in recent decades have delimited three subunits among African characiforms: a clade consisting of the families Distichodontidae and Citharinidae (Vari, 1979); a clade formed by the putatively monotypic family Hepsetidae; and the assemblage recognized alternatively as the ‘African Characidae’, Alestinae, or Alestidae by previous authors and hereafter referred to as the Alestidae. These studies have revealed that the three African subunits of the Characiformes do not jointly constitute a monophyletic unit, being instead dispersed across the phylogeny of the order. That conclusion is interesting both phylogenetically and in terms of the historical biogeographical relationships of the South American and African freshwater fish faunas.

Both the monophyly and higher-level phylogenetic relationships of the clade consisting of the Distichodontidae and Citharinidae have been the subject of in-depth analyses using morphological (Vari, 1979; Fink & Fink, 1981) and molecular (Ortí, 1997; Ortí & Meyer, 1997) evidence that consistently supports the

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*Corresponding author. E-mail: varir@si.edu hypothesis of the monophyly of the clade and/or its basal position within the Characiformes. Hypotheses as to the phylogenetic relationships of the Hepsetidae (Vari, 1995; Buckup, 1998; Oyakawa, 1998) align that family with the New World families Ctenoluciidae, Erythrinidae and Lebiasinidae, albeit with these hypotheses advancing alternative patterns of relationships among the four families. Preliminary information also indicates that the Hepsetidae can be defined on the basis of several derived attributes (Vari, 1995: 37).

The Alestidae (African members of the Characidae of Greenwood *et al.*, 1966), the third group among African characiforms, occurs across the range of the order in Africa. Maximum diversity in the Alestidae, both in numbers of genera and species, occurs in the coastal rivers of West Africa and the Congo River basin. Correlated with increasing distances from those regions is a decreasing diversity of alestids at both the generic and specific taxonomic levels. The approximately 105 species in the Alestidae (Paugy, 1984, 1986; Teugels & Thys van den Audenaerde, 1990; Géry, 1995, 1996) range from the diminutive species of the West African genus *Virilia*, some of which mature at 18.8 mm standard length, to the tigerfish, *Hydrocynus goliath* which at 1320 mm standard length achieves the greatest length of any characiform (Weitzman & Vari, 1998). Such a dramatic range in body size, 18.8–1320 mm, a 70× size range, is unique to members of the Alestidae among the families of the Characiformes hypothesized to be monophyletic on the basis of multiple synapomorphies.

Although Buckup (1998: 139) remarked that the monophyly of the Alestidae 'has never been disputed', a retrospective evaluation indicates that this assumption is predicated on a lack of evidence indicative of the nonmonophyly of the Alestidae rather than being derived from a robust phylogenetic analysis that yielded a series of hypothesized synapomorphies for the family. Previous phylogenetic studies that delved into the question of the monophyly of the Alestidae did so in passing and the resultant hypotheses of alestid monophyly were invariably incidental to phylogenetic analyses focused on other groups within the Characiformes (Vari, 1998: 120). All such hypotheses on the monophyly for the Alestidae were, furthermore, based on evidence derived from the sampling of a typically very limited subset of taxa in the Alestidae. In their recent publication focused on the question of the relationships of *Alestes* and *Brycinus*, Murray & Stewart (2002) proposed a series of synapomorphies for the African components of the Alestidae and its subunits. Although their analysis is hitherto the most encompassing study of that question, it included only a restricted number of alestid taxa and surveyed relatively few morphological systems.

The phylogenetic position of, and intrarelationships within, the African characiforms that constitute nearly all of the Alestidae of this study are yet to be examined in depth. Greenwood *et al*. (1966: 395) united the species now assigned to the Alestidae together with a large number of New World taxa into the Characidae. That family constituted the most speciose assemblage within the Characiformes (the Characoidei of Greenwood *et al*., 1966). This expansive Characidae, a concept that has been retained by some authors until the present time (Lévêque, 2001: 14), was, furthermore, the only characiform family common to the Americas and Africa. A series of phylogenetic analyses (Buckup, 1998; Lucena & Menezes, 1998; Toledo-Piza, 2000; this study) demonstrated that such a broadly encompassing Characidae constituted a nonmonophyletic group within the Characiformes.

Of particular note for the present study was the hypothesis that the African members of the Characidae (*sensu* Greenwood *et al*., 1966) constituted the sister group to a clade that encompassed more than just the Neotropical components of the Characidae. Several phylogenetic studies focusing on these components, including some alestids in the outgroup analysis, suggested a close relationship between the Alestidae and at least some components of the Characidae (Ortí & Meyer, 1997; Buckup, 1998; Zanata, 2000) and provided preliminary evidence for the monophyly of the Alestidae (Vari, 1998: 120; Zanata, 2000: 293). Some of these analyses, however, raised questions as to the monophyly of a group consisting of the New World Characidae and the African Alestidae. Of particular note relative to that question are the striking similarities between the monotypic African genus *Arnoldichthys* that was assigned to the Alestidae by recent authors and the South American characid genus *Chalceus*, a lineage of five mid-sized species (Zanata & Toledo-Piza, 2004). So pronounced are the similarities between these two genera that a species of *Chalceus* with erroneous locality data was described as a new genus and species of a supposedly African characid (= alestid) by Fowler (1906). In a study focused on the question of the phylogenetic relationships within the Neotropical characid genus *Brycon*, Zanata (2000) identified characters that supported the hypothesis of a close relationship of *Chalceus* with some genera of the Alestidae. An in-depth analysis of that hypothesized phylogenetic relationship lay, however, beyond the limits of her study.

Intrafamilial suprageneric and generic groupings within the Alestidae were similarly problematic. Roberts (1969: 443) divided the African components of the Alestidae (his African Characidae) into the subfamilies Hydrocyninae (consisting only of *Hydrocynus*) and Alestinae (including all remaining African genera herein assigned to the Alestidae). Géry (1977: 18) thereafter erected the family Alestidae for Roberts' Hydrocyninae and Alestinae and restricted the Characidae to the Neotropical taxa that were traditionally assigned to that family. Géry's conclusions were based on a melange of plesiomorphic and apomorphic characters that rendered it impossible to evaluate the monophyly of either his Alestidae or Characidae.

Vari (1979: 342) noted that the recognition of a separate Hydrocyninae rendered the Alestinae as delimited by Roberts (1969) nonmonophyletic. In order to resolve that issue, Vari (1979) synonymized the Hydrocyninae into the Alestinae but did not delve into the question of the relationships within the Alestinae (the African components of the Alestidae of this study). In her phylogenetic study of *Hydrocynus*, Brewster (1986) provided additional evidence indicative of the nonmonophyly of the Alestinae of Roberts (1969) and noted that the then-utilized classification of alestids was clearly unsatisfactory and indeed a major impediment to an understanding of the diversity in the group. Furthermore, the genera proposed and/or recognized within the Alestidae by many authors (e.g. Poll, 1957, 1967a; Géry, 1977; Paugy, 1986, 1990a) were delimited on a typological basis without evidence as to the naturalness (monophyly), or lack thereof, of these taxa.

Our study of phylogenetic questions involving the Alestidae was undertaken with several aims, specifically:

1. Examination of the hypothesis of the monophyly of the Alestidae tentatively proposed by Vari (1998).
2. Identification of synapomorphies that allow the proposal of a hypothesis of intrarelationships within the Alestidae and the definition of suprageneric clades and genera within the Alestidae.
3. Examination of the historical biogeography of the Alestidae.
4. Examination of the pronounced range of body sizes within the Alestidae in the context of the final phylogeny in order to determine the evolutionary framework for the apparent miniaturization and gigantism present in the family.
5. Evaluation of the fossil record of taxa assignable to the Alestidae within the context of the final phylogeny and analysis of the implications of such fossils for the minimum ages of higher-level clades within the family.

METHODS

PHYLOGENETIC PROCEDURES

Hypotheses of relationships were proposed using the cladistic or phylogenetic method first formalized by Hennig (1950, 1966) and subsequently developed by a series of other authors. Parsimony analysis was employed to generate hypotheses of phylogenetic relationships and of character state transformations using PAUP v. 4.0b10 (Swofford, 2000). A parallel analysis utilizing Hennig86 v.1.5 (Farris, 1988; Platnick, 1989) associated with Tree Gardener v.2.2. (Ramos, 1998) yielded the same results. Heuristic search was applied in both programs, with options 'stepwise addition', 'random addition-sequence' with '2000 replicates' in PAUP and 'mhennig*' and 'bb*' in Hennig86.

Character polarity was determined by outgroup comparison. Most multistate characters were analysed ordered according to morphoclines (similarity among the pertinent character states) except for characters 49 and 80, for which there was no obvious morphocline and which were treated as unordered. Rooting was fixed in the characiform *Xenocharax* (family Distichodontidae), which is apparently a basal representative of the Characiformes (Fink & Fink, 1981).

Character state distribution was examined using ACCTRAN optimization following de Pinna (1991: 367) under which ambiguous character distributions are resolved under the optimization that maximizes reversals rather than parallelisms within the resultant phylogenetic tree. The equally parsimonious DELTRAN option is also discussed at appropriate level(s) within 'Phylogenetic Reconstruction', below, in order to make the alternatives apparent to the reader and facilitate future lower level phylogenetic analyses.

Relationships for ingroup and outgroup taxa were resolved simultaneously, including all relevant terminals in a single analysis of global parsimony, as explained in Nixon & Carpenter (1993). Outgroup relationships are neither presented in the cladograms nor discussed in 'Phylogenetic Reconstruction', in so far as the sampling of outgroup taxa was of necessity insufficient to address questions of higher level phylogenetic relationships within the Characiformes.

The data matrix was assembled with the aid of Tree Gardener v. 2.2. (Ramos, 1998). Whenever possible, characters were typically assigned discrete, usually binary, states to minimize problems with the ambiguous ordering of multistate characters. Data for the analysis were extracted from multiple body systems so as to minimize the loading resulting from functionally constrained correlations and thus better determine the phylogenetic signal. All discretely codable examined features, including those found to be autapomorphic under the final most parsimonious hypothesis, were retained in the phylogenetic analysis.

Characters are defined and described in 'Character description and analysis' below, and are summarized in the table in Appendix 2. Missing entries in the data matrix are represented by '?' when the character state could not be checked due to lack of appropriate study material or as a consequence of the impossibility of coding the state for that taxon, or represented by '–' for inapplicable character states.

As a consequence of the unavailability of material of the species that could be cleared and counterstained, our observations of the terminal alestid taxon *Petersius conserialis* Hilgendorf, known only from two small river systems in East Africa (Skelton, 1994: 128), were restricted to alcohol-preserved specimens and radiographs of that material. Many characters involving internal features were coded as '?' for *P. conserialis* due to the resultant impossibility of determining the condition in that species for such features.

Ingroup taxa were chosen as representatives of all recognized genera of Alestidae based on the availability of specimens for clearing and staining. Such taxa typically were the type-species for a genus and/or demonstrated morphological variation that was either externally obvious or was previously discussed in the literature and therefore a potential source of phylogenetically useful information. In the case of the more speciose genera of the Alestidae, we attempted to include a diversity of species that represented the range of morphological variation in the nominal taxon and/or maximized the representation of species in the genus (Appendix 2).

Hypotheses of relationships within the Characiformes presented by recent authors (Ortí & Meyer, 1997; Buckup, 1998; Zanata, 2000) were additional sources of comparative information, as well as serving as a method to delimit the most appropriate outgroups for the Alestidae. Although the cladogram presented by Murray & Stewart (2002: fig. 6) indicated a sister-group relationship between the Alestidae and the Characidae (*sensu stricto*), no synapomorphies were proposed by those authors to support that scheme of relationships. In the absence of such evidence, the dichotomy between the Alestidae and Characidae proposed by Murray & Stewart (2002) collapses, with a consequent lack of resolution at the base of their phylogenetic scheme.

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; BMNH, The Natural History Museum, London, formerly, British Museum (Natural History); FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Cambridge; MEPN, Museo de la Escuela Politecnica Nacional, Quito; MNHN, Muséum National d'Histoire Naturelle, Paris; MUSM, Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima; MRAC, Musée Royal de l'Afrique Centrale, Tervuren; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, DC; USNM, Former United States National Museum, collections in NMNH; ZMH, Zoologisches Institut und Zoologisches Museum, Hamburg.

OSTEOLOGICAL PREPARATIONS

Samples of all material included as terminal taxa, except *Petersius conserialis* (see comments above concerning that species), were cleared and counterstained for cartilage and bone using a modification of the method outlined by Taylor & Van Dyke (1985). Whenever possible, two or more specimens of each species were prepared in that fashion in order to facilitate checks for anomalous features and also to allow for evaluation, when possible, of sexually dimorphic osteological features. Specimens that were examined via radiography were supplemental sources of osteological data and are indicated by (R).

Data from external morphology were based on the examination of the cleared and stained specimens prior to their processing as osteological preparations. In some instances these data were supplemented by information from other alcohol-preserved specimens of the species in the same or in other lots. Information from the literature provided supplemental evidence concerning character state distributions. Our morphological examination of *P. conserialis* was limited to externally apparent features and to those internal characters of phylogenetic interest which could be examined via radiography.

Genera recognized herein are those listed in Poll (1967a) and Paugy (1986), with the exception of *Clupeopetersius* (see remarks under 'Nomenclature', below). Identifications were based on the most recent available taxonomic treatment of each taxon; however, the lack of in-depth revisionary treatments for many African alestid species and genera makes it likely that various nominal species as now delimited actually represent species complexes. An example involves the material herein identified as *Virilia pabrensis*, which although agreeing with the published concept of the species, demonstrates some differences relative to the characters described to date for that species, most notably in size at maturity.

The holotype of *Phenacogrammus pabrensis* is an apparently mature male of 39.5 mm SL (Roman, 1966: pl. 4, fig. 8). In his paper in which he made *P. pabrensis* the type-species of *Virilia*, Roberts (1967b: 254) reported that mature males of *Phenacogrammus* (= *Virilia*) *pabrensis* were about 29–29.5 mm SL, a size significantly smaller than the holotype of the species (39.5 mm SL) as reported by Roman (1966). Roberts furthermore commented (1967b: 255) that 'males do not grow much after they mature', a remark that raises questions as to whether his material was conspecific with that of Roman (1966), in which the male holotype was about 33% longer.

Mature males of *Virilia pabrensis* as evidenced by pronounced sexual dimorphism of the anal fin that were examined in this study were 18.8–19.7 mm SL, a length approximately one-third smaller than Roberts' material and one-half that of Roman's holotype of the species. This range in reported sizes for mature males in different population samples of *V. pabrensis* raises questions as to the conspecificity of these samples. This question can only be addressed by a thorough analysis of *Virilia* across its geographical distribution, a project beyond the scope of this study.

Species indicated with an asterisk (*) in Appendix 1 were the source of the morphological data utilized in estimating the phylogenetic relationships of the Alestidae, and were also used as the basis for illustrations and/or specific observations reported in the text. Observations to produce the data matrix were focused on the first listed lot for each species and were supplemented, when necessary, by examination of specimens in the other cited conspecific lots. The remaining species in the list were the basis of additional observations pertinent to broader questions of character distribution. Whenever a character is mentioned in the text as being present in an outgroup genus without the citation of a species, the statement on the character distribution refers solely to a species listed in Appendix 1, and should not be taken to imply that the character is general across all members of the genus.

TERMINOLOGY

Osteological terminology follows Weitzman (1962) with the following modifications. Prevomer is substituted for vomer and opisthotic for intercalar, as in most recent papers discussing the osteology of the Characiformes. The use of epioccipital rather than epiotic follows Patterson (1975). The ossification traditionally termed the epihyal is referred to as the posterior ceratohyal, and the ceratohyal of many previous authors as the anterior ceratohyal, following Nelson (1969). Use of mesethmoid rather than ethmoid follows Fink & Fink (1981).

NOMENCLATURE

The group that is the primary focus of this study was referred to as the African Characidae under the taxonomically more encompassing concept of the Characidae proposed by Greenwood *et al*. (1966). In recent years the 'African Characidae' of some authors has been cited as the Alestinae by Poll (1967a: 2), followed by Roberts (1969: 442) and Vari (1979: 342). Géry (1977: 18; 1995: 39) and Buckup (1998: 138) alternatively used Alestidae for the assemblage. On some occasions the group has, in turn, been identified as the Alestiinae. The root for the familial level name is derived from *Alestes*; according to Steyskal (1980: 174) names that end in 'es' drop that syllable for their stems. Thus, the family root would be 'Alest' and the family name Alestidae, the form that we use in the following discussion. When citing previous authors who recognized the group as a subfamily we use Alestinae for consistency regardless of whether these authors used that form of the name or an alternative spelling.

Clupeopetersius was proposed by Pellegrin (1928: 82) as a replacement name for *Clupeocharax*, a name that he advanced two years earlier (1926: 159) to include *C. schoutedeni* Pellegrin, a species that was described in that same publication. His proposal of the replacement name *Clupeopetersius* was based on his opinion that *Clupeocharax* was preoccupied by *Clupeacharax* Pearson (1924: 46), a characid described from the Bolivian portions of the Amazon River basin. Notwithstanding the similarity in the two names, they do differ, and, as noted by Eschmeyer (1998: 1896), the change of name by Pellegrin (1928) was unnecessary. We consequently use *Clupeocharax*, the older available name, contrary to authors (e.g. Poll, 1967a; Paugy, 1990a) who followed Pellegrin (1928) and utilized *Clupeopetersius* for *C. schoutedeni*.

Several subfamilial units have been proposed for components of the Alestidae. Based on the results of our analysis, one of these, the Petersiini, would have to be dramatically restricted in order to be monophyletic. Continued recognition within the Alestidae of the Petersiini would, furthermore, necessitate the proposal of a number of additional suprageneric taxa so that all recognized subfamilies would be monophyletic. Such a complex subfamilial-level taxonomy of the Alestidae is premature in light of the unavoidable gaps in the taxonomic sampling within this analysis. We consequently identify clades in the phylogenetic analysis in terms of the included genera.

There remain significant questions about the naturalness of both the Characidae and the various subfamilies recognized within that family in the recent systematic literature. Of particular import for the purposes of the comparative discussions in this paper are the divergent published opinions as to the limits of the Neotropical characiform subfamily Tetragonopterinae. Weitzman & Malabarba (1998: 164) questioned whether the Tetragonopterinae was monophyletic but, nonetheless, continued to recognize that subfamily as it was utilized in the literature at that time. Reis (2003: 212), following up on the questions highlighted by Weitzman and Malabarba, alternatively restricted the Tetragonopterinae to *Tetragonopterus,* and removed the numerous other genera and species assigned to the Tetragonopterinae in most recent studies to 'Genera Incertae Sedis in Characidae' (Lima *et al*., 2003: 106).

Although this action ensured the monophyly of the restricted Tetragonopterinae (a genus, *Tetragonopterus*, of only three species; Reis, 2003; Benine, Dardis & Vari, 2004), it also eliminated the Tetragonopterinae as a ready descriptor for the assemblage formed by the numerous taxa that were traditionally assigned to that subfamily, many of which share some apparently derived attributes. We consequently follow Malabarba & Weitzman (2003) in utilizing the more encompassing concept of the Tetragonopterinae that existed prior to Reis (2003) in order to facilitate the discussion of character states and their distribution in the outgroup taxa of this study.

CHARACTER DESCRIPTION AND ANALYSIS

Discussion of the phylogenetically informative characters for the taxa examined in this study is arranged by discrete body systems presented in an overall anterior to posterior pattern. A brief description of each character is followed first by summaries of the recognized character states and then by the consistency index (CI) and retention index (RI) for each character. These brief character encapsulations are followed by a discussion of the condition of the feature in outgroup characiforms along with other remarks, when applicable, pertinent to the question of the polarity and/or utility of the feature in question based on the final most parsimonious hypothesis of relationships. These discussions focus on the outgroups utilized in the phylogenetic analysis and are supplemented, when appropriate, by comments on apparently homologous features in other groups of Characiforms in the New and Old Worlds. The occurrence of such apparent homologues in such outgroups is assumed to represent homoplasies within our present understanding of characiform relationships (Buckup, 1998; Weitzman & Malabarba, 1998; Malabarba & Weitzman, 2003; other papers cited therein).

ANTORBITAL, SUPRAORBITAL, INFRAORBITAL AND NASAL BONES

1. Presence or absence of antorbital: (0) present; (1) absent (CI = 50; RI = 0)

The antorbital in the Characiformes is typically a small bone positioned at the anteroventral margin of the ring of orbital ossifications (Figs 1, 2, 4). In his discussion of the osteology of *Lepidarchus*, Roberts (1966: 212) called attention to the absence in that genus of a series of bones, including the antorbital. The antorbital is present in all of the other taxa included in this analysis, with the exception of the erythrinid genus *Hoplias*, a distant outgroup more closely related to various groups of nonalestid characiforms (Vari, 1995: fig. 15; Buckup, 1998: 134; Oyakawa, 1998: 98). In light of the intervening phylogenetic distance, the absence of the antorbital in *Hoplias* is hypothesized to be homoplastic relative to the lack of the ossification in *Lepidarchus*. The lack of the antorbital consequently

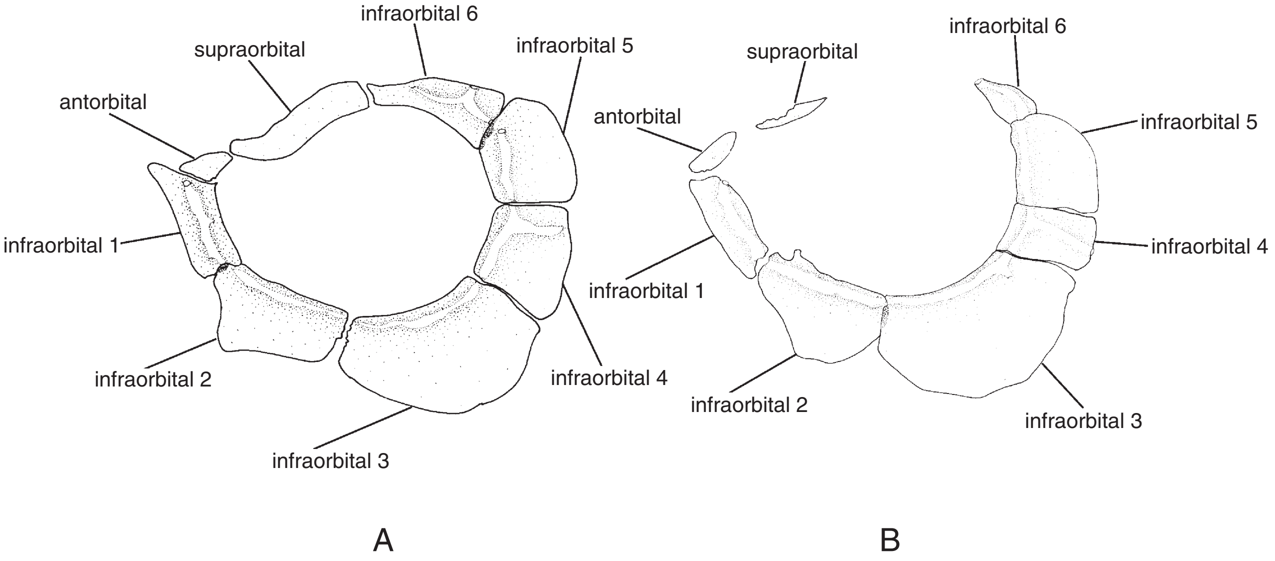

Figure 1. Infraorbitals, supraorbital, and antorbital of (A) *Brycinus macrolepidotus*, MZUSP 60303, 58.6 mm SL; and (B) *Chalceus macrolepidotus*, FMNH 85686, 93.3 mm SL; lateral view, anterior to left.

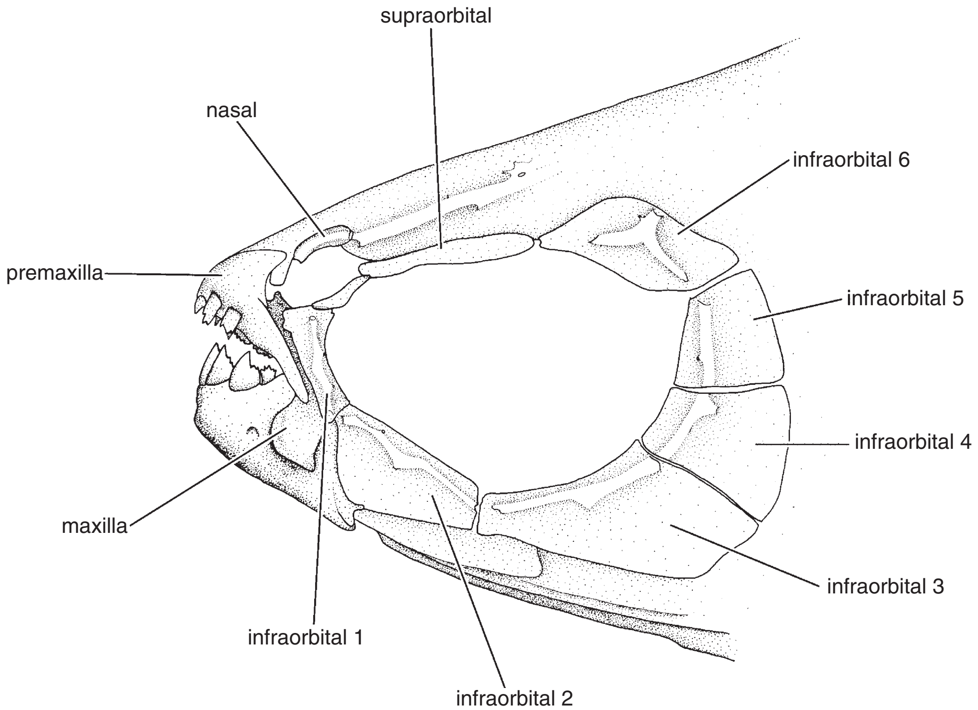

Figure 2. Jaws and surface bones of the lateral portion of the head of *Alestes baremoze* MZUSP 60301, 118.6 mm SL; left side, lateral view.

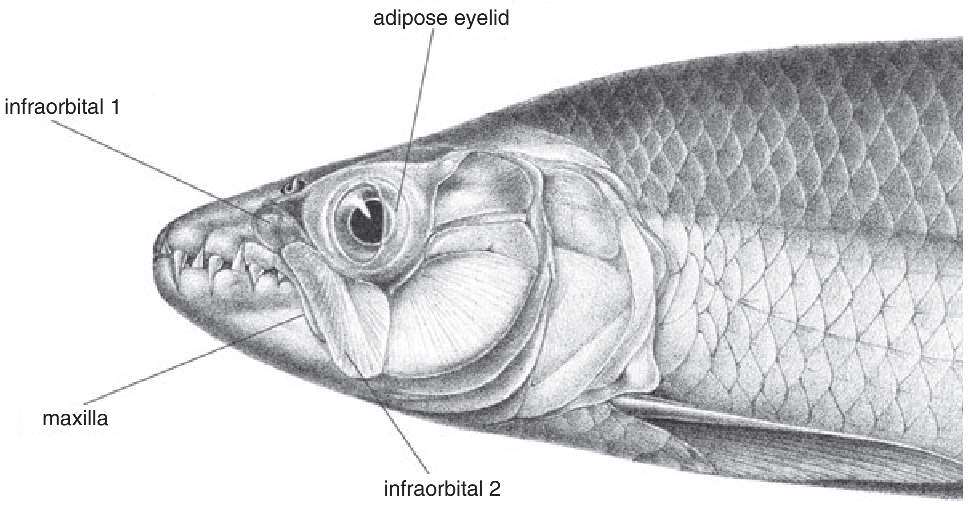

Figure 3. *Hydrocynus vittatus*, showing enlarged first and second infraorbitals, overlap of enlarged teeth of anterior portions of upper and lower jaws, position of posterior margin of maxilla, and pronounced degree of development of adipose eyelid overlying eye (taken from Boulenger, 1898: pl. 10, fig. 2).

is hypothesized to be autapomorphic for *Lepidarchus* within the Alestidae.

2. Presence or absence of supraorbital: (0) present; (1) absent (CI = 16; RI = 72)
The majority of taxa in the Characiformes possess a supraorbital, a flat ossification of variable shape and proportional size that is situated at the dorsal margin of the orbit and that overlaps the dorsolateral margin of the ventral blade of the lateral ethmoid to differing degrees (Figs 1, 2, 4). Within the Alestidae, the supraorbital is absent in the clade formed by *Ladigesia* and *Lepidarchus* and the clade consisting of *Hemmigrammopetersius*, *Micralestes*, *Virilia* and all

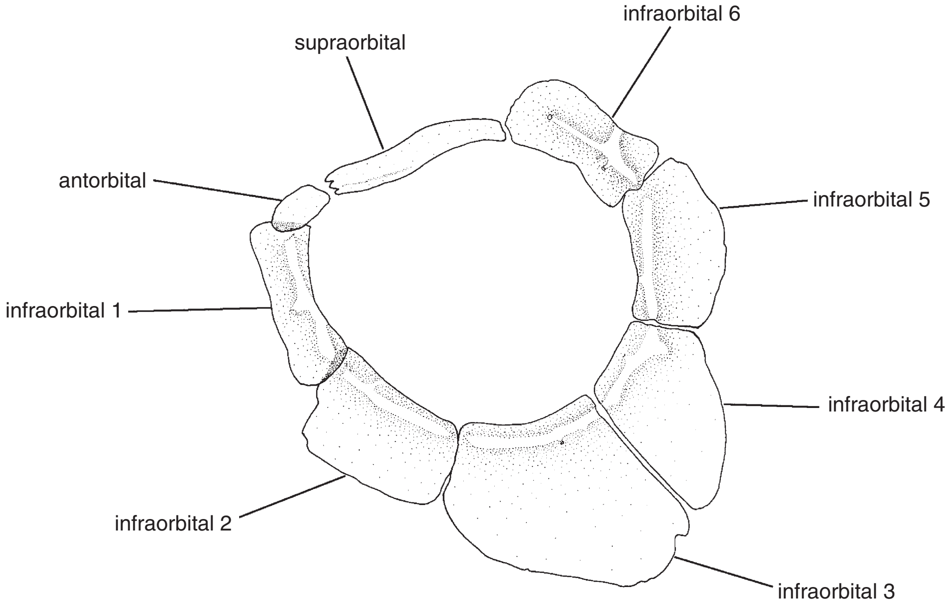

Figure 4. Infraorbitals, supraorbital, and antorbital of *Bryconalestes longipinnis*, USNM 193937, 76.2 mm SL; lateral view, anterior to left.

species of *Rhabdalestes* with the exception of *R. septentrionalis* (Boulenger). The absence of a supraorbital has been utilized to delimit a lineage within the New World family Characidae (Malabarba & Weitzman, 2003: fig. 2) and is absent in several taxa in the outgroups in this analysis (Characidae: *Astyanax*, *Charax*, *Cheirodon*, *Tetragonopterus*; Crenuchidae: *Crenuchus*; Erythrinidae: *Hoplias*). Under the final most parsimonious hypothesis of relationships, the absence of the supraorbital occurs homoplastically within the Alestidae in the two cited intrafamilial clades and between those lineages and the noted outgroups.

3. Form of ventral surface of supraorbital: (0) relatively smooth and without distinct ventral process; (1) with distinct ventrally directed process, anterior portion of which contacts blade-like ventrolateral process of lateral ethmoid (CI = 25; RI = 62)

A well-developed ventral projection of the supraorbital described as state 1 for this character was observed among examined alestids in *Alestes baremoze* (Joannis), *A. dentex* (Linnaeus), *Arnoldichthys spilopterus* (Boulenger), *Bryconaethiops boulengeri* Pellegrin, *B. macrops* Boulenger, *B. microstoma* Günther, *Bryconalestes derhami* (Géry & Mahnert), *B. intermedius* (Boulenger) and *B. longipinnis* (Günther). Several examined outgroup taxa (e.g. the African *Hepsetus* and the New World *Bryconops* and *Serrasalmus*) also have some degree of ornamentation of the ventral surface of the supraorbital. These taxa lack, however, ventral projections of the main body of the supraorbital of a form comparable to that present in the nine listed alestid taxa. The examined cleared and stained specimens of *Hydrocynus brevis* Günther and *H. forskahlii* Cuvier have a slight indication of a process on the ventral surface of the supraorbital, but larger whole specimens of both species lack a distinct elaboration in that region of the bone and in light of that absence we code *H. brevis* and *H. forskahlii* as having state 0 for this character.

Although *Alestes macrophthalmus* Günther is a member of a clade whose other members are characterized by the presence of a well-developed ventral projection on that bone, the ventral portions of the supraorbital in the cleared and stained material of that genus is only somewhat irregular. *Alestes macrophthalmus* is consequently coded as having state 0 for this character.

4. Form of supraorbital: (0) relatively straight or gently sigmoid with anterior portion not distinctly angled anterodorsally; (1) distinctly sigmoid with anterior portion distinctly angled anterodorsally (CI = 100; RI = 100)

The supraorbital of most examined characiforms is relatively straight or only gently sigmoid with the anterior portion of the ossification lacking a distinct angle relative to the remainder of the bone. State 1, the presence of a distinct anterodorsal angle in the supraorbital, is unique to *Brycinus bimaculatus* (Boulenger), *B. brevis* (Boulenger) and *B. macrolepidotus* Valenciennes among examined alestids.

5. Continuity of orbital ring: (0) incomplete, with lateral margin of frontal forming portion of dorsal margin of orbital rim; (1) complete, with dorsal margin of orbital rim bordered by sixth infraorbital and supraorbital or in some instances solely by latter ossification (CI = 16; RI = 82)

A dorsally continuous orbital ring bordered by the infraorbitals and supraorbital is common to diverse characiforms (Figs 1A, 2, 4), with the degree of completeness of the orbital ring primarily a function of the extent of development of the supraorbital. Both the reduction in the degree of development of the supraorbital (*Brachypetersius altus* (Boulenger), *Chalceus* (Fig. 1B), *Phenacogrammus*) and the absence of that ossification (*Ladigesia*, *Lepidarchus*, *Micralestes* and all *Rhabdalestes* species with the exception of *R. septentrionalis*) result in a contribution of the frontal to the orbital rim.

Although most of the taxa in the analysis that demonstrate a reduction of the degree of development of the supraorbital tend to be species of a small body size, a reduction of the supraorbital is not invariably correlated with a smaller body size across the Alestidae. *Brachypetersius notospilus* (Pellegrin), a species with a relatively small body size, retains a complete orbital ring. A nearly complete orbital ring is, in turn, present in *B. gabonensis* Poll, a species that also attains only a small adult body size. A direct correlation between the degree of development of the supraorbital and body size similarly fails to apply across the Characiformes given that the ossification is absent in the Erythrinidae, represented in the outgroups of this study by *Hoplias,* a genus that achieves large to very large body size, and also in various members of the Tetragonopterinae that attain body sizes significantly larger than those achieved by the taxa in the Alestidae that lack this ossification.

6. Relative position of anterior portion of first infraorbital and antorbital: (0) anterior border of first infraorbital extending anterior to anterior border of antorbital; (1) anterior border of first infraorbital either aligned with anterior border of antorbital or situated slightly posterior to that point (CI = 33; RI = 85)

In the Alestidae, the first infraorbital always extends to some degree anterior to the anterior limit of the antorbital, with some species in the family having a significant portion of the infraorbital situated forward of that landmark (e.g. *Brycinus macrolepidotus* (Fig. 1A), *Chalceus epakros* Zanata & Toledo-Piza, *C. guaporensis* Zanata & Toledo-Piza, *Clupeocharax*, *Tricuspidalestes*). Other species in the Alestidae, in contrast, lack such a well-developed extension of the first infraorbital despite having the anterior border of the first infraorbital extending forward of the anterior border of the antorbital (e.g. *Brachypetersius gabonensis*, *B. notospilus*, *Chalceus macrolepidotus,* Fig. 1B). Continuity between these conditions renders it impossible to parse the degree of development of this extension of the first infraorbital beyond the anterior limit of the antorbital into two or more characters. The extension of the first infraorbital anterior to the antorbital, regardless of the degree of the extension, is consequently coded as a single feature.

An extension of the first infraorbital distinctly anterior to the antorbital was also observed in *Crenuchus*, *Hemiodus* and *Xenocharax* among examined outgroups. The most common condition present in the other examined outgroup taxa is to have the anterior limits of these two bones aligned, albeit with some variation within *Brycon* in which some species of the genus have the anterior border of the antorbital situated anterior to the limit of the first infraorbital (e.g. *B. dentex* Günther, *B. oligolepis* Regan).

7. Degree of development of first infraorbital: (0) first infraorbital not overlapping ascending process of maxilla and falling distinctly short of lateral portion of premaxilla; (1) first infraorbital totally or nearly totally overlapping ascending process of maxilla and with anterior border of infraorbital reaching at least posterolateral portion of premaxilla (CI = 33; RI = 91)

In all alestids other than *Chalceus*, *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes*, the anterior portion of the first infraorbital is proportionally distinctly wider than the form of that bone present in the examined outgroups. This widened form in the majority of alestids consequently extends further anteriorly than in the outgroup condition, reaching to, or nearly to, the lateral portion of the premaxilla with a consequent overlap of the lateral surface of the ascending process of the maxilla by the first infraorbital (Fig. 2; see also Brewster, 1986: fig. 22, for this condition in *Alestes dentex*).

Such a lateral overlap of the maxilla by the first infraorbital is not, however, solely a function of the degree of development of the first infraorbital in all of these taxa. *Clupeocharax* and *Tricuspidalestes,* for example, have wide infraorbitals that, nonetheless, fail to distinctly overlap a significant portion of the maxilla and are consequently coded as state 0 for this character. *Brachypetersius gabonensis*, alternatively, has a proportionally narrower infraorbital that, nonetheless, covers the proximate portion of the maxilla and the condition in that species is coded as state 1. A relatively wide anterior portion of the first infraorbital was previously reported by Lucena (1993) as present in the alestids *Alestes leuciscus* Günther, *Hemmigrammopetersius rhodesiensis* (Ricardo-Bertram) and *Hydrocynus forskahlii*.

Our observations of *Petersius* were restricted to whole alcohol-preserved specimens. Nonetheless, it is apparent that the genus has a pronounced degree of overlap of the first infraorbital over the lateral surface of the maxilla, albeit with the extent of the overlap between these bones less than that present in some other alestids (e.g. *Brycinus*). In light of the degree of overlap we code *Petersius* as having state 1.

Oyakawa (1998: 41) utilized the degree of extension of the first infraorbital over the maxilla in his analysis of the phylogenetic relationships of the Neotropical characiform families Erythrinidae, Lebiasinidae and Pyrrhulinidae (the latter two families are equivalent to the Lebiasinidae of Greenwood *et al.*, 1966). Although some degree of overlap characterizes the members of the Erythrinidae, Lebiasinidae and Pyrrhulinidae (*sensu* Oyakawa, 1998), the overall morphology of the first infraorbital in those families differs significantly from the form of the bone present in the Alestidae. In these Neotropical families the first infraorbital covers only a small region of the basal portion of the ascending process of the maxilla and, furthermore, falls short of the premaxilla. This condition, which was also observed in this study in the Neotropical genus *Acestrorhynchus*, is distinct from the more pronounced degree of overlap of the first infraorbital over portions of the maxilla and premaxilla present in the Alestidae and is thus considered nonhomologous with the latter condition.

8. Degree of anterior extension of first and second infraorbitals: (0) first and second infraorbitals not covering lateral surface of premaxilla; (1) first and second infraorbitals greatly enlarged and covering at least part of lateral surfaces of premaxilla and maxilla (CI = 100; RI = 100)

The possession of anteriorly enlarged first and second infraorbital bones extending over the lateral surface of the maxilla was identified as a synapomorphy for the species of *Hydrocynus* by Brewster (1986: 190, fig. 7; synapomorphy 16). As noted in character 7, most examined alestids have an enlarged first infraorbital covering a major portion of the ascending process of the maxilla (Fig. 2). The first infraorbital in the species of *Hydrocynus* is, however, proportionally significantly more extensive than that occurring in other members of the Alestidae (Fig. 3). As a consequence, the first infraorbital in *Hydrocynus* entirely covers not only the lateral surface of the ascending process of the maxilla but also laterally overlaps a significant portion of the posterolateral surface of the premaxilla.

The second infraorbital in *Hydrocynus* is similarly enlarged anteriorly beyond the condition present in other alestids and laterally overlaps a portion of the flat posteroventral portion of the maxilla and a relatively broad region of the posterodorsal surface of the lower jaw (Fig. 3). The degree of overlap of the maxilla by the first and second infraorbitals within the species of *Hydrocynus* is ontogenetically variable, with larger specimens of the genus having the maxilla completely covered laterally.

No comparable pronounced overlap of the upper jaws bones by the first and second infraorbitals was observed in the other taxa examined in this study. Although all genera of the New World family Prochilodontidae have a pronounced overlap of the maxilla by the anterior infraorbitals (Castro & Vari, 2004: 37), this overlap is a consequence of the realignment of the entire upper jaw posterodorsally from the location typical for that complex in other characiforms. That revamping is nonhomologous with the condition in *Hydrocynus* that retains an alignment of the jaw that is comparable to that present in the majority of characiforms. A hypothesis of the nonmonophyly of the conditions in these two taxa is furthermore supported by the phylogenetic data that indicate that the Prochilodontidae are most closely related to the Neotropical families Curimatidae, Anostomidae and Chilodontidae (Vari, 1983; Castro & Vari, 2004: 58).

9. Sensory canal of first and second infraorbitals: (0) with distinct bony lamellae present dorsal and particularly ventral to laterosensory canal segments in each bone; (1) distinct bony lamella dorsal and ventral to laterosensory canal segments absent and with these infraorbitals consisting primarily of ossified laterosensory canal segment (CI = 100; RI = 100)

The first and second infraorbitals in characiforms typically have the laterosensory canal segments bordered dorsally and particularly ventrally by distinct ossified lamellae (Figs 1, 2, 4). Such a morphology is general to all genera of the Alestidae, with the exception of *Lepidarchus*, in which both infraorbitals are reduced to tubular ossifications lacking ossified lamellae other than for a very slightly developed, plate-like process that is present along the anterodorsal portion of the first infraorbital; an autapomorphic condition.

In *Triportheus* and some other taxa in the Neotropical Characidae (*Agoniates*, *Brycon chagrensis* (Kner & Steindachner), *B. dentex*, *B. guatemalensis* Regan, *B. meeki* Eigenmann & Hildebrand, *B. striatulus* (Kner & Steindachner), *Lignobrycon*) the ventral lamellar portion of the anterior portion of the first infraorbital is reduced and the sensory canal in that region of the bone approximates the ventral margin of the ossification. Nonetheless, the remaining lamellar portions of the first infraorbital in these New World taxa are fully developed. That form of the first infraorbital is thus considered to be nonhomologous with the condition in *Lepidarchus*.

In the Neotropical serrasalmine *Serrasalmus*, the first infraorbital is reduced either to a bony canal or retains only very reduced bordering lamellae. This reduction is a consequence of reduction in the space available for that ossification as a consequence of restructurings of the adjoining bones. Furthermore, the first infraorbital is well ossified, a condition that contrasts with the poorly ossified bone that is characteristic of *Lepidarchus*. It is also noteworthy that a reduction of the lamellar portions of the first infraorbital is not universal within the Serrasalminae, with such structures present within the subfamily in *Colossoma*, *Mylossoma* and *Utiaritichthys* (see Machado-Allison, 1983: fig. 11b–d). Neither is there any phylogenetic evidence to indicate that the Serrasalminae and Alestidae are closely related. In light of all of these differences, the reduction of the first infraorbital in *Serrasalmus* is considered nonhomologous with that present in *Lepidarchus*.

10. Presence or absence of dorsomedial process of second infraorbital: (0) absent; (1) present (CI = 33; RI = 50)
The dorsal portion of the second infraorbital in characiforms typically has a slightly curving margin without any distinct projections (Figs 1A, 2, 4). All species of *Chalceus* other than for *C. erythrurus* alternatively have a distinct, dorsomedially orientated process that arises from the medial surface of the second infraorbital and is orientated in the direction of the lateral surface of the ventral wing of the lateral ethmoid (Fig. 1B). A somewhat similar process was also observed in the Neotropical characids *Brycon coxeyi* Fowler and *B. oligolepis*. Its presence in the *Brycon* species represents a homoplasy relative to the structure on that bone present in *Chalceus* when evaluated either within the context of the overall most parsimonious hypothesis of relationships for the Alestidae proposed herein, or the hypothesis of relationships within *Brycon* under which *B. coxeyi* and *B. oligolepis* are well embedded within the phylogeny of that genus (Zanata, 2000: fig. 6).

Only one species among the examined alestids, *Phenacogrammus major* (Boulenger), has a process of the second infraorbital reminiscent of that present in the majority of the species of *Chalceus*, albeit less developed. Furthermore, on at least one side of the examined cleared and stained specimen of *P. major* there occur two such processes on the second infraorbital rather than the single structure that is present in *Chalceus*. Notwithstanding those differences, the condition in *P. major* is tentatively coded herein as homologous to the process present in *Chalceus*. Studies of additional species of *Phenacogrammus* are necessary to determine the generality of this modification of the second infraorbital within that genus.

11. Presence or absence of third infraorbital: (0) present; (1) absent (CI = 100; RI = 100)
The vast majority of characiforms have a variably shaped third infraorbital situated along the ventral and often posteroventral margin of the orbital ring (Figs 1, 2, 4). A third infraorbital is uniquely absent in *Lepidarchus* among examined alestids and outgroups, a derived loss that is hypothesized to be autapomorphic for the genus.

12. Presence or absence of fourth infraorbital:
(0) present; (1) absent (CI = 100; RI = 100)
The majority of characiforms and most of the alestid and outgroup taxa included in this study have six infraorbitals surrounding the orbit, with a fourth infraorbital positioned at the posterior of the orbital rim (Figs 1, 2, 4). A fourth infraorbital is absent in *Ladigesia* and *Lepidarchus*, a derived loss that may be associated with the diminutive body size of those species. Such a correlation is also present in various characiforms of small body size in Africa (e.g. some species of *Nannocharax*; Vari, 1979: 301) and the Neotropics (e.g. *Carnegiella*; Weitzman, 1954: fig. 7 and *Spintherobolus*; Weitzman & Malabarba, 1999: 15; see also references in latter paper)

13. Shape of fourth infraorbital: (0) anterior and posterior margins of fourth infraorbital running approximately in parallel, with width of dorsal and ventral portions of bone approximately equivalent; (1) posterior margin of fourth infraorbital distinctly angled anterodorsally at least on posterodorsal portion of bone, with width of dorsal portion of bone distinctly narrower than ventral margin (CI = 50; RI = 96)
A relatively square or rectangular morphology of the fourth infraorbital is common to characiforms in general and characids in particular; it also occurs in numerous alestids (Figs 1, 2). A subgroup of alestids (see Appendix 2) differs from that general characiform condition in having an anterodorsally angled margin along at least the posterodorsal portion (Fig. 4), with the reduction in the degree of development of that region even more pronounced in some of these taxa (e.g. *Bathyaethiops*, *Duboisialestes*). Regardless of the degree of reduction, this modification results in a distinct difference in the width of the dorsal margin relative to the extent of the ventral margin of the fourth

infraorbital, a hypothesized derived condition based on outgroup comparisons. In light of the absence of the fourth infraorbital in *Ladigesia* and *Lepidarchus,* the condition of this character could not be coded for those genera.

Looking at other characiforms we find a similar disparity between the widths of the dorsal and ventral margins of the fourth infraorbital in a subgroup of the Neotropical genus *Brycon* (*B. insignis* Steindachner and *B. opalinus* (Cuvier)). These species are, however, deeply embedded in the phylogeny of the genus and their congeners lack this condition (Zanata, 2000: fig. 6). A similar disparity in the margins of the fourth infraorbital is found in the Neotropical genus *Bryconops*, a taxon of uncertain phylogenetic position that is, however, not considered to be a component of the Alestidae under the final most parsimonious hypothesis of relationships.

We were unable to code the condition of this character in *Serrasalmus* and *Charax* due to the lack of a separate fourth infraorbital in those Neotropical genera. The absence of that bone is likely a consequence of the fusion of the third and fourth infraorbitals. Notwithstanding that complication, it is noteworthy that neither *Serrasalmus* nor *Charax* demonstrate modifications of the dorsal portions of the combined ossification that are characteristic of state 1 for this character.

14. Presence or absence of ossified fifth infraorbital and associated laterosensory canal: (0) present; (1) absent (CI = 100; RI = 100)

The majority of characiforms and most of the taxa of the Alestidae examined in this study have six infraorbitals surrounding the anteroventral through posterodorsal margins of the orbit, with a fifth infraorbital forming the portion of the series at the posterior part of the orbital margin (Figs 1, 2, 4). A fifth infraorbital is, however, absent in *Ladigesia* and *Lepidarchus*, a loss that is hypothesized to be derived. As was the case with the fourth infraorbital (see discussion in character 12), there is often a correlation between the loss of the fifth infraorbital and small to diminutive body size. Such a correlation applies in the case of *Ladigesia* and *Lepidarchus*, which are miniatures or near miniatures (*sensu* Weitzman & Vari, 1988). Various other characiforms, most often members of the New World family Characidae of small body size, also lack ossified fifth infraorbitals (e.g. *Axelrodia risesi*, Weitzman & Fink, 1983: fig. 13; *Paracheirodon innesi,* Weitzman & Fink, 1983: fig. 8; *P. simulans,* Weitzman & Fink, 1983: fig. 6). The absence of that ossification in nonalestid characiforms is clearly homoplastic with the lack of the bone in *Ladigesia* and *Lepidarchus* in light of the results of this study and those of Buckup (1998).

15. Presence or absence of sixth infraorbital: (0) present; (1) absent (CI = 100; RI = 100)

The majority of characiforms and most of the taxa of the Alestidae examined in this study have six infraorbitals surrounding much of the border of the orbit, with the sixth infraorbital positioned in the posterodorsal portion of the series (Figs 1, 2, 4). A sixth infraorbital is, however, absent within the Alestidae in *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, a loss that is hypothesized to be derived. Such a loss also occurs in various New World characiformes, usually also of small to diminutive body size, that share reductions of other portions of the infraorbital series (see comments in characters 12 and 14).

16. Junction of fifth and sixth infraorbitals along margin of orbit: (0) relatively smoothly continuous and forming continuous arch or with minor indentation; (1) with very well-developed indentation (CI = 100; RI = 100)

A smoothly continuous junction between the fifth and sixth infraorbitals along the posterior margin of the orbit is typical among examined characiforms (Fig. 1; see also *Brycon meeki*, Weitzman, 1962: fig. 8) or there is at most a slight indentation in the posterior margin of the orbit in the area of articulation of these two bones. In the species of *Alestes* and *Bryconaethiops* there occurs, however, a deep indentation along the orbital rim at the junction of those bones (Fig. 2) apparently as a consequence of the reduction of the extent of development of the anterodorsal portion of the fifth infraorbital. This character could not be coded for *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* among examined alestids as a consequence of their lack of a sixth infraorbital.

17. Presence or absence of nasal bone: (0) present; (1) absent (CI = 100; RI = 100)

A nasal bone is nearly universally present across the Characiformes and its absence in *Lepidarchus* is considered to be an autapomorphy for the genus.

18. Position of anterior margin of nasal: (0) falling short of lateral process of mesethmoid (= lateral ethmoid wing of Weitzman, 1962); (1) extending anteriorly to overlie or extend beyond lateral process of mesethmoid (CI = 33; RI = 90)

The nasal demonstrates a certain degree of variation in its overall length within the Alestidae and across examined outgroups; however, it is difficult to unambiguously parse that variation into multiple character states. The one discrete character that we were able to identify is whether the nasal falls short of the lateral process of the mesethmoid vs. reaching or surpassing that process, and we herein limit our coding of the overall length of the nasal to those two conditions. The majority of members of the Alestidae have state 0 of this character, but comments on the coding of the character for the species of *Bryconaethiops* in the matrix are appropriate.

An examination of an ontogenetic series of *Bryconaethiops boulengeri* demonstrates a proportional increase in the anterior extent of the nasal with increasing body size. The only available material we have of *B. microstoma* is of relatively small size with the nasal bone in these specimens falling short of the lateral process of the mesethmoid. In light of the ontogenetic increase in the degree of development of the bone in its congeners, it is, nonetheless, likely that larger specimens of *B. microstoma* would demonstrate proximity between the nasal and lateral process of the mesethmoid. Given the small size of our available material of this species, we code the character as unknown for *B. microstoma* until such time as material of the species of larger body size becomes available.

The condition of the nasal bone for this feature could not be coded for *Lepidarchus* as a consequence of its absence in that genus. The coding of this character is also problematic in some instances in the outgroup because of the pronounced differences in the form of the lateral process of the mesethmoid in Neotropical and African taxa such as *Crenuchus*, *Hemiodus*, *Xenocharax* and the Cheirodontinae in which the mesethmoid is a narrow, relatively elongate bone and in which the nasal, although not proportionally shortened, nonetheless, falls distinctly short anteriorly of the lateral process of the mesethmoid. These taxa are consequently coded as '?' in the matrix.

Cranium

19. Form of mesethmoid: (0) with distinct, triangular, anteromedial process and without broad, dorsal expansion over anterodorsal portion of premaxilla; (1) without distinct, anteromedial process but with dorsal expansion extending over anterodorsal portion of premaxilla (CI = 50; RI 50)

The majority of alestids have the contralateral premaxilla separated medially, at least in part, by an anteromedial, variably anteriorly attenuate process of the mesethmoid. The mesethmoid, in turn, either lacks any processes extending over the anterodorsal portion of the premaxilla, or such processes, if present, are relatively small. In *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes* the anteromedial process of the mesethmoid is significantly reduced or completely absent (Fig. 5) and the dorsal portion of the bone is expanded into an anteriorly broadly rounded, approximately horizontally aligned process extending over the anterodorsal surface of the median portions of the contralateral premaxilla. Outgroup comparisons failed to reveal any comparable modifications of the mesethmoid among other examined characiforms and these restructurings of that bone in the three cited alestid genera are consequently considered to be derived.

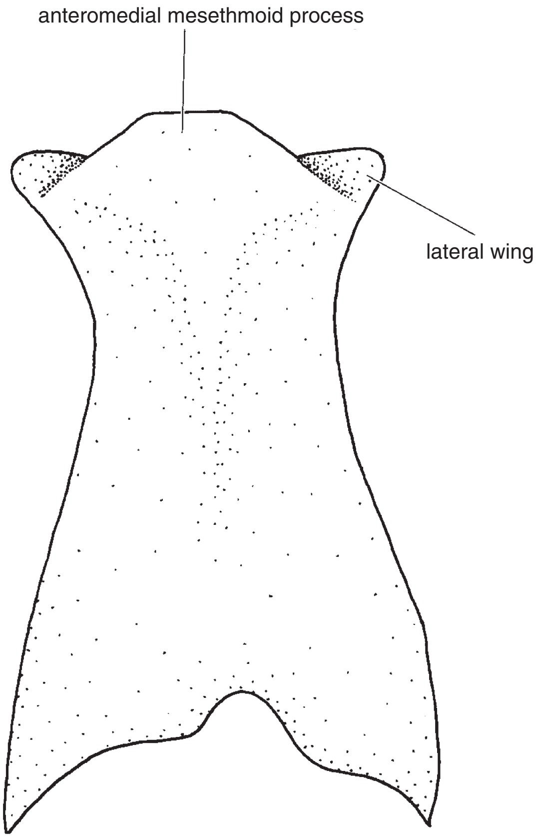

Figure 5. Mesethmoid of *Tricuspidalestes caeruleus*, USNM 365952, 29.9 mm SL, dorsal view, anterior at top.

Although *Cheirodon* has an abbreviated anteromedial process, it lacks any anterodorsal processes extending over the premaxillae. Instead, the premaxillae in *Cheirodon* have short processes passing dorsal to a portion of the mesethmoid, a condition different from the modifications of the mesethmoid that is common to *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes*.

The pronounced restructuring of the mesethmoid characteristic of the species of *Hydrocynus*, in turn, results in a system that at first appearance seems similar to the condition common to *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes*. As noted in the discussion of character 20, the overall morphology of the mesethmoid in *Hydrocynus* differs, however, in numerous details from the form of that bone in *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes* and is

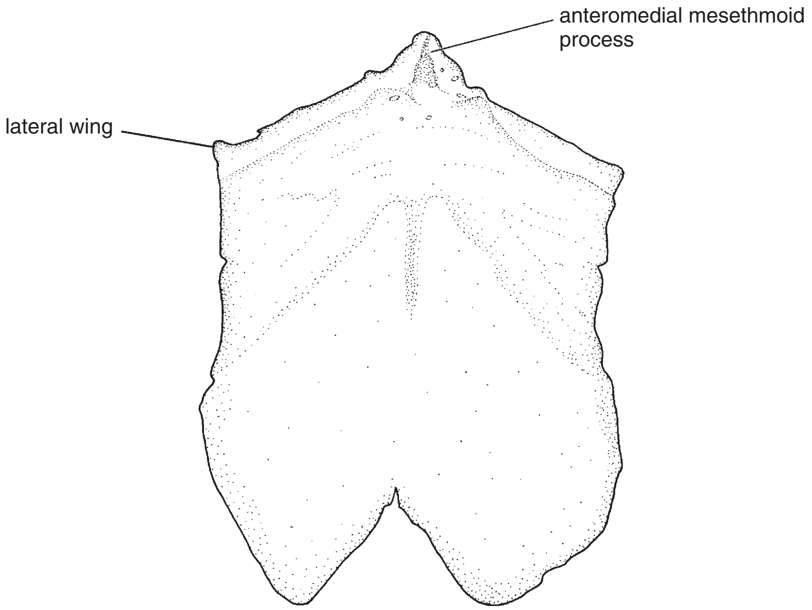

Figure 6. Mesethmoid of *Chalceus spilogyros*, MZUSP 76069, 122. 7 mm SL; dorsal view, anterior at top.

considered nonhomologous with the modifications of the mesethmoid in those three genera.

The anterior portion of the neurocranium in *Crenuchus*, *Hemiodus* and *Xenocharax* is modified to a degree that makes it impossible to code those genera for this character.

20. Degree of development of anterior portion of mesethmoid: (0) with distinct medial process; (1) without distinct medial process (CI = 100; RI = 100)
As noted in the discussion of the previous character, the mesethmoid in the majority of alestids and many outgroup characiforms has a variably developed, median mesethmoid process (Figs 6, 7) separating the contralateral premaxillae to differing degrees. In contrast, the species of *Hydrocynus* have a truncate medial portion of the mesethmoid, with a resultant contact of the contralateral premaxillae along their entire medial margins. In her discussion of the osteology of *Hydrocynus*, Brewster (1986: 166, 184, fig. 1) detailed the series of modifications of the overall form of that ossification and identified the medial structure of the mesethmoid in that genus as the ‘median rostral process. It is difficult to homologize the individual components of the anterior portion of the mesethmoid in *Hydrocynus* vs. the processes present on the bone in other examined characiforms as a consequence of the pronounced restructuring of the mesethmoid in that genus. Notwithstanding that procedural limitation, the morphology of the truncate structure identified by Brewster as the ‘median rostral process’ is unique to the members of *Hydrocynus* among examined characiforms and is consequently considered to be derived.

21. Lateral margin of anterior portion of mesethmoid: (0) without distinct lateral, shelf-like process; (1) with distinct lateral, shelf-like process (CI = 100; RI = 100)
The anterior portion of the mesethmoid has the form of an anteriorly attenuate triangle both in the majority of examined alestids (Figs 6, 7) and outgroup characiforms. A subset of the species of the Alestidae (Appendix 2) possess in addition a distinct lateral, shelf-like process on each side of the anteriorly directed, triangular medial process of the mesethmoid (Fig. 8). This process extends ventral to the primary anteromedial portions of the premaxilla and partially supports the ventral surfaces of that bone. The character could not be coded for *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes* due to the pronounced restructurings of that portion of the mesethmoid in those genera.

22. Ventral diverging lamellae of mesethmoid: (0) lamellae reduced or absent; (1) two lamellae well-developed (CI = 50; RI = 93)
Weitzman (1962: 19) described the portion of the ventral region of the mesethmoid (the ethmoid of that author) posterior to the mesethmoid–vomer articulation in the Neotropical characid *Brycon meeki* as bearing posterolaterally directed lamellae on each side.

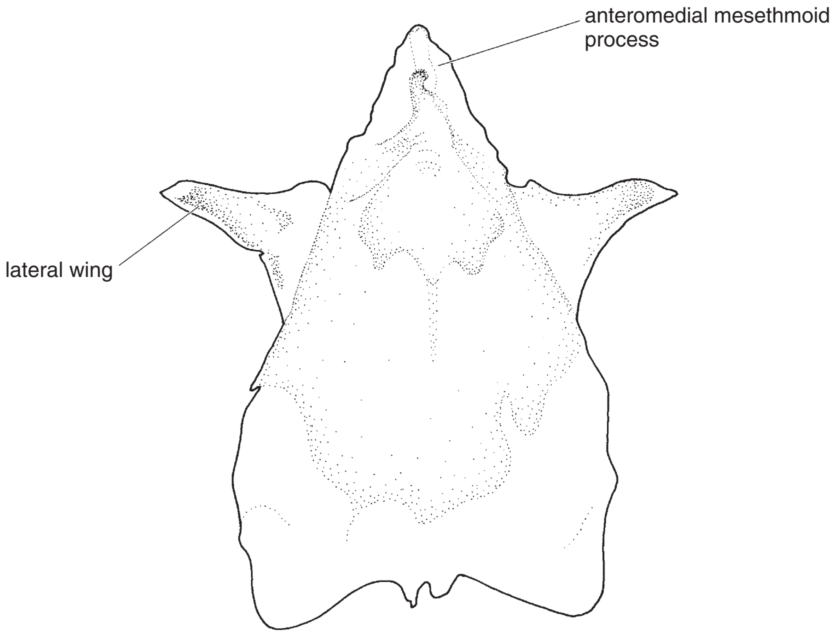

Figure 7. Mesethmoid of *Alestes baremoze*, MZUSP 60301, 118.6 mm SL; dorsal view, anterior at top.

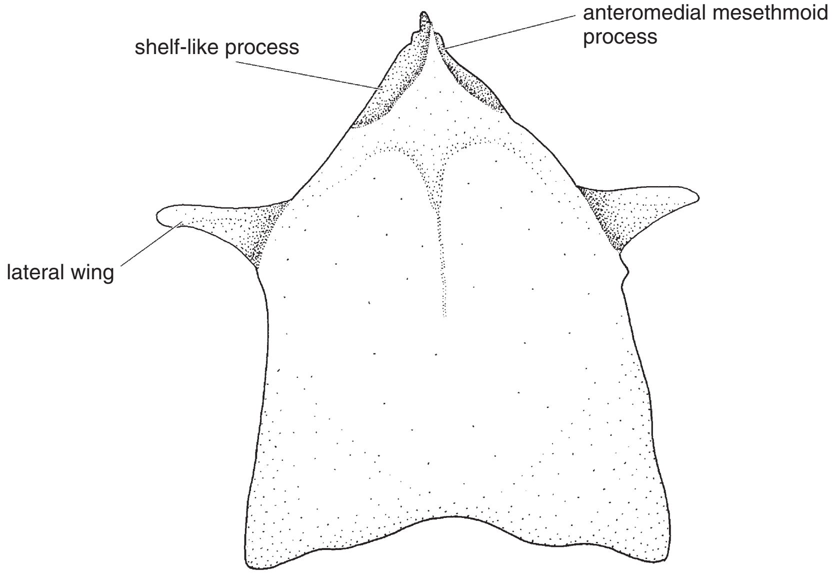

Figure 8. Mesethmoid of *Phenacogrammus aurantiacus*, MZUSP 22853, 67.0 mm SL; dorsal view, anterior at top.

The absence of such lamellae in some alestids was reported by Lucena (1993) for *Alestes leuciscus*, *Hemmigrammopetersius rhodesiensis* and *Hydrocynus forskahlii*, and was found in this study to characterize all examined species of the Alestidae with the exception of *Chalceus*. In her discussion of the well-developed ventral lamellae in the Neotropical subfamily Cynodontinae, Toledo-Piza (2000: 17) reported the reduction or absence of these structures in the Neotropical characiform families Ctenoluciidae, Erythrinidae, Gasteropelecidae, Lebiasinidae, along with most species of *Acestrorhynchus*. None of these taxa are hypothesized to be phylogenetically proximate to the Alestidae (Vari, 1995; Buckup, 1998; Lucena & Menezes, 1998) and the lack of well-developed lamellae in these taxa is consequently considered to be nonhomologous with the absence of those structures in most alestids.

23. Degree of development of lateral wings of mesethmoid (= lateral ethmoid wings of Weitzman, 1962: 19): (0) reduced; (1) well-developed (CI = 50; RI = 80)

In his description of the mesethmoid of *Brycon meeki*, Weitzman (1962: 19) noted the presence on that ossification of a lateral ethmoid wing that was positioned posterior, lateral and somewhat ventral to the mesethmoid spine. The lateral wing of the mesethmoid (= lateral ethmoid wing of Weitzman, 1962) on each side of the mesethmoid has a triangular, laterally pointed form and along its dorsal surface usually supports the ventral surface of the posterior portion of the ascending premaxillary process. Most of the examined characiform taxa have well-developed lateral mesethmoid wings (Figs 7, 8) that support a significant portion of the premaxilla. In contrast, *Chalceus* (Fig. 6) and *Arnoldichthys* have the anterolateral process of the mesethmoid greatly reduced and that structure consequently supports only a small portion of the premaxilla.

Coding the form of the lateral wing of the mesethmoid in some examined outgroup characiforms proved problematic. In *Crenuchus*, *Hemiodus*, *Hepsetus* and *Xenocharax* the overall forms of the mesethmoid differ significantly from the morphology of that ossification that is present in the Alestidae. This variation engendered difficulties in the evaluation of the homology of the components of the mesethmoid between these various taxa. Although coding these outgroup taxa as lacking the mesethmoid wing might at first seem appropriate, the uncertainty as to homology of components of the mesethmoid makes it more appropriate to code the presence of the wing as unknown in these outgroups.

24. Form of lateral portion of mesethmoid wings: (0) terminating in relatively rounded or pointed process; (1) terminating laterally in distinct concavity (CI = 100; RI = 100)

The lateral mesethmoid wings in *Hydrocynus* are thick, blunt, transverse processes with a slight overall curvature ventrally in the transverse plane, a morphology that is hypothesized to represent an apomorphic feature for this genus (Brewster, 1986: 166, 189: figs 1, 26, 28, 30). Although characiforms demonstrate a degree of variation in the overall morphology of the mesethmoid wing ranging from having a distinctly pointed structure (e.g. most alestids, Figs 7, 8) to a more triangular form (e.g. *Brycon falcatus*), in none of the examined outgroup characiforms did we observe lateral mesethmoid wings with a concave lateral border in combination with the presence of anterior and posterior processes such as those characterizing the species of *Hydrocynus*. Neither do examined outgroup characids have a direct articulation of the lateral process of the mesethmoid with the premaxilla.

In *Hydrocynus*, in contrast, the anterolateral portion of the lateral mesethmoid wing is more elongate than is the form of that structure typical for other examined characiforms; the anterolateral surface of the wing consequently articulates with a concavity on the posterior surface of the premaxilla. The concave surface of the mesethmoid wing and the posterolateral process of the mesethmoid also jointly serve as an area of attachment for the ligament extending from the mesethmoid to the maxilla and premaxilla. The highly restructured mesethmoids of *Xenocharax*, *Hemiodus*, *Crenuchus* and *Hoplias* render it impossible to code those taxa for this character.

25. Ventrolateral expansion of projection of vomer extending from main body of bone: (0) absent; (1) present (CI = 100; RI = 100)

The vomer in characiforms bears two anterolateral projections of varying form extending towards the upper portions of the maxillae; they are situated below the lateral wings of the mesethmoid. A concavity located proximate to the lateral margin of the vomerine projection in the area between that process and the main body of the vomer serves as an area of attachment for the ligaments arising from the ectopterygoid and palatine. For the purposes of our discussion, projections of the vomer encompass both the lateral expansions situated along the same plane as the main body of the bone and the ventral protruding process extending from such lateral expansions given the difficulty in ascertaining the exact homologies of these processes.

Well-defined lateral projections of the vomer serving as an area of attachment of ligaments are usually present in *Chilobrycon*, *Lignobrycon*, *Salminus*, *Triportheus* and *Brycon* (albeit with the lateralmost portion of the projections reduced in those species of *Brycon* with elongate heads such as *B. alburnus* Böhlke and *B. insignis*). Although a relatively well-developed projection of the vomer is present in *Charax*, the ectopterygoid and palatine ligaments in that genus insert on the median portion of the vomer in a mode distinct from, and apparently nonhomologous with, the form of attachment typical of the species of *Brycon*. In the case of *Serrasalmus*, there occur ventrally directed projections of the ventral portion of vomer that differ to such a degree from the processes present in other examined taxa that it rendered it impossible to code the character for this genus.

26. Orientation of inferior lamella of lateral ethmoid: (0) orientated anteromedially; (1) orientated directly anteriorly (CI = 50; RI = 50)

Although the extent of the development of the inferior lamella differs across the characiform groups examined in this study, the typical condition in those taxa is an inferior lamella with an anteromedial orientation, which contacts either the vomer or the lateral limit of the area of articulation of the vomer and the mesethmoid. In three of the examined genera in the Alestidae (*Clupeocharax*, *Lepidarchus* and *Tricuspidalestes*) the inferior lamella, although elongate, is, however, orientated directly anteriorly and extends lateral of the lateral margins of the vomer, a condition absent elsewhere among examined taxa and which is consequently considered to be derived.

In the case of the examined species of *Hemmigrammopetersius*, the inferior lamella of the lateral ethmoid is highly reduced, being represented only by a short anterior process. In *Virilia* the process is, in turn, completely absent. It was, thus, impossible to code these two alestid genera for this character. Similarly, the pronounced modification of the lateral ethmoid in *Hepsetus* among the examined outgroups makes it impossible to code this character for that genus.

27. Extent of development of inferior lamella of lateral ethmoid: (0) well developed and extending to vomer anteriorly; (1) reduced and falling short of contact with vomer anteriorly; (2) inferior lamella absent (CI = 100; RI = 100)

As noted in character 26, contact anteriorly of the inferior lamella of the lateral ethmoid with the vomer is common among the taxa under consideration in this study. Such a morphology of that structure is also present in various examined outgroup characiforms. In the examined specimens of *Hemmigrammopetersius* the process is, however, distinctly reduced, and is represented by only a short anterior process on the lateral ethmoid. In *Virilia* the process is, in turn, completely absent. It was impossible to code the condition of this character for *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes* because of the dramatically altered morphology of the inferior lamella of the lateral ethmoid in those genera. It is similarly impossible to code the condition of the character for *Hepsetus* in light of the pronounced restructuring of the lateral ethmoid in that genus.

28. Posteriorly directed, pointed process on posterior surface of lateral wing of lateral ethmoid: (0) absent; (1) present (CI = 50; RI = 0)

The posterior surface of the lateral wing of the lateral ethmoid is typically unelaborated in characiforms. *Micralestes elongatus* Daget and *Rhabdalestes septentrionalis* have, however, a distinct, posteriorly directed, pointed bony process located on the posterior surface of the lateral wing of the lateral ethmoid; a condition that is hypothesized to be derived.

29. Posterior bony tube on lateral ethmoid: (0) absent; (1) present (CI = 100; RI = 100)

The main body of the lateral ethmoid in the region anterior to the orbital cavity is pierced by a foramen for the passage of the olfactory nerve in all characiforms. A cleared and stained specimen of *Alestes macrophthalmus* (176.3 mm SL) is unique within the material examined in our analysis in having a posterior bony tube arising from the posterior surface of the lateral ethmoid. This structure surrounds the proximate portion of the olfactory nerve and posteriorly contacts and interdigitates with the anteriorly directed bony tube on the orbitosphenoid.

Brewster (1986: 170) reported that larger specimens of *Hydrocynus* (400 mm SL) have a process of the lateral ethmoid sutured to the tubular process of the orbitosphenoid that envelopes the olfactory bulb and nerve, a condition apparently comparable to that observed in this study to be present in *Alestes macrophthalmus*. The cleared and stained specimens of *Hydrocynus* (39.7–140.4 mm SL) examined in this study lack such a tubular process of the lateral ethmoid, and an examination of a whole specimen of *H. brevis* (USNM 72790; *c.* 525 mm SL) revealed a distinct gap between the anterior bulbous portion of the orbitosphenoid and the rear of the lateral ethmoid. Nor were we able to find any posterior bony process on the latter ossification associated with the olfactory nerve. It is possible that this feature is variable within the genus; however, in light of our observations we code *Hydrocynus* as lacking the posterior process of the lateral ethmoid.

Xenocharax has an osseous contact between the orbitosphenoid and lateral ethmoid that is superficially reminiscent of the positionally comparable articulation between those bones that is present in *Alestes macrophthalmus*. The conditions of the contact between the lateral ethmoid and orbitosphenoid in the two taxa differ, however, in numerous details, the most notable of which is the fact that the processes of these two bones in *Xenocharax* form a strut rather than a bony tube, and thus fail to envelope a portion of the olfactory canal as is the case in *A. macrophthalmus*. More significantly, the structure in *Xenocharax* is more dorsally situated than is the bony tube present in *A. macrophthalmus*. In light of these differences, these posterior bony processes of the lateral ethmoid in *A. macrophthalmus* and *Xenocharax* are considered nonhomologous.

Weitzman (1962: 20) noted that *Brycon meeki* has a tubular process arising from the posterior surface of the lateral ethmoid, which encloses a portion of the olfactory nerve. The specimens of *Brycon* examined in this study have a short flange along the medial surface of the ventral process of the lateral ethmoid that is presumably comparable to the more developed process described by Weitzman. This process in *Brycon* is, however, more medially located than is the tubular structure present in *Alestes macrophthalmus* and is thus considered nonhomologous with the process characteristic of the latter species.

30. Posterior portion of lateral ethmoid with narrow process not associated with olfactory tract contacting orbitosphenoid ventrally: (0) absent; (1) present (CI = 100; RI = 100)

In the serrasalmine genera *Piaractus* and *Serrasalmus* there occurs a direct contact between the elongate, anteriorly directed process arising from the ventral portion of the orbitosphenoid and a posteriorly directed process arising from the posteromedial portion of the lateral ethmoid. *Serrasalmus*, furthermore, has an interdigitating suture between the two bones, perhaps as a consequence of the larger size of the examined cleared and stained specimen of that genus. Although the articulation between the orbitosphenoid and lateral ethmoid is entirely cartilaginous in the cleared and stained specimen of *Piaractus* examined in this study, an ossified process occurs in that region in larger individuals (see Machado-Allison, 1983: fig. 10a). Regardless of the presence or absence of such interdigitations between the processes of the orbitosphenoid and lateral ethmoid, the resultant area of contact between these bones in *Piaractus*, *Serrasalmus* and other members of the Serrasalminae (see Jégu & Santos, 2002: fig. 13) is positioned distinctly ventral to the olfactory tract and consequently is considered nonhomologous with the condition discussed in character 29 for *Alestes macrophthalmus*.

31. Presence or absence of rhinosphenoid: (0) present; (1) absent (CI = 20; RI = 50)

The rhinosphenoid is a median ossification in the orbital region whose possession is unique to a subset of characiforms. When present, the rhinosphenoid is situated medial of the contralateral lateral ethmoids and anterior to the orbitosphenoid; it is attached to the latter either directly or via an intermediate cartilage (e.g. *Brycon meeki*, Weitzman, 1962: fig. 3). Basal characiforms, represented in this analysis by the *Xenocharax* (family Distichodontidae), lack a rhinosphenoid, but that ossification is present in a number of other characiform groups including many subunits of the New World family Characidae. Géry (1995) noted that the lack of this ossification apparently characterizes the African members of the Alestidae, an observation confirmed in some species of the group by Murray & Stewart (2002). Our more encompassing analysis demonstrates that the ossification is consistently absent in all examined members of the Alestidae (e.g. *Brycinus nurse* (Rüppell), Fig. 9; see also *Hydrocynus forskahlii*, Brewster, 1986: fig. 1B).

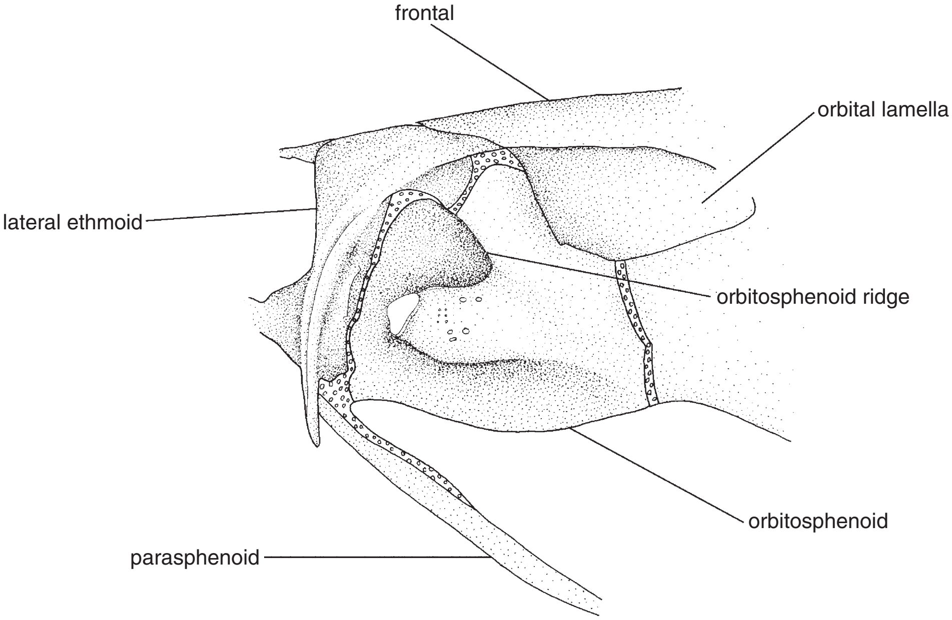

Figure 9. Orbital region of *Brycinus nurse*, USNM 339724, 107.4 mm SL; lateral and slightly ventral view, anterior at left; small circles indicate cartilage.

32. Presence or absence of distinct ridge on anterodorsal portion of orbitosphenoid: (0) absent; (1) present (CI = 50; RI = 66)

The association of the anterodorsal portion of the orbitosphenoid and the posterodorsal process of the lateral ethmoid varies both ontogenetically and phylogenetically. This renders it difficult to unambiguously code the contact, or lack thereof, between those portions of these two ossifications. One distinct feature in that region that can, nonetheless, be coded unambiguously is the presence or absence of a distinct, ridge-like process on the anterodorsal portion of the orbitosphenoid (Fig. 9) contacting a corresponding process of the lateral ethmoid in some species of *Brycinus* (Appendix 2). In light of the absence of this feature in examined outgroup characiforms, we consider the presence of the structure in those species of *Brycinus* to be derived.

33. Degree of lateral expansion of orbitosphenoid: (0) anterolateral portion of orbitosphenoid without expansion lateral to olfactory bulb; (1) anterolateral portion of orbitosphenoid with anteriorly directed expansion that at least partially overlaps lateral surface of olfactory bulb (CI = 50; RI = 94)

Most characiforms have a relatively flat and laterally unelaborated orbitosphenoid that has the olfactory nerve exiting either from the median opening situated anterior to the anteroventral margin of the orbitosphenoid or through a variably developed foramen along the anterior surface of that bone. Starks (1926: 167) noted that some species of *Alestes* have an anteriorly directed bony process on the orbitosphenoid that at least partially encloses the olfactory bulb and nerve. Roberts (1969: 441) subsequently reported the presence of a comparable process in additional species of *Alestes* along with *Bryconaethiops* and *Hydrocynus*.

Based on an examination of a subset of the species in the Alestidae (Géry & Mahnert, 1977: 18) used the presence of a orbitosphenoid-lateral ethmoid bone tube as a defining character for that family. Vari (1979: 341), in turn, suggested that such a form of contact between the orbitosphenoid and lateral ethmoid might be an apomorphy shared by the members of the African Characidae (= African components of the Alestidae of this study). Subsequently, Murray & Stewart (2002: 1891) hypothesized that the presence of 'orbitosphenoid tube for olfactory nerve' was synapomorphic for the members of the Alestidae; a family that, as delimited by those authors, encompassed only African taxa.

The more encompassing observations in the present study indicate that the presence of a process of the orbitosphenoid enveloping the lateral surface of the olfactory bulb is, at least to some degree (Fig. 9), limited to a subset of the Alestidae rather than being universal for all taxa in the family (see Appendix 2). The degree of development of the process is variable both intraspecifically and apparently ontogenetically (see comments in the next paragraph) and we consequently code the expansion of the anterolateral portion of the orbitosphenoid as present whenever it extends lateral of the olfactory lobe, regardless of whether or not it forms a distinct tubular structure.

Although the cleared and stained specimens of *Hydrocynus* examined in this study demonstrate only a moderate expansion of the portion of the orbitosphenoid situated lateral to the olfactory bulb, Brewster (1986: 170) reported that the large specimens of the genus that she examined (400 mm SL or more) have a distinct orbitosphenoid process that she stated was sutured anteriorly to a comparable posteriorly directed process of the lateral ethmoid. The examination of a large whole specimen of *H. brevis* (USNM 72790; *c.* 525 mm SL) revealed, however, a distinct gap between the anterior bulbous portion of the orbitosphenoid and the rear of the lateral ethmoid (see also character 29) without an anterior process of the orbitosphenoid. Thus, the degree of development of the bulbous anterior portion of the orbitosphenoid described by Brewster in larger specimens of *Hydrocynus* is intragenerically variable. Brewster (1986: fig. 1) illustrated a less developed process on the orbitosphenoid in a small specimen of *Hydrocynus*, labelling it OSP. That abbreviation is absent in the list of abbreviations in her paper, but likely refers to the orbitosphenoid process.

Although Weitzman (1962: 20) reported a tubular process enclosing the olfactory nerve in the Neotropical characid *Brycon*, the structure in question is a short process arising from the lateral ethmoid and is as such considered to be nonhomologous with the anterior tubular process of the orbitosphenoid that is present in many members of the Alestidae.

34. Degree of contribution of orbital lamella of frontal to articulation between orbitosphenoid and frontal: (0) orbital lamella of frontal relatively anteroposteriorly elongate and forming all, or nearly all, of articulation between orbitosphenoid and frontal; (1) orbital lamella of frontal relatively anteroposteriorly short, with major portion, or nearly all, of articulation between orbitosphenoid and frontal being with main body of frontal (CI = 50; RI = 80)

The orbital lamella of the frontal (*sensu* Weitzman, 1962: 21) in most members of the Alestidae is an anteroposteriorly elongate process of the ventral surface of the frontal (Fig. 9) that completely, or nearly completely, separates the orbitosphenoid from the main dorsal portion of the frontal. In *Arnoldichthys*, in contrast, the anteroposterior extent of the lamella is somewhat reduced; that process is, in turn, significantly shortened in *Chalceus*. As a consequence of these reductions of the orbital lamella, the extent of the contact of the dorsal margin of the orbitosphenoid with the main body of the frontal in both genera is significantly increased. If we look at the examined outgroup characiforms we find that there is also a proximity, at least to a degree, of the anterodorsal portion of the orbitosphenoid and the main body of the frontal in *Crenuchus*, *Hoplias* and *Xenocharax*. The proportional extent of the direct articulation of the orbitosphenoid with the main body of the frontal in those genera is, however, less pronounced than is the contact zone present in *Arnoldichthys* and *Chalceus*. The reductions in the degree of the orbital lamellae of the frontal in *Arnoldichthys* and *Chalceus* are thus considered nonhomologous with the diminution of those processes that occurs in the cited outgroup taxa.

35. Alignment of orbital lamella of frontal and adjoining portions of orbitosphenoid: (0) aligned approximately in parallel to supraorbital laterosensory canal segment in frontal; (1) aligned distinctly anteromedially to varying degrees and divergent from supraorbital laterosensory canal segment in frontal (CI = 33; RI = 71)
The frontal bears a ventral process, the orbital lamella, articulating with the lateral surface of the dorsal portion of the orbitosphenoid and pterosphenoid (Fig. 9). In the majority of the examined species of the Alestidae, the orbital lamella and the immediately adjoining portion of the orbitosphenoid have an approximately anteroposterior alignment and along their areas of articulation these structures approximately parallel the course of the supraorbital laterosensory canal segment in the frontal. In the species of *Chalceus* and *Arnoldichthys*, in contrast, the orbital lamella and the proximate portions of the orbitosphenoid have a distinct anteromedial alignment and as a consequence have an orientation that either distinctly (*Arnoldichthys*) or dramatically (*Chalceus*) diverges anteriorly from the alignment of the supraorbital laterosensory canal. Among examined outgroup characiforms such a comparable anteromedial alignment of the orbital lamellae was only found to occur in *Crenuchus* and *Hoplias*.

36. Presence and degree of development of frontal fontanel: (0) fontanel reaching mesethmoid anteriorly; (1) fontanel restricted to posterior portion of frontal with anterior limit of opening located only slightly anterior to epiphyseal bar; (2): fontanel absent (CI = 20; RI = 69)
In the majority of characiforms, the contralateral parietals and, to varying degrees, the frontals are separated by the median frontoparietal fontanel. Fontanels occur in the distichodontid *Xenocharax,* a member of the basal characiform clade, and in numerous noncharaciform ostariophysans (Vari, 1995: 15). Vari also reported that the species of *Alestes* (*sensu lato*) exhibit notable variation in the degree of development of the fontanel. Some species of the then broadly defined *Alestes* had fontanels extending anterior to the transverse epiphyseal bar that joins the contralateral frontals (e.g. *A. baremoze*, *A. leuciscus*, see Monod, 1950: figs 90, 92; and *A. liebrechtsii* Boulenger, see Myers, 1929: fig. 1), whereas the fontanel was absent in other species of *Alestes* (e.g. *A. grandisquamis* Boulenger, see Myers, 1929: fig. 2; *A. macrolepidotus* (Valenciennes), see Monod, 1950: fig. 99).

Recent studies (e.g. Géry & Mahnert, 1977; Paugy, 1986) have assigned both *A. grandisquamis* and *A. macrolepidotus* to *Brycinus* based on their shared lack of the fontanel and other differences in the overall morphology of the neurocranium. An absence of frontoparietal fontanels is of wide occurrence across the Characiformes, occurring in the Neotropical families Erythrinidae, Hepsetidae, Lebiasinidae (Weitzman, 1964: fig. 2) and Parodontidae (Roberts, 1974: fig. 56), along with other components of the order. The reduction or absence of the frontoparietal fontanel is an obviously homoplastic feature in light of the occurrence of this opening in characiforms of diverse lineages within the order (Vari, 1995: 15), and there is, furthermore, notable variation in the development of the opening even in closely related species of various genera (Vari & Vari, 1989: fig. 1; Vari, 1991: fig. 10).

The varying degrees of development of the frontoparietal fontanels, when present, among different groups of characiforms renders it difficult to determine the plesiomorphic condition of that opening within the order and to a degree raises questions as to the utility of this character for recovering information on phylogenetic relationships at higher levels of inclusiveness. Alternatively, the absence of a frontal fontanel was interpreted as derived by Lucena (1993) and proposed by that author as a synapomorphy for the clade consisting of *Chalceus*, *Brycon* and various taxa herein assigned to the Alestidae.

Despite such uncertainties, it is noteworthy that the majority of species in the Alestidae have contralateral frontals that are in contact anteriorly resulting in a reduction in the anteroposterior extent of the frontal fontanel. Extensive contact between the contralateral frontals and a consequent absence of the frontal portion of the fontanel occurs in *Arnoldichthys*, *Brycinus bimaculatus*, *B. brevis*, *B. carolinae* (Paugy & Lévêque), *B. imberi* (Peters), *B. kingsleyae* (Günther), *B. macrolepidotus*, *B. nurse*, *Chalceus epakros*, *C. guaporensis* and *Petersius conserialis*. According to Brewster (1986: 168) the frontal portion of the fontanel is also absent in *Hydrocynus*, an observation based on skeletal preparations of standard lengths greater than those available in this study, all of which retain the aperture. Alternatively, the alestids *Bathyaethiops* and *Lepidarchus* have a frontal fontanel reaching anteriorly to the mesethmoid.

This extensive fontanel in *Bathyaethiops* and *Lepidarchus* is rare in the Alestidae, but is common in the examined outgroups. Within the context of the final most parsimonious hypothesis of relationships, the extensive fontanel in those two genera represents a reversal of the reduced frontal fontanel that is widespread across the Alestidae. This reversal is perhaps correlated with the relatively small body size in the species of *Bathyaethiops* and *Lepidarchus*.

In the case of the Neotropical outgroup genus *Salminus* there occurs a certain degree of variation in the extent of the fontanel, with the frontal fontanel in juveniles of the genus (84.1 mm SL) represented solely by a small aperture situated anterior to the epiphyseal bar. Adults of *Salminus,* in turn, have the contralateral frontals and parietals completely conjoined medially in adults. As such, the apparent method of reduction of the opening in *Salminus* involves the posterior expansion of a portion of the frontal proximate to the transverse epiphyseal bar, a condition that differs from that in Alestidae.

The condition of the presence and degree of development of the fontanel in *Salminus* is consequently coded as unknown. *Salminus*, furthermore, does not appear to be closely related to the Alestidae based on molecular data, but rather to *Brycon* (Ortí, 1997: fig, 10; Ortí & Meyer, 1997: fig. 10) or to *Brycon* plus *Henochilus*, a species endemic to eastern Brazil (Castro *et al*., 2004: fig. 5). A close phylogenetic position of *Salminus* with *Brycon* is also supported by evidence from heterochromatin patterns and karyotypes (Margarido & Galetti, 1999: 360) and sperm ultrastructure (Pompiani, 2003).

Murray & Stewart (2002: 1892) utilized the presence vs. absence of the fontanel as a feature for the purposes of their phylogenetic analysis, but did not divide that character between the frontal and parietal portions of the aperture. Because of the incongruence of the occurrence of these reductions of the components of the fontanel anterior and posterior to the epiphyseal bar within the Alestidae, we herein treat the development of the fontanel in the frontal and parietal as separate characters (nos. 36 and 37). Contrary to Murray & Stewart (2002), the coding of the feature in our analysis is based on the condition in the adults since many examined taxa demonstrate ontogenetic variation in the presence of the feature (see also character 37). These developmental transitions would result in significant loss of information if data from juveniles and adults were subsumed into a single character.

37. Presence or absence of parietal fontanel: (0) present in adult specimens; (1) absent in adult specimens
(CI = 20; RI = 71)
The parietal portion of the frontoparietal fontanel is absent in *Arnoldichthys*, *Brycinus bimaculatus*, *B. brevis*, *B. carolinae*, *B. imberi*, *B. kingsleyae*, *B. macrolepidotus*, *B. nurse*, *Chalceus epakros*, *C. guaporensis*, *Hydrocynus brevis* and *H. forskahlii* within the Alestidae and in *Brycon pesu* Müller & Troschel, *Hepsetus* and *Hoplias* within the outgroup.

Variation in the size of the parietal fontanel correlated with the stage of development of the specimen was observed in some of the taxa included in this analysis. *Brycon pesu* has the fontanel present in specimens of approximately 27.0 mm SL, but absent by about 49.7 mm SL. Specimens of *Brycinus macrolepidotus* of 39.2 mm SL retain a parietal fontanel whereas an individual of that species of 77.6 mm SL has the parietals in contact with each other along the midline with a resultant obliteration of the fontanel. *Arnoldichthys* and some species of *Chalceus* apparently follow the same ontogenetic pattern, with the parietal fontanels present in small individuals of these genera but absent in specimens of 55.8 mm SL (in alcohol) and 69.2 mm SL (cleared and stained), respectively. Cleared and stained individuals of *Hydrocynus brevis* (140.4 mm SL) and *H. forskahlii* (120.0 mm SL) have parietal fontanels present, but larger specimens of these species lack those apertures (see also Brewster, 1986: 168) and we consequently code these species as state 1 for this character.

Boulenger (1909: 231) reported that *Petersius conserialis* differs from the other species that he assigned to that genus in its relatively large body size and 'the complete closing up of the parietal fontanelle.' This account of the species was based on the holotype of the species that had a 'total length 145 millim [= millimeters]' (Boulenger, 1909: 231). Myers (1929: 5), Hoedeman (1951: 5), Poll (1967a: 28) and Géry (1995: 40) followed Boulenger in attributing the lack of a parietal fontanel to *P. conserialis*. Alternatively, Murray & Stewart (2002: 1892) noted that 'smaller specimens' of *P. conserialis* of unspecified body size have the fontanel present between the parietals and posterior part of the frontals, but apparently did not examine adults of the species in which the extent of the opening is significantly reduced.

A parietal fontanel is present, albeit not extensive, in all specimens of *P. conserialis* examined in this study, some of which reach a total length (approximately 135 mm TL) comparable to that of the holotype of the species (145 mm TL). More significantly, there is minimal difference in the proportional extent of the parietal fontanel across the size range of specimens of *P. conserialis* examined in this study (97.3–111.4 mm TL). These observations reduce the likelihood that the aperture would be completely absent in the only somewhat larger holotype of the species notwithstanding Boulenger's (1909) statement to the contrary. We consequently code the parietal fontanel as being present in *Petersius*.

38. Presence or absence of contact between frontal and pterotic: (0) frontal and pterotic bones in contact;
(1) pterotic excluded from contact with frontal by sphenotic (CI = 100; RI = 100)

Lepidarchus is unique among the taxa examined in this study in lacking a contact of the frontal with the pterotic. This loss of contact between these ossifications is apparently a consequence of the reduction in the degree of development of the anterior portion of the pterotic and the associated expansion of the sphenotic into the resultant space between the pterotic and frontal (see Roberts, 1966: fig. 1).

39. Position of sphenotic spine relative to anterior portion of articular fossa for hyomandibular on sphenotic and prootic: (0) sphenotic spine located proximate to anterior limit of articular fossa that extends, in turn, to posterior margin of orbital opening;
(1) sphenotic spine located distinctly anterior to anterior limit of articular fossa that is, in turn, situated distinctly posterior to posterior margin of orbital opening (CI = 20; RI = 33)

In nearly all examined species in the Alestidae and outgroup characiform taxa the anterior limit of the articular fossa for the hyomandibular is positioned proximate to the posterior margin of the orbital cavity. In taxa with that morphology, the anterior terminus of the fossa is located along the vertical through the anterior limit of the ascending arm of the prootic. This repositioning results in a proximity of the anterior terminus of the fossa and the ventral limit of the lateral spine of the sphenotic. In the species of *Hydrocynus* the anterior limit of the articular fossa is distinctly separated along the horizontal axis from both the posterior margin of the orbital cavity and from the ventral portion of the lateral sphenotic spine (see Brewster, 1986: fig. 1b).

Such a separation of those structures, although unique to *Hydrocynus* among examined members of the Alestidae, also occurs in various examined outgroup taxa (*Charax*, *Hepsetus*, *Hoplias*, *Salminus*, *Serrasalmus*), all of which are characterized by proportionally elongate heads and/or strong jaws. Nonetheless, the overall most parsimonious hypothesis of relationships indicates that the condition in *Hydrocynus* is synapomorphic for the species of that genus, albeit homoplastically present in various outgroup taxa.

In her analysis of *Hydrocynus*, Brewster (1986: 189, fig. 3) proposed that the presence of a 'strut' on the ventromedial portion of the sphenotic was synapomorphic for members of that genus and noted that an apparently similar process on the sphenotic was present in the Neotropical genus *Serrasalmus*. The species of *Hydrocynus* have a distinct ridge-like process on the sphenotic extending from the sphenotic spine to the region of the articular fossa for the hyomandibular. This ridge apparently represents the 'strut' described by Brewster for *Hydrocynus*, whereas *Serrasalmus* has a distinct strut-like process on the ventral portion of the sphenotic resulting from the presence of an extensive fenestra situated in the portion of the lateral process of the sphenotic that lies immediately above the strut. That condition differs from the ridge-like process of that portion of the sphenotic present in *Hydrocynus*.

The character defined herein, based on the proximity, or lack thereof, of the sphenotic spine and articular fossa is apparently correlated functionally with the process that Brewster termed a 'strut' in *Hydrocynus*. We utilize the more obvious separation between the spine and fossa as the character for the purposes of our phylogenetic analysis.

40. Form of ventral portion of sphenotic spine:
(0) sphenotic spine blade-like and progressively ventrally attenuating; (1) sphenotic spine with process posteriorly, with spine distinctly thickened a short distance dorsal to ventral margin (CI = 33; RI = 60)

The distinctive morphology of the ventral margin of the sphenotic spine was utilized by Brewster (1986: 191, 192, fig. 3; the sphenotic process of that author) as a synapomorphy for a clade consisting of *Hydrocynus* and what she termed *Alestes sensu stricto* – the *Alestes* of this study. Brewster reported that those taxa have 'a well-developed, ventrally thickened sphenotic process.' In their subsequent analysis Murray & Stewart (2002: 1891) followed Brewster's proposed polarity and used the thickening of the ventral portion of the sphenotic spine as a synapomorphy for *Hydrocynus* and *Alestes*.

Our observations confirm that the portion of the sphenotic spine located somewhat dorsal to the ventral margin is posteriorly thickened in these two genera, with a moderate expansion characteristic of the species of *Alestes* and a more pronounced development of the process present in the species of *Hydrocynus*. Nonetheless, in light of the intergradation of the degrees of development of this process across the species of *Alestes*, in some of which the thickening of the sphenotic spine approaches the degree of development of the structure in *Hydrocynus*, we did not parse the degree of development of the process into two or more characters. Rather, we code the presence of the process in *Alestes* and *Hydrocynus* as a single derived character regardless of the degree of development. The overall most parsimonious hypothesis of relationships arrived at in this study indicates that this derived modification of the sphenotic spine was arrived at independently in *Alestes* vs. *Hydrocynus*. Among examined outgroups, only *Hemiodus*, a South American genus phylogenetically distant from the Alestidae (Buckup, 1998: fig. 6), was found to have a somewhat comparable process of the sphenotic spine.

41. Form of parasphenoid: (0) relatively straight anteroposteriorly and with posterior portion of bone aligned approximately along longitudinal axis of anterior portion of vertebral column; (1) with distinct anteroposterior curvature and with posterior portion of bone located distinctly ventral to longitudinal axis through anterior portion of vertebral column (CI = 25; RI = 40)

In many characiforms the portion of the parasphenoid situated ventromedial to the orbit is straight, whereas in many members of the Characidae (e.g. *Brycon*, see Weitzman, 1962: fig. 3) and Alestidae (Fig. 9) it is more or less strongly curved ventrally. Roberts (1969: 406) interpreted a straight parasphenoid as plesiomorphic within the Characiformes and he consequently considered the curved morphology to be derived. That hypothesis was, however, underpinned by assumptions as to basal groups within the Characiformes that were subsequently found to be erroneous (Fink & Fink, 1981).

Brewster (1986: 185) compared *Hydrocynus* with members of the Alestidae and suggested that a markedly ventrally convex parasphenoid was the derived morphology for the bone; he thus hypothesized that the straight form of the parasphenoid present in *Hydrocynus* was plesiomorphic (see Brewster, 1986: fig. 1b; NB: our cleared and stained specimens of the genus demonstrate straighter parasphenoids than the form of the ossification illustrated in that figure). Subsequently, Murray & Stewart (2002: 1890) coded *Hydrocynus* as having a 'ventrally depressed' (presumably ventrally curved) parasphenoid, although without any comment as to why their characterization of the feature differed from that of Brewster (1986).

As noted above, the form of the parasphenoid in *Hydrocynus* is more appropriately characterized as straight. Under the more complex description of the character that we utilize herein, the condition in *Hydrocynus* is distinct from that present in other alestids, *contra* the coding of this feature by Murray & Stewart (2002). Within the context of the comparisons in this study, state 0, which is limited within the Alestidae to *Chalceus guaporensis* and *Hydrocynus*, is derived; however, that character state is also present in *Hepsetus*, *Hoplias* and *Salminus* among examined outgroup taxa.

42. Presence or absence of intercalar: (0) present; (1) absent (CI = 100; RI = 100)

The intercalar (= opisthotic of Weitzman, 1962) is a small ossification located on the posterior portion of the ventral surface of the neurocranium in the region of contact of the basioccipital, pterotic and prootic. When present, the intercalar serves as the area of attachment on the neurocranium for a ligament extending to the dorsal portions of the pectoral girdle (see also characters 130, 131). An intercalar is nearly universally present in examined characiforms, but was found to be uniquely absent within the Alestidae in *Ladigesia* and *Lepidarchus*, two of the alestid taxa that are adult at among the smallest body sizes of all the taxa examined in this study. Such a loss fits the pattern of reduction in the degree of development of various ossifications in characiforms of diminutive size (Weitzman & Vari, 1988: 445). The intercalar is, however, present in some other alestid species of adult body sizes comparable to those of *Ladigesia* and *Lepidarchus*; thus, its absence in those genera may not be solely a function of their overall body size.

43. Presence or absence of third post-temporal fossa located entirely in epioccipital: (0) absent; (1) present (CI = 33; RI = 90)

The most widespread, and hypothesized, plesiomorphic arrangement of the post-temporal fossae among characiforms consists of a dorsal and posterolateral pair of fossae situated on each side of the neurocranium (Vari, 1979: 289; 1983: 37; Weitzman, 1962: fig. 5). A third post-temporal fossa situated entirely within the epioccipital occurs in all examined species of the Alestidae (e.g. *Hydrocynus forskahlii,* Fig. 10) with the exceptions of *Arnoldichthys*, *Chalceus*, *Ladigesia* and *Lepidarchus*.

This form of epioccipital aperture was previously described for some components of the Alestidae, along with members of the Neotropical families Curimatidae (Vari, 1983: 37), Hemiodontidae (included here as a outgroup represented by *Hemiodus*) and Parodontidae (Roberts, 1974: figs 5, 59). Brewster (1986: 168) interpreted the presence of this form of third post-temporal fossa in the African Characidae (= most of the Alestidae if this study) as being homoplastic with respect to the occurrence of the opening in the cited Neotropical families, a conclusion that is in keeping with the phylogenetic hypotheses advanced by Vari (1983, 1989) and Buckup (1998).

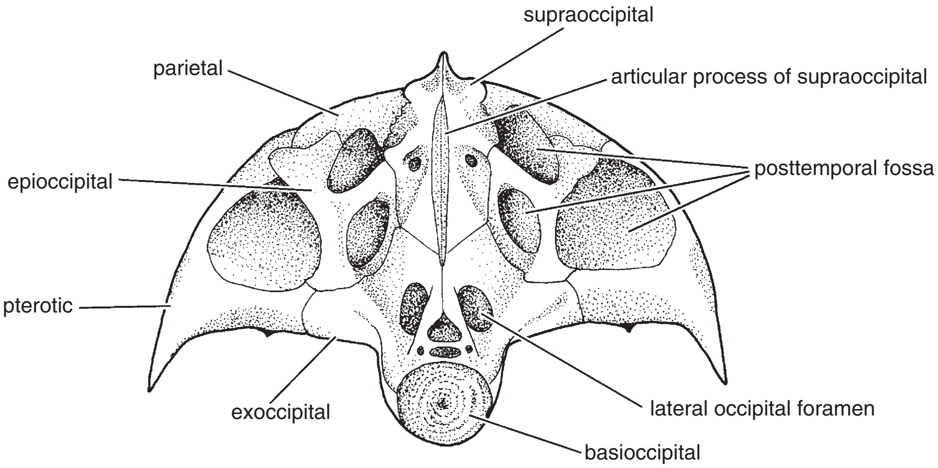

Figure 10. Posterior region of neurocranium of *Hydrocynus forskahlii* (modified from Brewster, 1986: fig. 2).

Although a third post-temporal fossa also occurs within the African characiform families Citharinidae and Distichodontidae and the South American family Cynodontinae, it is bordered by both the epioccipital and exoccipital (Vari, 1979: 289) rather than being located entirely within the epioccipital, as is the case when it is present in members of the Alestidae. The Citharinidae and Distichodontidae are basal members of the Characiformes and thus the opening between the exoccipital and epioccipital in those two families is hypothesized to have arisen independently of that form of the opening in most members of the Alestidae.

Toledo-Piza (2000: 27) confirmed the presence of a post-temporal fossa bordered by the epioccipital and exoccipital in all genera of the Cynodontidae and also reported the presence of such an opening in *Gilbertolus atratoensis* Schultz, *Gnathocharax*, *Heterocharax*, *Lonchogenys* and *Roestes*. Although *Gnathocharax*, *Heterocharax* and *Lonchogenys* have somewhat uncertain phylogenetic relationships, they clearly lie outside the scope of this study given the lack in those genera of the synapomorphies for the Alestidae

Based on a series of synapomorphies, Lucena & Menezes (1998: fig. 1) hypothesized that *G. atratoensis* and *Roestes* constitute a monophyletic subfamily that they termed the Roestinae. Under that hypothesis the Roestinae is most closely related to the Cynodontinae, and those two subfamilies together constitute the Cynodontidae. Lucena & Menezes also advanced several synapomorphies that united the Cynodontidae and Acestrorhynchidae, the latter of which lacks a third post-temporal fossa, as sister groups. In light of that phylogenetic evidence, the presence of a fossa in most species of the Alestidae, on the one hand, and the Cynodontidae, on the other, is considered homoplastic.

Within the final most parsimonious hypothesis of relationships, the absence of the third post-temporal fossa in *Arnoldichthys* and *Chalceus* is plesiomorphic. The lack of that aperture in the more derived alestid genera *Ladigesia* and *Lepidarchus* is, however, a reversal that may be correlated with the relatively small body size of those taxa (see also character 44). Contrary to Murray & Stewart (2002: 1898–9) who reported the absence of the fossa in *Brycinus sadleri* (Boulenger), we found it to be present in all of the cleared and stained material of that species examined in this study.

44. Relative size of post-temporal fossae: (0) dorsal and ventral fossae not distinctly different in size; (1) dorsal fossa significantly smaller than ventral fossa (CI = 100; RI = 100)

In the majority of characiforms (e.g. *Brycon meeki*; Weitzman, 1962: fig. 5), including nearly all examined taxa in the Alestidae, the dorsal and ventral post-temporal fossae are of approximately the same size, albeit with the latter typically being somewhat larger than the former.

In *Lepidarchus* the dorsal fossa is dramatically smaller than the ventral fossa, occupying only a small area delimited by the bridge formed by the posterior process of the epiotic on one side and the dorsally adjoining portion of the semicircular system on the other side. The small size of the available specimens of *Lepidarchus* and the limited degree of ossification of the neurocranium in the cleared and stained material of the genus make it possible that the relatively small dorsal fossa would disappear in somewhat larger and likely more extensively ossified individuals of the genus. Roberts (1966: fig. 2) illustrated a specimen of *Lepidarchus* with apparent continuity of the dorsal and ventral posttemporal fossae due to the lack of contact between the adjoining portions of the parietal and epiotic. Such continuity is limited to a subset of the cleared and stained specimens of the genus examined in this study.

Comment is appropriate on the relative size of these fossae in very small specimens of *Hydrocynus*, such as that illustrated by Brewster (1986: fig. 2), a figure that is, in turn, the basis for our Figure 10. As shown in that illustration, the dorsal fossa in such specimens is apparently much smaller than the ventral fossa. This apparent disparity in the sizes of the two fossae is partially a function of the orientation of the openings in the illustration. Furthermore, our larger cleared and stained specimens of the genus demonstrate much less disparity between the proportions of the two openings and parallel the relative size of the apertures in most members of the Characiformes. *Hydrocynus* is consequently coded as state 0 for this character. The state of this character could not be coded in the outgroup taxon *Serrasalmus* as a consequence of the pronounced modifications of that portion of cranium in that genus.

45. Presence or absence of lateral occipital foramen: (0) absent; (1) present (CI = 33; RI = 33)

Characiforms typically have a well-developed lateral occipital foramen that occupies a large portion of the posterior surface of the exoccipital in the region lateral to the foramen magnum and the cavum sinus imparis (Fig. 10). *Lepidarchus*, in contrast, lacks any indication of this opening in the examined cleared and stained specimens. That opening is also absent, apparently homoplastically, in *Hemiodus*, *Hepsetus* and *Hoplias* among examined outgroup characiforms, taxa that are hypothesized to be distant phylogenetically from the Alestidae (Vari, 1995; Buckup, 1998).

46. Presence or absence of paired, vertically elongate processes along posterior margin of supraoccipital, which envelope anterodorsal portion of neural complex: (0) absent; (1) present (CI = 95; RI = 60)

The medial neural complex in characiforms is located in the anterior portion of the vertebral column dorsal to the scaphium and claustrum and above the neural arches of the third and fourth vertebrae. In most examined outgroup characiforms, the anterior portion of the neural complex abuts the posterior surface of the supraoccipital midsagitally, with the anterior surface of the complex sometimes vertically divided anteriorly into parallel vertical ridges. When present, the resultant contralateral flanges on anterior surface of the neural complex lie to each side of, and contact, the posterior portion of the vertically elongate medial ridge that often extends along the rear of the supraoccipital.

Nearly all members of the Alestidae (Appendix 2) have the association of the adjoining portions of the neural complex and supraoccipital reversed from the condition typical for characiforms. In these taxa the supraoccipital has a paired vertically aligned, ridge-like process positioned on each side of the midline of the posterior portion of the bone rather than possessing a single, medial, vertical process (see Fig. 10 for condition in *Hydrocynus*). These paired vertical processes on the supraoccipital jointly bracket a lengthy portion of the anterodorsal margin of the neural complex.

Outgroup comparisons failed to reveal comparable paired vertical processes of the supraoccipital in examined characiforms other than in the Neotropical genus *Serrasalmus*. The elaborations of the posterior margin of the supraoccipital in *Serrasalmus* are, however, located distinctly more ventrally on the supraoccipital than are the vertical processes that are present on that ossification in most members of the Alestidae. In light of their positional differences, the forms of the modifications of the supraoccipital in the Alestidae and *Serrasalmus* are considered to be nonhomologous.

Paired vertical processes of the supraoccipital are absent within the Alestidae in *Arnoldichthys*, *Chalceus* and *Lepidarchus*. The absence in *Arnoldichthys* and *Chalceus*, correlating as it does with their basal position in the family, presumably reflects the retention of the plesiomorphic condition. The absence in *Lepidarchus*, which is internested within the phylogeny of the Alestidae, is perhaps reflective of the small body size of the single species in the genus and the associated reduction in the degree of ossification of various components of its skeleton, including the supraoccipital.

47. Relative position of ventral margin of lagenar portion of basioccipital: (0) situated ventral to, or aligned with, joint between parasphenoid and basioccipital; (1) situated distinctly dorsal to joint between parasphenoid and basioccipital (CI = 20; RI = 60)

The basioccipital forms the basal portion of the lagenar capsule, the bulla containing one of the three otoliths, the asteriscus. In the majority of examined characiforms and alestids, the ventral margin of the bulla is situated to varying degrees ventral to the horizontal plane through the longitudinal joint between the posterior portion of the parasphenoid and the ventral margin of the more medial portions of the basioccipital (e.g. *Brycon meeki*, see Weitzman, 1962: fig. 3).

In the species of *Alestes*, *Bryconaethiops* and *Hydrocynus* the ventral margin of the bulla instead lies somewhat to distinctly dorsal to the horizontal plane through the line of articulation between the posterior portion of the parasphenoid and the basioccipital (see Brewster, 1986: fig. 1b, for the condition of this region in *Hydrocynus*). Based on the overall morphology of that portion of the cranium, in particular the proportional development of the various portions of the basioccipital, it appears that this shift in the relative position of these structures in *Alestes*, *Bryconaethiops* and *Hydrocynus* is a consequence of the dorsal shift of the bulla in these genera rather than a ventral expansion of the medial portions of the basioccipital.

Larger specimens of *Bryconaethiops* have a proportionally more pronounced difference between the relative positions of the ventral margin of the bulla and the basioccipital-parasphenoid articulation than are characteristic of *Alestes* and *Hydrocynus*. Although the degree of separation of these structures increases ontogenetically in *Bryconaethiops*, the absence in this analysis of adults of all species of the genus renders it premature to code the condition in *Bryconaethiops* as a separate character. *Petersius conserialis* is coded as having state 1 based on information from radiographs of available specimens. A dorsal position of the bulla (state 1) is present in *Bryconops* and *Salminus* among examined characiform outgroups.

48. Area of insertion of Baudelot's ligament on neurocranium: (0) located on portion of basioccipital posteroventral to lagenar capsule; (1) located on portion of basioccipital anteroventral to lagenar capsule (CI = 100; RI = 100)

In characiforms Baudelot's ligament extends from the medial surface of the pectoral girdle anteriorly to an insertion on the posteroventral portion of the neurocranium. In most members of the order examined in this study, this ligament inserts on the portion of the basioccipital situated posteroventral to the lagenar capsule (e.g. *Brycon melanopterus* (Cope)) (Fig. 11). In *Bryconalestes* and various other alestids of smaller body size (see Appendix 2), the insertion of Baudelot's ligament on the basioccipital is shifted to the area

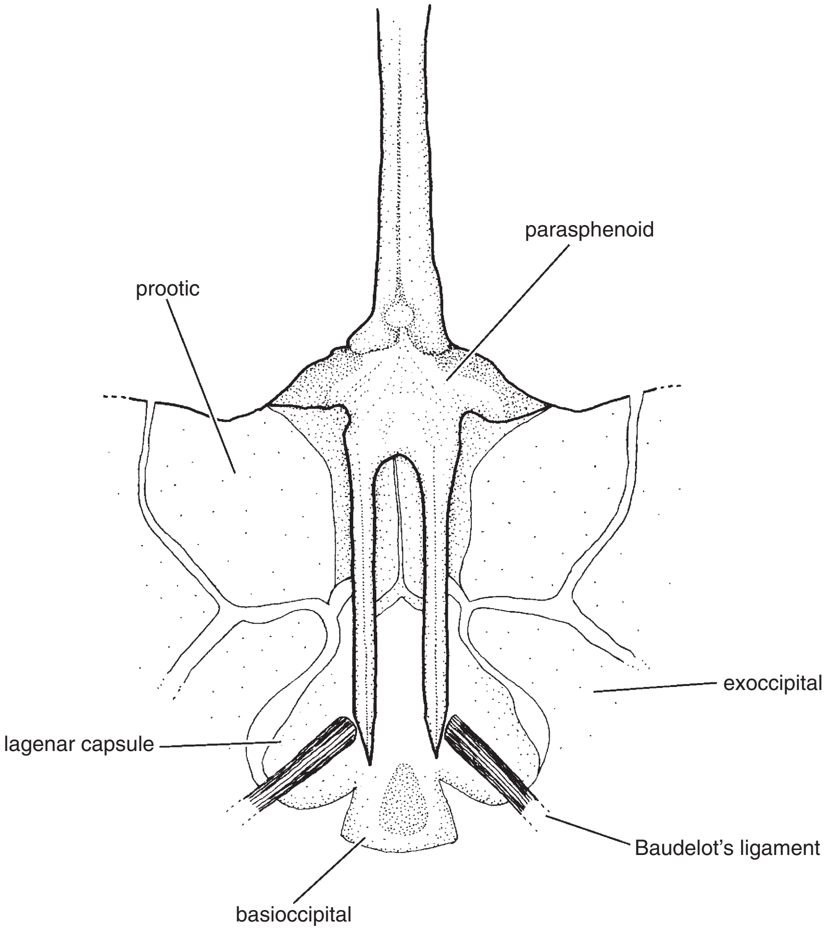

Figure 11. Posteroventral region of neurocranium of *Brycon melanopterus*, MZUSP 6626, 113.7 mm SL, showing area of attachment of Baudelot's ligament; ventral view, anterior at top.

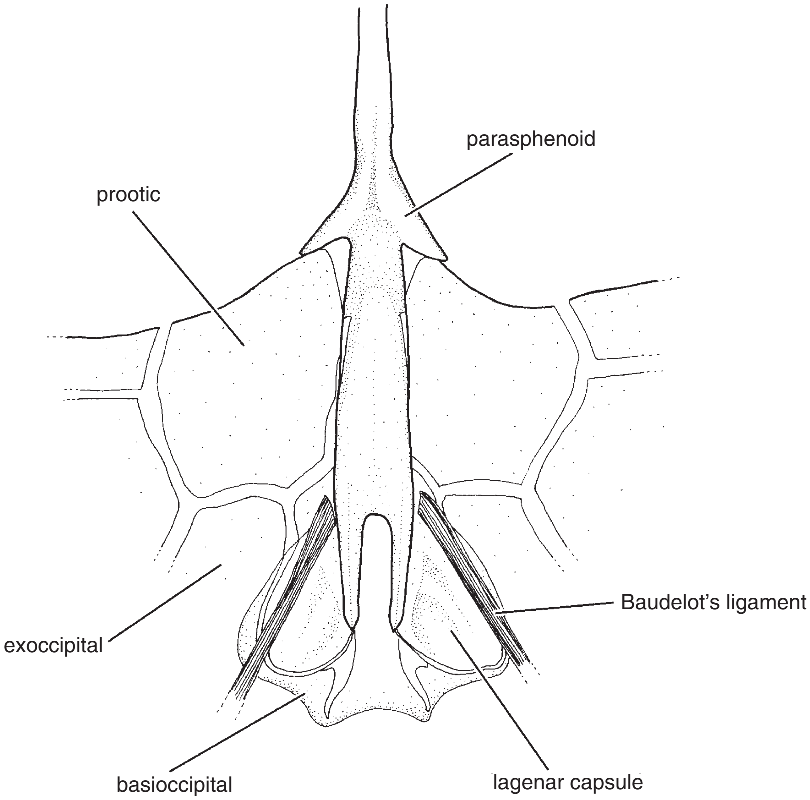

Figure 12. Posteroventral region of neurocranium of *Bryconalestes longipinnis*, MZUSP 60307, 64.2 mm SL, showing area of attachment of Baudelot's ligament; ventral view, anterior at top.

anteroventral to the bulla of the lagenar capsule (Fig. 12). An anterior insertion of the ligament on the neurocranium also occurs among examined outgroups in the New World tetragonopterins and *Cheirodon*. These taxa, however, have a drastically different overall morphology of the posteroventral portion of the neurocranium than that present in the Alestidae.

In the Alestidae, regardless of the area of insertion of Baudelot's ligament on the cranium, the basioccipital has contralateral, horizontally elongate processes extending ventral to the lagenar capsules, with the ligament invariably attaching somewhere along these basioccipital processes. In tetragonopterins and *Cheirodon*, in contrast, these processes are absent, a loss that necessitates the anterior shift of the area of attachment of the ligament on the neurocranium described above.

Dentition

49. Number of tooth cusps: (0) one throughout ontogeny; (1) two; (2) three or more at some point in ontogeny (CI = 33; RI = 20)

Characiforms are notable for variation in the form of dentition across the order, with the Alestidae demonstrating notable differences both ontogenetically and phylogenetically. Although the majority of alestids have tri- to multicuspidate dentition as adults, two genera in the family, *Clupeocharax* and *Lepidarchus*, have unicuspid dentition throughout ontogeny, a feature perhaps associated with their relatively small body size, such as is the case in some Neotropical characiforms (e.g. *Xenurobrycon*, Weitzman & Fink, 1985: figs 59–64; *Priocharax*, Weitzman & Vari, 1988: fig. 2). Conical dentition was also observed in *Charax*, *Hepsetus*, *Hoplias* and *Salminus* among examined outgroup taxa.

Although the anterior dentition in all but smaller individuals of the species of *Hydrocynus* is distinctly unicuspid (Brewster, 1986: fig. 7), it is ontogenetically a secondary condition. The ontogenetically earliest jaw teeth of *Hydrocynus* are conical (Brewster, 1986: fig. 6) and sequentially replaced during development first by tricuspid teeth (Brewster, 1986: 172–3, fig. 4) along the length of both jaws and finally with strong conical teeth on the anterior portions of both the upper and lower jaws (Fig. 3; see also Brewster, 1986: fig. 7 and character 50). We consequently code the condition in *Hydrocynus* as state 2 for this character, in light of the form of the teeth during the intermediate ontogenetic stage.

Oral teeth with two cusps were observed only in the outgroup *Xenocharax* in this analysis, but such teeth are general to all members of the Citharinidae and Distichodontidae at some point in ontogeny (Vari, 1979: 275). Poll (1967a) based his proposal of *Tricuspidalestes*, which included *Phenacogrammus caeruleus* Matthes, on the apparent presence of exclusively tricuspid jaw teeth in that species. Our examination of cleared and stained specimens of *Tricuspidalestes* indicates that the jaw dentition in that genus actually consists of an admixture of tri- and pentacuspid teeth. *Duboisialestes* demonstrates variation in the number of cusps on the teeth of each jaw, with the maximum number ranging between 5 and 12 per tooth (Poll & Gosse, 1995: 145).

50. Ontogenetic shift from tricuspid to unicuspid teeth in anterior portion of jaws: (0) not as in state 1; (1) teeth in both jaws all tricuspid at some point in ontogeny, but with anterior teeth in adults strongly conical (and distinctly overlapping in upper and lower jaws) and posterior teeth remaining tricuspid (CI = 100; RI = 100)

Among the taxa examined in this study, *Hydrocynus brevis* and *H. forskahlii* are unique in having unicuspid teeth on the anterior portions of each jaw that are apparently ontogenetically derived from the tricuspid teeth universal across both jaws earlier in ontogeny (Fig. 3; see also Brewster, 1986: fig. 4 and character 49). These ontogenetically intermediate tricuspid teeth are, in turn, replacements for the unicuspid jaw teeth present earlier during development in individuals of *Hydrocynus* (Brewster, 1986: fig. 6).

According to Brewster (1986: 189, figs 5, 7), the adult dentition of all species of *Hydrocynus* consists of strong conical teeth on the anterior portions of both jaws. This morphology of these teeth was utilized by Brewster as a synapomorphy for the members of the *Hydrocynus* (her character 14). Our results are congruent with her conclusion.

Another striking aspect of the conical dentition in the anterior portion of the jaws of *Hydrocynus* is the degree to which the elongate teeth in the two jaws alternatively overlap the lateral surface of the opposing jaw (Fig. 3; see also Eastman, 1917: pl. 87a; Gregory & Conrad, 1938: fig. 17). This attribute is unique to *Hydrocynus* among examined characiforms.

51. Presence or absence of compressed jaw teeth: (0) not as in state 1; (1) teeth in both upper and lower jaws compressed, distally expanded and overlap proximate teeth in each jaw (CI = 100; RI = 100)

Duboisialestes is unique within the Alestidae in its dramatically compressed teeth, with the consequent distinct overlap of the widened proximate teeth of each jaw along their adjoining margins (see Poll, 1967a: fig. 30; Poll & Gosse, 1995: fig. 215). Although a degree of overlap of teeth on the dentary, but not the premaxilla, occurs within the Alestidae in some species of *Brycinus*, the overlap of the dentary teeth in that genus is a result of a posterior elaboration of the involved teeth, a different modification of the teeth than that characterizing *Duboisialestes*. The form of the dentition in *Micralestes acutidens* (Peters), although also being expanded along the plane of the cusps, differs from that present in *Duboisialestes* in overall form and is thus considered nonhomologous.

UPPER JAW

Various authors (Roberts, 1969: 441; Vari, 1979: 341; Brewster, 1986: 203) have drawn attention to the unusual forms of the upper jaw in what has been termed the African Characidae (the Alestidae of this study with the exception of *Chalceus*). Brewster (1986) specifically identified the overall upper jaw morphology as a synapomorphy for her African Characidae (the African components of the Alestidae of this study), albeit without providing a detailed analysis of the upper jaw across that assemblage, an endeavour peripheral to the questions she was addressing in that paper. In actuality, the generalization by previous authors that the upper jaw in the Alestidae is derived subsumes a number of features pertinent at different levels of the phylogeny. We now analyse those attributes as a series of independent characters.

52. Form of posterolateral portion of premaxilla: (0) represented by short process, usually with concave posterior surface that accommodates proximate portion of maxilla; (1) represented by elongate, pedicle-like process, always without concave posterior surface (CI = 50; RI = 95)

In all examined taxa of the Alestidae, with the exception of *Arnoldichthys*, *Chalceus* and *Lepidarchus*, the posterolateral portion of the premaxilla has a pedicle-like process extending distinctly beyond the posterior limit of the premaxillary dentition and over the lateral surface of the proximate portion of the maxilla, terminating posteriorly in a pointed or rounded tip (Fig. 13).

This was previously reported by Roberts (1969: 441) in various species of *Alestes* (the *Alestes* and *Brycinus* of this study), *Bryconaethiops*, *Micralestes and Phenacogrammus*. The morphology of the premaxilla contrasts with that present in most characids and other examined characiform outgroups, in all of which the posterior limit is located more or less immediately posterior to the point of implantation of the posteriormost premaxillary tooth. Furthermore, in these outgroups the posterior portion of the premaxilla terminates in a

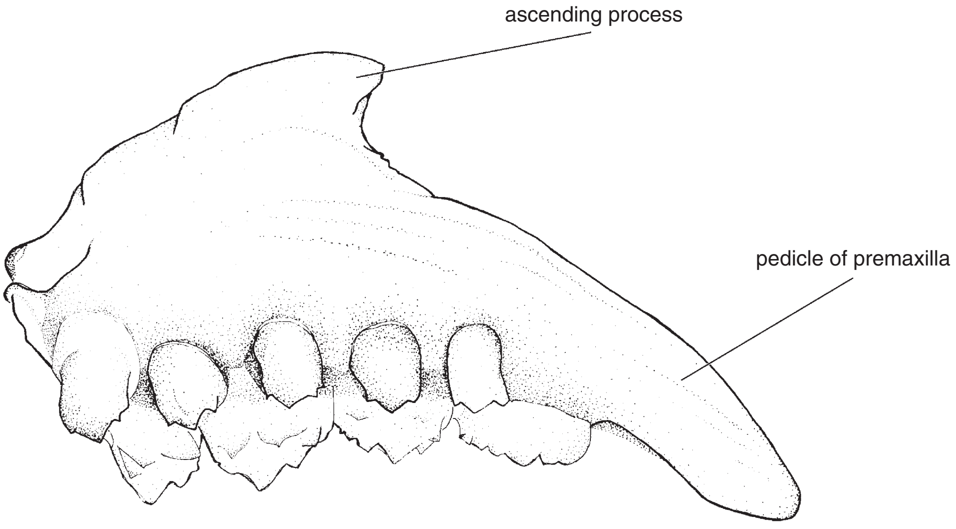

Figure 13. Premaxilla and premaxillary dentition of *Brycinus macrolepidotus*, MZUSP 60303, 58.6 mm SL; right side, lateral view, anterior to left.

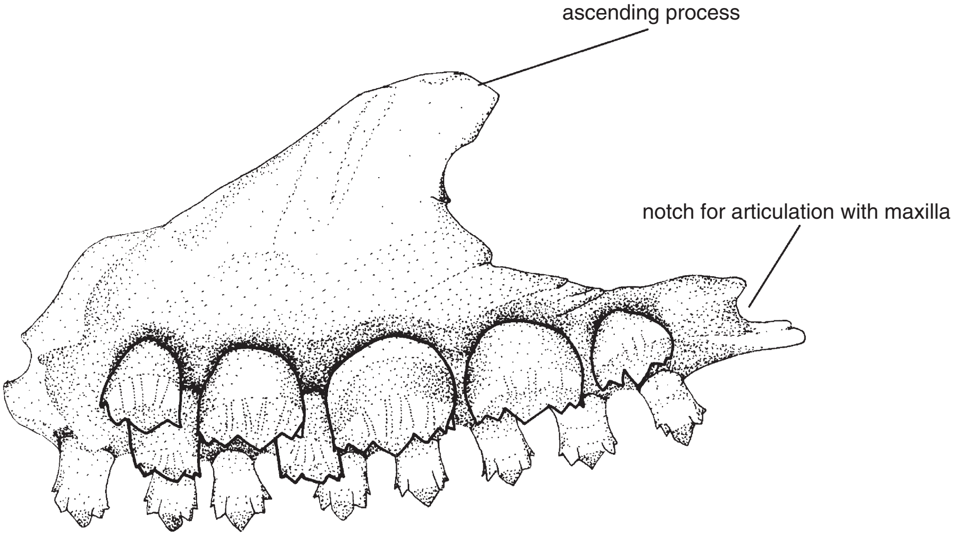

Figure 14. Premaxilla and premaxillary dentition of *Chalceus erythrurus*, MZUSP 20385, 104.6 mm SL; right side, medial view, anterior at left.

distinct, approximately vertically aligned, notch (Fig. 14) that accommodates the proximate portion of the maxilla.

The only other characiforms we encountered with a comparable pedicle-like premaxillary process are the Neotropical serrasalmines *Colossoma macropomum* (Cuvier) (Machado-Allison, 1982: fig. 22b, although not *C. bidens* (Spix & Agassiz) (Greenwood, 1976, fig. 2a), *Piaractus* (Machado-Allison, 1982: fig. 22a) and *Mylesinus*. These taxa are all components of one of the major subclades of the Serrasalminae (Machado-Allison, 1983: fig. 1). However, among the more basal members of that subfamily, the pedicle-like process is absent in *Acnodon* (Jégu & Santos 1990: fig. 10), *Myleus* (Jégu & Santos, 2002: fig. 5), *Ossubtus* (Jégu, 1992: fig. 7c), *Tometes* (Jégu, Santos & Belmont-Jégu, 2002a: fig. 6; Jégu *et al.*, 2002b: fig. 6) and *Utiarichthys* (Machado-Allison, 1983: fig. 4c).

Pristobrycon, the one member of the second major lineage within the Serrasalmine for which information on the form of the premaxilla is available, also lacks a pedicle (Machado-Allison, 1983: fig. 5). Given that only a derived subunit of the monophyletic Serrasalminae (Machado-Allison, 1983) has a pedicle-like expansion of the premaxilla, it is most parsimonious to hypothesize that the process arose independently in

Colossoma macropomum, Piaractus and *Mylesinus* vs. the Alestidae.

Forms of the posterior portion of the premaxilla among alestids that differ from the typical bauplan for that family occur in *Arnoldichthys*, *Chalceus* (Fig. 14), *Clupeocharax*, *Hydrocynus*, *Lepidarchus* and *Tricuspidalestes*. The morphology of the premaxilla in the basal alestids *Arnoldichthys* and *Chalceus* is comparable to that in the examined outgroups and thus represents an apparent retention of the plesiomorphic condition within the context of the final phylogeny.

Brewster (1986: 189) described the premaxilla in *Hydrocynus* as being vertically expanded distally and considered this restructuring to be an apomorphy for the genus. While more robust and ventrally curved (see Brewster, 1986: fig. 5) than the form present in nearly all other alestids, the basic pattern of the premaxilla is shared with other members of that family (a posteriorly unnotched pedicle extending over a portion of the maxilla). Thus, the form of the posterior portion of the premaxilla in *Hydrocynus* is considered to be homologous to the pedicle-like extension present in most other genera in the Alestidae.

The alestid genera *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes,* whose members are of small to diminutive body size, are all characterized by associated reductions in the degree of development of the posterior portion of the premaxilla. In *Clupeocharax* and *Tricuspidalestes* the posterolateral process, although proportionally shorter than the form in other alestids is, nonetheless, proportionally longer than the form present in outgroups and, furthermore, lacks a notch along its posterior limit. As such, the form of the posterior portion of the premaxilla in *Clupeocharax* and *Tricuspidalestes* is considered homologous with the pedicle-like, unnotched process that is present in most other alestids (state 1).

Lepidarchus, in contrast, lacks the posterior pedicle of the premaxilla that is typical of other alestids and, furthermore, has a notch at the posterior limit of the bone (see Roberts, 1966: fig. 2). Possession of this form of premaxilla may be correlated with the series of paedomorphic features of the genus (see 'Miniaturization and Gigantism in the Alestidae', below). Regardless of the underlying cause resulting in a reversal from the condition of this portion of the premaxilla otherwise universal in the African component of the Alestidae, the possession of the apparently plesiomorphic condition in *Lepidarchus* results in its being coded as state 0 for this character.

In his discussion of the osteology of *Ladigesia*, Géry (1968: 80, fig. 3) reported that the premaxilla of that genus is elongate with 'its distal end bifid' and that this bone 'receives' the anterior margin of the maxilla. Our observations confirm that *Ladigesia* shares the elongate pedicle found in other alestids, but we found no indication in the examined material of the genus of a posterior notch on the pedicle of the premaxilla such as was cited by Géry (1968).

In their analysis of a component of the Alestidae, Murray & Stewart (2002: 1889) reported on the extension of the premaxilla beyond the posterior limit of the dentition (their character 3) and the presence of a maxillary pedicle (their character 6) in various alestids. These two attributes apparently refer to the same feature, state 1 of this character. In their description of the morphology of the extension of the premaxilla, they referred to the posterior portion of the bone as tubular. We find that although the process is somewhat rounded in cross-section, that portion of the premaxilla is, however, transversely flattened to varying degrees and is, furthermore, solid rather than hollow.

53. Form of posterior portion of premaxilla: (0) tapering and not transversely flattened; (1) distinctly vertically expanded and transversely flattened (CI = 100; RI = 100)
Brewster (1986: 171, 189, fig. 5; apomorphy 8 of that paper) identified the proportionally deeper distal portion of the premaxilla in *Hydrocynus*, which contrasts with the posteriorly tapering premaxilla typical of other characiforms, as a synapomorphy for the species of that genus. Our observations indicate that the vertical expansion of the distal portion of the premaxilla is indeed unique to *Hydrocynus* among examined taxa. Furthermore, the transverse flattening of that portion of the bone is a correlated derived attribute of the premaxilla that is distinctive for *Hydrocynus* within the Alestidae.

The flattening of the distal portion of the premaxilla in that genus was utilized by Murray & Stewart (2002: 1889) as part of a multistate character dealing with the degree of extension of the premaxilla beyond the posterior limit of the premaxillary dentition. In so far as the feature in question is one of the forms of that portion of the ossification rather than the extent of its development posteriorly, we follow Brewster (1986) in recognizing the form of the posterior portion of the premaxilla as a separate character in this analysis.

54. Presence or absence of ascending process of premaxilla: (0) absent; (1) present (CI = 50; RI = 50)
A distinct ascending process of the premaxilla (*sensu* Vari, 1979) extending posterodorsally over the mesethmoid is common to a diversity of taxa across the Characiformes other than for basal groups such as the Distichodontidae (represented herein by *Xenocharax*) and Citharinidae (Vari, 1979: 271) in which the ascending process, if homologous with that in other characiforms, is, however, proportionally quite short.

In the taxa under consideration we find several exceptions to this generalized characiform morphology. In *Lepidarchus* the ascending process, albeit present, is significantly reduced relative to its form in other alestids. This reduction is autapomorphic for *Lepidarchus* within the context of the final phylogeny and parallels the various reductions in the degree of development of other bones in that genus; a trend presumably associated with the small body size of its single species. Although reduced, the ascending process in *Lepidarchus* is present and, thus, coded as state 1.

In the case of the species of *Hydrocynus*, the entire dorsal portion of the premaxilla and proximate regions of the mesethmoid are dramatically restructured in such a fashion that the conjoined contralateral halves of upper jaw can pivot posterodorsally on the anterior portion of the mesethmoid; modifications previously described by Brewster (1986: 189; apomorphies 5 and 7 of that study). Although it seems likely that the irregular short processes on the dorsal surface of the premaxilla that Brewster (1986: fig. 5, AP) identified as the ascending process may represent its residual components, they are reduced to such a degree as to be effectively absent and are consequently coded as state 0 in this study. This pronounced reduction may represent the absence of the 'dorsal process of the premaxilla' reported for that genus by Murray & Stewart (2002: 1889).

Coding of the ascending process in the outgroup *Crenuchus* is problematic. *Crenuchus* bears what might be interpreted as an ascending process extending lateral to the anteriorly attenuate medial portion of the mesethmoid. If such a homology is correct (it is coded as such here), the process is, nonetheless, broader and laterally less distinct than that present in many other characiforms. The question of the presence or absence of the process in *Crenuchus* does not, however, have any import for the polarity decisions of that character within the Alestidae.

55. Presence or absence of interdigitations between contralateral premaxillae: (0) premaxillae without medial interdigitations; (1) premaxillae with medial interdigitations (CI = 20; RI = 85)

The form of the junction between the contralateral premaxilla varies within the Alestidae. Whereas in many of the taxa there is a simple juxtaposition of the medial surfaces of the contralateral premaxillae, in others there is a distinct series of interdigitations locking the two premaxilla into a single functional unit (Fig. 13; Appendix 2).

The presence of interpremaxillary sutures was considered an apomorphic character for the Citharinidae and Distichodontidae by Vari (1979: 273). According to Vari, such sutures had been previously reported within the Characiformes for *Brycon* (Weitzman, 1962: 32), *Hydrocynus* (Eastman, 1917: 757, pl. 85), and were discovered in his study in the alestids *Alestes baremoze*, *Bryconaethiops* and in the Neotropical genera *Serrasalmus* and *Triportheus*. Based on a series of derived characters (the possession of a rhinosphenoid and tooth form and distribution among others), Vari proposed that the South American genera with such interdigitations were most closely related to Neotropical characiforms lacking interdigitating premaxillary sutures. As such, the presence of these sutures was considered to be an independent acquisition in the Alestidae (the African Characidae of Vari, 1979) and the cited Neotropical outgroup taxa; a conclusion supported by subsequent higher level phylogenetic studies (e.g. Zanata, 2000).

Brewster (1986: 185, 189; apomorphy 6 of that study) proposed that the presence of medial synarthritic interdigitations along the length of the adjoining surfaces of the premaxillae was a derived feature for *Hydrocynus*. Although their degree of development in larger specimens of *Hydrocynus* is more pronounced than is the case for processes present in the other members of Alestidae with such an articulation of the contralateral premaxillae, the underlying morphology of the interdigitations and presence of intervening ligaments between the premaxillae of *Hydrocynus* is homologous with that typical for all members of the Alestidae. The condition in *Hydrocynus* cannot therefore be delimited as a condition unique to that genus. We consequently code the condition in *Hydrocynus* as equivalent to that in the other alestids that possess such interdigitations.

The lack of cleared and stained specimens of *Petersius conserialis* made it impossible to critically evaluate the presence or absence of interdigitations between the premaxillae. Nonetheless, there is clearly a relatively limited area of contact between the contralateral premaxillae in *Petersius* without any external indication of interdigitations joining these ossifications. Furthermore, processes joining the contralateral premaxillae were also reported to be absent in that genus by Murray & Stewart (2002). We consequently code *Petersius* as lacking those structures. Murray & Stewart (2002) reported that interdigitations are absent in *Brycinus lateralis* (Boulenger) and *B. leuciscus* (Günther), species that, however, possess such interdigitations in the cleared and stained specimens examined in this study.

56. Form of articulation between premaxillae and mesethmoid: (0) with single shallow articular fossa along dorsomedial portion of premaxilla articulating with medial process of mesethmoid; (1) with deep articular fossa on dorsomedial portion of posterior surface of premaxilla and with second, more laterally situated fossa articulating with lateral process of anterior portion of mesethmoid (CI = 100; RI = 100)

In her analysis of the monophyly of *Hydrocynus*, Brewster (1986: 185) noted that the genus was characterized by what she termed a 'double premaxillary (ethmoid) facet.' The medial of these facets reported by Brewster is apparently homologous with the less distinct depression on the posteromedial surface of the premaxilla contacting the anterolateral portion of the mesethmoid in other members of the Alestidae and many characiforms.

This articular facet is, however, much more pronounced in *Hydrocynus* than it is in the examined outgroups. The more posterolaterally positioned of the two facets on the premaxilla in *Hydrocynus*, situated immediately medial to the proximal limit of the maxilla, hinges on the lateral process on the anterior portion of the mesethmoid (the lateral supraethmoid wing of Brewster) and its possession is unique to this genus among examined characiforms. Brewster (1986: 189) treated these modifications of the premaxilla as two distinct synapomorphies for *Hydrocynus* (her synapomorphies 9 and 10); however, in so far as they appear to be components of the same functional complex, we utilize them as a single feature in this analysis.

57. Number of functional rows of teeth on premaxilla: (0) one row; (1) two rows; (2) three rows (CI = 20; RI = 57) The number of rows of functional teeth on the premaxilla demonstrates considerable phylogenetic and ontogenetic variation across the Characiformes, with two rows present in the more generalized members of basal characiform groups (e.g. *Xenocharax*, family Distichodontidae; Daget, 1960, fig. 4). Both increases and decreases in this apparently basal number of rows occur between and within various lineages of characiforms.

The presence of a single regular tooth row, with the individual teeth in that series arranged in a distinct, smooth arch and with all the teeth having a similar shape and number of cusps was interpreted by L.R. Malabarba (1998: 203) as a synapomorphy for the Cheirodontinae, a component of the Neotropical family Characidae. Malabarba hypothesized that the plesiomorphic condition for characiforms was represented by two rows of functional premaxillary teeth; a suggestion congruent with hypotheses of higher level relationships within the Characiformes.

Turning to the taxa of immediate interest we find that the presence of two rows of teeth on the premaxilla is general across the Alestidae other than for *Clupeocharax*, *Hydrocynus* and *Lepidarchus,* all of which retain only a single row, and *Bryconaethiops* and *Chalceus*, both of which have three rows. Although the presence of one row is common to *Clupeocharax*, *Hydrocynus* and *Lepidarchus*, this reduced number is apparently a consequence of differing underlying causes.

In the case of *Hydrocynus* the teeth on the premaxilla are proportionally massive, thereby reducing the available space on the premaxilla for multiple rows, notwithstanding the robust morphology of the premaxilla in the genus (see Brewster, 1986: figs 5, 7). In *Clupeocharax* and *Lepidarchus* the teeth are, in contrast, proportionally small, but these genera demonstrate a distinct reduction in the relative cross-dimensions of the premaxilla, a trend that is particularly striking in the case of *Lepidarchus*. Despite the differences between the two conditions, it is nonetheless, inappropriate to make an *a priori* assumption of the nonhomology of the single row present in *Hydrocynus* on the one hand, vs. that in *Clupeocharax* and *Lepidarchus*, on the other and they are coded as equivalent. Such a hypothesis of nonhomology is, however, congruent with the overall most parsimonious hypothesis of relationships.

One row of teeth occurs in the Neotropical genera *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* among examined outgroup taxa. We code the condition in *Hepsetus* as unknown, since that genus is characterized by a limited overlap of the two rows of teeth towards the posterior limit of the outer tooth row, an arrangement of the premaxillary dentition that is different from that present in nearly all genera of the Alestidae. The possession of three rows is limited to *Bryconaethiops* and *Chalceus* within the Alestidae and to *Brycon* and *Triportheus* in the examined outgroups.

The presence of several rows of teeth on the premaxilla has been utilized, at least in part, by various authors as a feature to relate *Brycon*, *Chalceus* and *Triportheus* (e.g. Eigenmann & Allen, 1942; Weitzman, 1962; Lucena, 1993) and consequently requires further comment. The homology between the rows of premaxillary teeth in *Brycon, Chalceus* and *Triportheus* is at best questionable and Zanata (2000: 78) demonstrated that the arrangement found in *Chalceus* is nonhomologous with that present in *Brycon*, although both genera share an increased number of tooth rows.

In *Brycon* the premaxilla bears one outer row that includes several to a number of cuspidate teeth and an inner one consisting of two large teeth (see character 60). Between these two rows are one or two rows similar in overall arrangement to the outer row. These intermediate rows commence medially between the inner and outer rows and the posterior teeth in that series commence posterolateral to the two teeth constituting the inner row. These teeth are, furthermore, more or less aligned with those of the outer row at the lateral limit of the premaxilla.

Chalceus has a different arrangement of the premaxillary dentition, characterized by well-defined inner and outer rows extending across the width of the premaxilla, and with a short row of two teeth present between the rows. In light of these differences in tooth arrangement, the three or more rows in *Brycon* is considered nonhomologous with the three premaxillary rows in *Chalceus*. The condition of the premaxillary dentition in *Triportheus* is comparable to that present in *Brycon* and the differences in the dentition of *Triportheus* vs. *Chalceus* are comparable to those between *Chalceus* and *Brycon* described above.

Bryconaethiops has an arrangement comparable to that present in *Chalceus* (two primary rows with a less developed intermediate third row, but with only a single rather than two pair of teeth in the third intermediate row). As such, the arrangement of the premaxillary dentition in *Bryconaethiops* and *Chalceus* is positionally homologous, although the final most parsimonious hypothesis indicates that these genera are not sister taxa, and as such the tooth arrangement apparently arose independently in each genus.

The form of the premaxilla and associated dentition in the African *Hepsetus* demonstrates a number of features that are unique to that genus within the Characiformes. The most distinctive of these modifications is the elongate, tooth-bearing process of the premaxilla extending posteriorly from the main body of the bone and continuing medial to the anterior portion of the maxilla. Roberts (1969: 418, figs 16, 29) identified this process as an autogenous element that he termed the accessory ectoptyergoid. Fink & Fink (1981: 316) noted that this structure situated medial to the maxilla was fused to the posterior portion of the main body of the premaxilla in the specimens that they examined in their study.

Continuity between the process and the main body of the premaxilla in *Hepsetus* in both small and midsized cleared and stained specimens was confirmed by Vari (1995: 23) and was found to be universal in the material of *Hepsetus* examined in this study. Although the dentition on this process demonstrates minimal, or more often no, overlap with the posterior portions of the tooth row running along the lateral margin of the main body of the premaxilla, a case could be made for considering the arrangement of the dentition on the premaxilla of *Hepsetus* as representing two rows of teeth. These are a lateral row of larger teeth on the anterior portion of the dentigerous surface of the bone and a medial row of smaller teeth borne on the posterior process of the premaxilla.

However, this pattern of premaxillary dentition differs dramatically from the arrangement in all other characiforms with two or more rows of premaxillary teeth, all of which are characterized by the combination of a complete, or near complete, overlap of these rows on the anterior portion of the premaxilla and an absence of a posteromedial process to the premaxilla. The unique bauplan of the premaxilla and its associated dentition introduces uncertainty into the question of the homology of the teeth on the posterior process of the premaxilla in *Hepsetus*. Given their location, the teeth on the posterior process may represent a medially shifted posterior portion of the premaxilla and its associated dentition with a resultant break in the series. Regardless of whether that homology hypothesis is, or is not, correct, the location of the 'inner row' of premaxillary dentition in *Hepsetus* is positionally nonhomologous with the anteriorly positioned inner row that typifies other characiforms, characterized by the presence of two rows of premaxillary teeth. *Hepsetus* thus cannot be coded for this character. The same uncertainty applies to the coding of *Hepsetus* for character states for characters 58, 59, 61, 62, 63 and 64.

58. Separation of inner and outer tooth rows on premaxilla: (0) tooth rows well defined and separated from each other, with margins of adjoining teeth of inner tooth row situated close to each other; (1) tooth rows less distinct, with gaps between first and second, and second and third, teeth of inner row, and with two teeth of outer row partially repositioned in resultant gaps in inner tooth row (CI = 50; RI = 85)

Most examined taxa in the Alestidae with multiple rows of premaxillary teeth have a continuous inner row without any notable gaps between the adjoining teeth and also possess a discrete outer row of teeth. In *Hemmigrammopetersius*, *Virilia* and most, but not all, species of *Rhabdalestes* (Appendix 2), the teeth of the inner row become proportionally more spaced out along the premaxilla, with a consequent distinct gap between the first and second, and second and third teeth of that tooth series.

The two teeth of the outer premaxillary series are, in turn, partially shifted into the resultant spaces in the inner series. As a consequence of this rearrangement, the species of *Hemmigrammopetersius* and *Virilia*, and most species of *Rhabdalestes*, on first examination appear to have a single tooth row on the premaxilla with the orientation of the teeth sequentially alternating to some degree towards and away from the oral cavity.

In the two specimens of *Brachypetersius gabonensis* that we examined, there occurs a gap between the second and third teeth of the inner row on the premaxilla, but not between the first and second teeth. Furthermore, the tooth of the outer row positioned proximate to the space between the second and third teeth of the inner row in this species is not shifted into the resultant gap in a manner comparable to that typical of alestids with two gaps in the inner tooth row of the premaxilla.

Because of these differences in the premaxillary dentition of *B. gabonensis* relative to state 1, we code this species as having state 0. It was impossible to code this character for *Clupeocharax*, *Hydrocynus* and *Lepidarchus* in the Alestidae and *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* in the outgroup as a consequence of their possession of only one row of teeth on the premaxilla. *Hepsetus* was coded as unknown for the reasons discussed in character 57.

59. Number of teeth in outer tooth row of premaxilla:
(0) six or more; (1) five; (2) four; (3) three; (4) two
(CI = 33; RI = 87)
Although variation exists in the form and arrangement of dentition on the premaxilla both within the Alestidae and across the examined outgroups, for the purposes of this analysis it is appropriate to utilize the number of teeth in the outer row as a character independent of a determination of the methods by which the number of teeth has been achieved. It was impossible to code this character for *Clupeocharax*, *Hydrocynus* and *Lepidarchus* in the Alestidae and *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* in the outgroup as a consequence of the presence of only one row of teeth on the premaxilla in these taxa. *Hepsetus* was coded as unknown for the reasons discussed in character 57.

60. Composition of inner tooth row on premaxilla:
(0) represented by row of teeth that generally decrease gradually in size towards posterior portion of premaxilla; (1) represented solely by pair of large teeth
(CI = 100; RI = 100)
In the majority of characiforms with more than one row of cuspidate teeth on the premaxilla, the teeth of the inner row progressively gradually decrease in size posteriorly from the premaxillary symphysis and lack distinctly larger teeth. In the case of the outgroup taxon *Brycon*, the inner row is represented by two large teeth. Although various authors have proposed that there are two teeth present in the inner row in *Piaractus*, one of the outgroup taxa of this study, Machado-Allison (1982: 29) noted that his studies of the ontogeny of the premaxillary dentition of the genus indicated that the inner row actually encompasses four or five teeth. This character could not be coded for various ingroup (*Clupeocharax*, *Hydrocynus* and *Lepidarchus*) and outgroup taxa (*Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hepsetus*, *Hoplias* and *Serrasalmus*) lacking an inner row of dentition on the premaxilla.

61. Number of teeth in inner tooth row of premaxilla:
(0) five or more; (1) four or fewer (CI = 33; RI = 81)
Most members of the Alestidae have four teeth on the inner row of the premaxilla, whereas six are present in that series in *Arnoldichthys*, 5-10 occur in *Chalceus*, and only three are present in *Rhabdalestes septentrionalis*. Examined outgroup taxa possessing two rows on the premaxilla have five or more teeth on the inner row, a count that is consequently considered state 0 for this character. The presence of four teeth in the inner row of the premaxilla was also proposed as a synapomorphy for a clade within the New World family Characidae by Malabarba & Weitzman (2003: 84). The occurrence of that number of teeth in that lineage is homoplastic relative to the presence of four teeth in some members of the Alestidae in light of the phylogenetic hypotheses proposed herein and by Malabarba & Weitzman (2003: fig. 2). The lower number in *R. septentrionalis*, if shared with other congeners not examined in this study, would be a potential synapomorphy for a subunit of that genus.

It was impossible to code this character for various components of the Alestidae. *Clupeocharax*, *Hydrocynus* and *Lepidarchus* have only one row of teeth present on the premaxilla. In *Tricuspidalestes*, the dentition of the two rows interdigitate in such a fashion that it is difficult to unambiguously determine the number of teeth on the inner row. It was also impossible to code the Neotropical outgroup genera *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* for this character as a consequence of the presence of only one row of premaxillary teeth in these taxa. *Hepsetus* was coded as unknown for the reasons discussed in character 57.

62. Degree of development of posterior portion of third tooth of inner premaxillary tooth row: (0) tooth not expanded posteromedially; (1) tooth expanded posteromedially (CI = 100; RI = 100)
Alestes, *Brycinus* and *Bryconaethiops* share a posteromedial expansion of the third tooth of the inner premaxillary tooth row unique to those genera among examined characiforms (Fig. 15). This expansion typically results in the overlap of the anterior margin of the fourth tooth of the inner premaxillary row by the posterior portion of the third in that series when these teeth are examined from a directly medial view. This character could not be coded for *Clupeocharax*, *Hydrocynus* and *Lepidarchus* within the Alestidae or *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* in the outgroup as a consequence of the presence of only one row of premaxillary teeth in these taxa. *Hepsetus* was coded as unknown for the reasons discussed in character 57.

63. Distribution of cusps on distal margin of first through third teeth of inner premaxillary tooth row:
(0) cusps aligned in nearly straight line or in gentle arch; (1) cusps arranged in distinctly pronounced arch
(CI = 33; RI = 89)
The margin of the dentition of the teeth of the inner premaxillary tooth row among alestids and examined

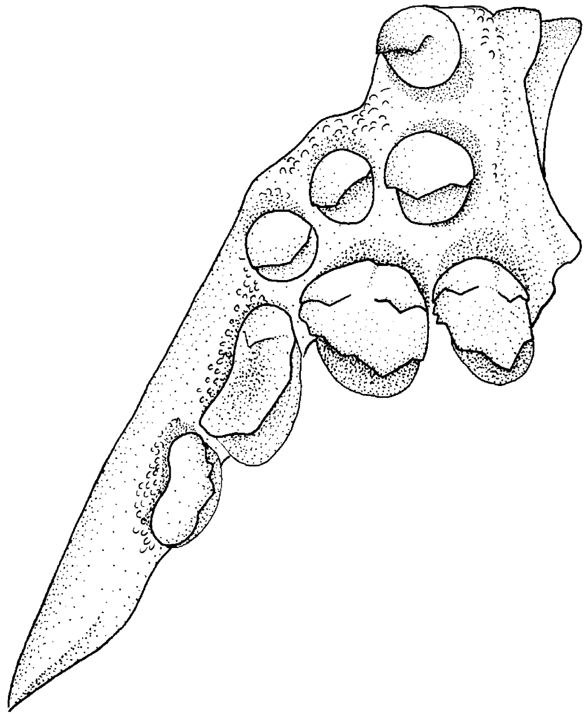

Figure 15. Premaxilla and premaxillary dentition of *Bryconaethiops microstoma*, USNM 339722, 55.1 mm SL; right side, ventral view, anterior at top.

characids typically has the cusps on the first through third teeth positioned either in a nearly straight line or in a gently curved arch when these teeth are examined from a ventral view. In *Alestes*, *Brycinus*, *Bryconaethiops* and *Bryconalestes* the cusps are arranged in a pronounced arch (Fig. 15) that is convex in the direction of the oral cavity. This arrangement is hypothesized to be derived within the context of outgroup comparisons.

The only somewhat comparable arrangement of the cusps on these premaxillary teeth that we encountered in our outgroup comparisons occurs in the species of *Triportheus*. In that genus the overall form of the first through third teeth of the inner premaxillary tooth row differs, however, significantly from that present in *Alestes, Brycinus, Bryconaethiops and Bryconalestes*. In light of that different morphology and within the overall most parsimonious hypothesis of relationships arrived at in this study, the occurrence of the arched arrangement of the cusps in *Triportheus* is considered nonhomologous with the occurrence of a somewhat comparable positioning of the cusps in *Alestes*, *Brycinus*, *Bryconaethiops* and *Bryconalestes*.

This character could not be coded for *Clupeocharax*, *Hydrocynus* and *Lepidarchus* among alestids and *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* in the outgroup as a consequence of the presence of only one row of premaxillary dentition in these taxa. *Hepsetus* was coded as unknown for the reasons discussed in character 57.

64. Included cusps on first through third teeth on inner tooth row on premaxilla: (0) absent; (1) present (CI = 100; RI = 100)

In most examined alestids and outgroups the cusps along the distal margin of the teeth of the inner row of the premaxilla are arranged either in a nearly straight line or as a varyingly formed arch when examined from a ventral view. Regardless of the overall pattern, the immediately adjoining cusps at each margin of the series of cusps are approximately in line with the proximate cusps. In *Alestes*, *Brycinus* and *Bryconaethiops* the cusp at each limit of the cusp series of the third tooth is shifted towards the central portion of the tooth when examined from a ventral view (Fig. 15). As a consequence, these terminal cusps are included within the arch of the remaining cusps along the oral margin of the teeth.

The homology of these included terminal cusps in *Alestes*, *Brycinus* and *Bryconaethiops* is problematic. One possibility is that these structures may be equivalent to the cusps at the end of the cusp series in some species of *Bryconalestes*, which are shifted slightly out of alignment of the rest of the series. Alternatively, these structures in *Alestes*, *Brycinus* and *Bryconaethiops* may represent a *de novo* development of cusps in that portion of the tooth. Regardless of the exact homology of these included cusps, no further centrally positioned cusps were discovered either in examined outgroups or other alestids, and the possession of such included cusps is consequently hypothesized to be derived.

This character could not be coded for *Clupeocharax*, *Hydrocynus* and *Lepidarchus* in the Alestidae and *Charax*, *Cheirodon*, *Crenuchus*, *Hemiodus*, *Hoplias* and *Serrasalmus* in the outgroup as a consequence of the presence of only one row of premaxillary teeth in these taxa. *Hepsetus* was coded as unknown for the reasons discussed in character 57.

65. Association of premaxilla and maxilla: (0) movably attached; (1) ankylosed (CI = 100; RI = 100)

Nearly all examined members of the Alestidae share with most characiforms a mobile ligamentous connection of the anterodorsal region of the maxilla with the posterodorsal portion of the premaxilla. Species of *Hydrocynus* alternatively have dense connective tissue bands that immovably conjoin the highly restructured premaxilla and maxilla. Although a tight, immobile association of the premaxilla and maxilla also occurs elsewhere within the Characiformes in the genera *Belonophago*, *Eugnatichthys*, *Hemistichodus*, *Ichthyborus*, *Mesoborus*, *Microstomatichthyoborus*, *Paraphago* and *Phago*, which together constitute a clade within the Distichodontidae (Vari, 1979: 274, fig. 4), the overall upper jaw morphology in those genera differs significantly from that in *Hydrocynus*. Furthermore, those taxa are more closely related to the remaining genera of the Distichodontidae and to members of the Citharinidae (Vari, 1979: fig. 47) all of which retain mobility between the premaxilla and maxilla. As such, the presence of an immobile joint between bones of the upper jaw bones in these eight genera is considered nonhomologous to the form of the articulation in *Hydrocynus*.

Brewster (1986: 189) utilized the possession of a laminar, edentate maxilla that is ankylosed to the premaxilla as a derived feature for the species of *Hydrocynus*. Lack of dentition associated with the maxilla is, however, general across the Alestidae and the posterior portion of the maxilla (albeit not all of the bone) is lamellar in numerous characiforms (see discussion in character 74). We consequently restrict the character herein to the presence or absence of ankylosis between the premaxilla and maxilla.

66. Area of insertion of premaxillary-maxillary ligament on maxilla: (0) on anterior surface; (1) on lateral surface (CI = 20; RI = 82)

In the examined outgroup characids, the ligament extends from the posterior terminus of the premaxilla to the maxilla, attaching onto the anterior margin of the latter. All alestids, with the exception of *Arnoldichthys*, *Chalceus*, *Clupeocharax*, *Hemmigrammopetersius*, *Lepidarchus* and *Tricuspidalestes*, have, in contrast, a posteroventral extension of the pedicle of the premaxilla over the lateral surface of the anterodorsal portion of the main body of the maxilla. Superimposition of the premaxilla over the anterior portion of the maxilla in these taxa renders inaccessible the site on the maxilla onto which the ligament inserts in many characiforms. This restructuring presumably necessitated a shift of the area of attachment of the ligament from the anterior to lateral surface of the premaxilla.

The basal alestid genera *Arnoldichthys* and *Chalceus* demonstrate the condition of the area of attachment for the premaxillary-maxillary ligament that is present in outgroups, an apparent retention of the plesiomorphic condition within the context of the final phylogeny. The other four alestid genera that lack the apparently derived version of the area of attachment (*Clupeocharax*, *Hemmigrammopetersius*, *Lepidarchus* and *Tricuspidalestes*) are deeply internested within the final phylogenetic tree, but all achieve only relatively small body size and demonstrate reductions of various bones. The posteriorly proportionally shorter or absent pedicle in these genera in which the posterior terminus only approximates the anterior limit of the main body of the maxilla, allows space for the apparent secondary attachment of the premaxillary-maxillary ligament onto the anterior portion of the maxilla.

In the case of *Hydrocynus* the posteroventral portion of the premaxilla is closely and tightly applied to the lateral surface of the maxilla, with the adjoining surfaces of those bones immovably conjoined by a strong mass of ligamentous tissue. Because of its location and function, this ligament mass is considered to be the homologue of the more discrete ligament connecting the premaxilla and maxilla in most other alestids. It was impossible to code this character in *Hemiodus*, *Piaractus* and *Serrasalmus* in the examined outgroups as a consequence of their diverse modifications of the upper jaw.

67. Anterodorsal portion of ascending process of maxilla: (0) terminates in relatively rounded or pointed process; (1) terminates in concave surface (CI = 33; RI = 92)

The anterodorsal portion of the ascending process of the maxilla in most characiforms attaches to the lateral wing of the mesethmoid via a distinct maxillary-mesethmoid ligament that arises from the rounded or varyingly tip of the ascending process of the maxilla (Fig. 16). The majority of examined taxa in the Alestidae (Appendix 2) have instead a distinct concavity at the tip of the ascending process of the maxilla (Figs 17, 18) resulting in a bifurcated anterior margin to the ossification. This feature was previously reported by Lucena (1993) for species of the Alestidae that were identified as *Alestes leuciscus*, *Hemmigrammopetersius rhodesiensis* and *Hydrocynus forskahlii*.

68. Alignment of ascending process of maxilla when viewed dorsally: (0) medially curved, with distinct angle relative to axis of posterior portion of maxilla; (1) relatively straight and aligned approximately parallel to axis of posterior portion of maxilla (CI = 100; RI = 100)

Brewster (1986: 202) noted that Neotropical characids typically have a somewhat medially directed ascending process of the maxilla. When viewed dorsally, this process forms a distinct angle relative to the axis of the main body of the bone. By contrast, in all examined alestids, with the exception of the basal genera *Arnoldichthys* and *Chalceus*, the axis of the process is aligned with that of the main body of the bone. As a consequence of this modification, the maxilla in these taxa appears to be straight, or nearly straight, when viewed dorsally.

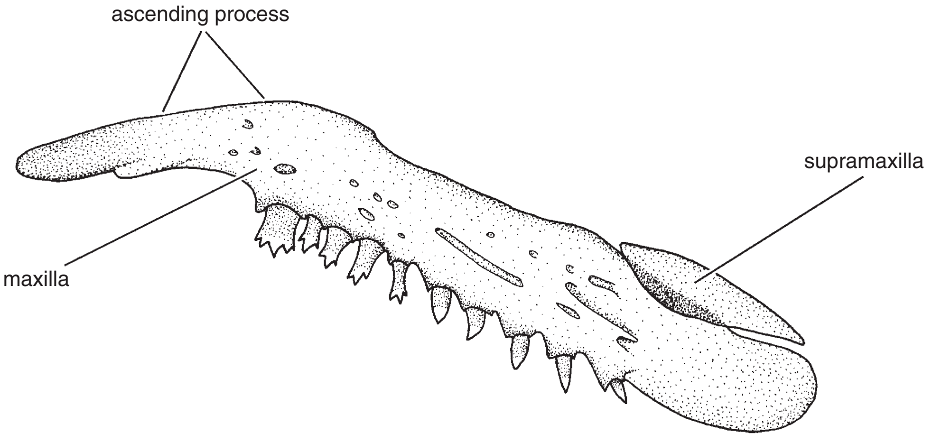

Figure 16. Maxilla, supramaxilla, and maxillary dentition of *Chalceus erythrurus*, MZUSP 20385, 104.5 mm SL; lateral view, anterior at left.

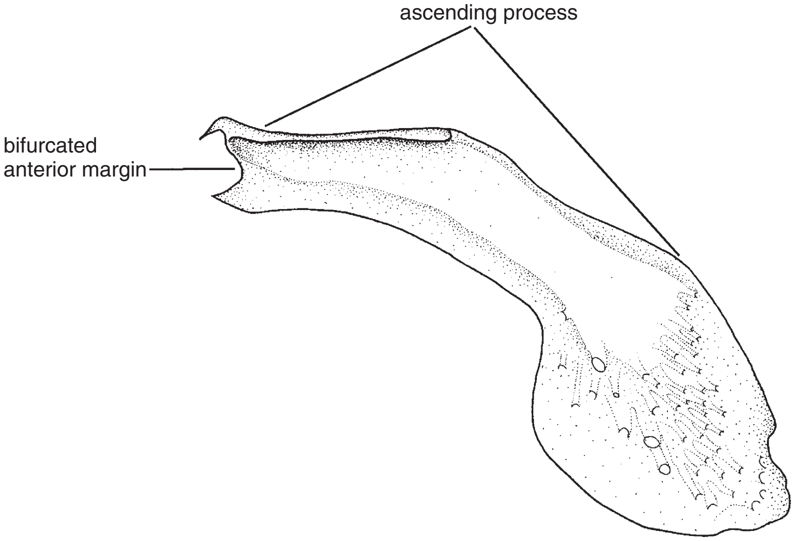

Figure 17. Maxilla of *Brycinus macrolepidotus*, MZUSP 60303, 58.6 mm SL; lateral view, anterior at left.

69. Relative length of ascending process of maxilla with respect to greatest length of lamellar portion of maxilla:
(0) ascending process shorter than lamellar portion;
(1) ascending process about as long as, or longer than, lamellar portion (CI = 33; RI = 91)

In examined outgroup characiforms the ascending process of the maxilla is shorter than the lamellar portion situated posteroventral to the posterior terminus of the premaxilla. By contrast, in all examined alestid taxa, with the exception of *Arnoldichthys*, *Chalceus* (Fig. 16), *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes,* the maxilla has a proportionally elongate ascending process (Figs 17, 18). As such, the ascending process in most alestids is longer, to distinctly longer, than the lamellar portion of the bone situated posteroventral to the terminus of the premaxillary pedicle.

Although *Arnoldichthys* and *Chalceus*, the sister groups to all other alestids, have a relatively short ascending process, they do achieve a moderate body size; thus the relative proportions of the components of the maxilla apparently represent the retention of the plesiomorphic condition within the final phylogeny. In *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes*, genera deeply embedded within the final phylogeny of the Alestidae that are of relatively to distinctly small body size, the short relative proportions of the ascending process vs. the lamellar portion of the maxilla are apparently associated with the reduction of the overall robustness of the premaxilla and the absence or shortening of the premaxillary pedicle in those three genera.

This reduction in the robustness of the premaxilla results in the apparent secondary anterodorsal expan-

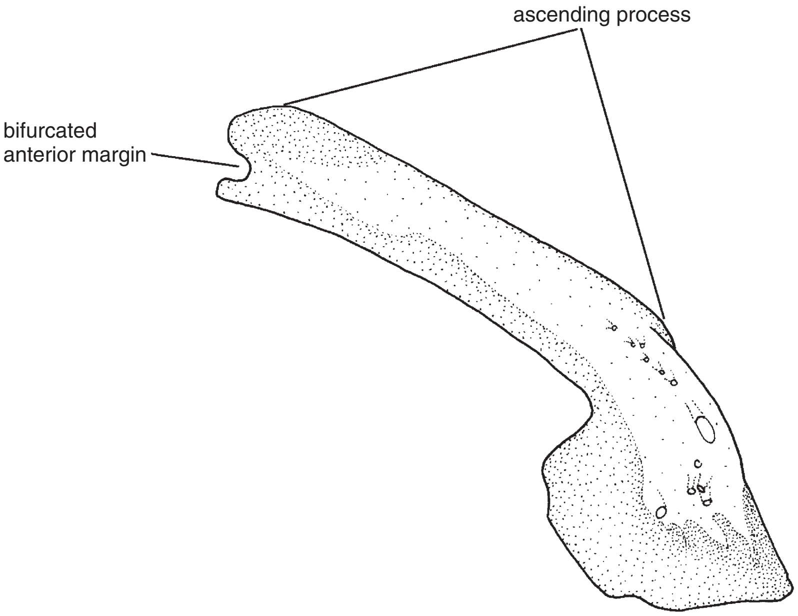

Figure 18. Maxilla of *Bryconaethiops microstoma*, USNM 339722, 55.1 mm SL; lateral view, anterior at left.

sion of the lamellar portion of the maxilla. Despite the differences in the overall morphology of the premaxilla and maxilla in *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes* vs. the hypothesized plesiomorphic condition as typified in outgroups, we code the condition of the ascending process of the maxilla in these three genera as equivalent to the morphology of that structure present in the outgroup given the degree of similarity in the overall morphology of the maxilla of these taxa.

70. Presence of distinct dorsolateral expansion on ascending process of maxilla: (0) absent; (1) present (CI = 100; RI = 100)

The ascending process of the maxilla is usually rod-like or, at most, has some limited dorsally or dorsolaterally situated expansions in nearly all examined alestids and outgroups (Figs 16, 17). *Bryconaethiops* uniquely possesses a pronounced dorsolaterally positioned expansion on the ascending process (Fig. 18). We were unable to code this feature for *Hemiodus* among examined outgroups, in light of the pronounced modifications of the ascending process of the maxilla in that genus.

71. Extent of expanded portion of ascending arm of maxilla: (0) extending beyond posterior limit of premaxilla; (1) terminating at posterior limit of premaxilla (CI = 100; RI = 100)

In most alestids and outgroups the rotund ascending arm of the maxilla is continuous with a transversely thickened region located along the anterodorsal portion of the lamellar portion. This expanded region of the maxilla, in turn, extends distinctly beyond the posterior limit of the premaxilla. *Hydrocynus* is unique among examined taxa in having a transversely expanded portion of the anterodorsal region of the maxilla terminating at the posterior limit of the premaxilla. As a consequence of this modification, the entirety of the maxilla is relatively flat posterior to the terminus of the premaxilla. This lack of thickening of the dorsal margin of at least the anterior portion of the main body of the maxilla, presumably represents the 'lamellar' aspect of the maxilla that was hypothesized to be a derived feature for the species of *Hydrocynus* by Brewster (1986: 189), a polarity of the feature congruent with the hypothesis arrived at in this analysis.

72. Position of posterior margin of maxilla: (0) falling short of, or aligned with, vertical through lateral blade of lateral ethmoid; (1) extending slightly beyond vertical through lateral blade of lateral ethmoid; (2) extending distinctly beyond vertical through lateral blade of lateral ethmoid (CI = 40; RI = 88)

In most examined outgroups, the posterior limit of the maxilla is situated posterior to the vertical through the approximately vertically directed, lateral blade of the lateral ethmoid. In members of the Alestidae other than the basal lineages *Arnoldichthys*, *Chalceus* and *Hydrocynus*, the maxilla terminates short of, or barely reaches, the vertical through the lateral blade of the lateral ethmoid (Figs 2, 19, 20).

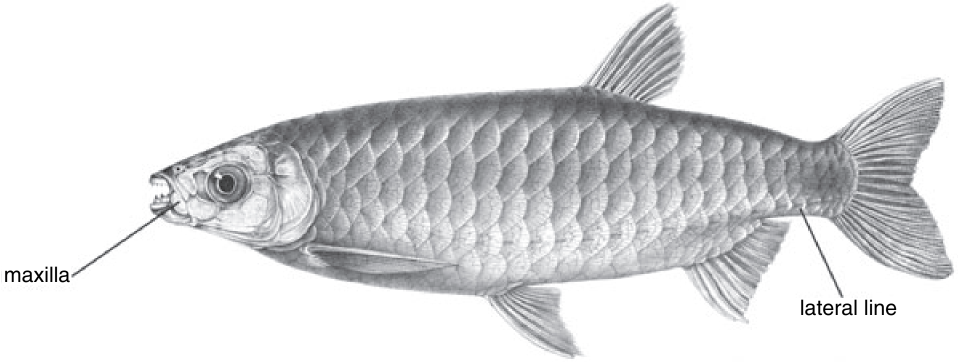

Figure 19. *Brycinus grandisquamis*, showing position of posterior margin of maxilla, position of laterosensory canal of lateral line, and poorly developed and effectively absent adipose eyelid (taken from Boulenger, 1889: pl. 35, fig. 3).

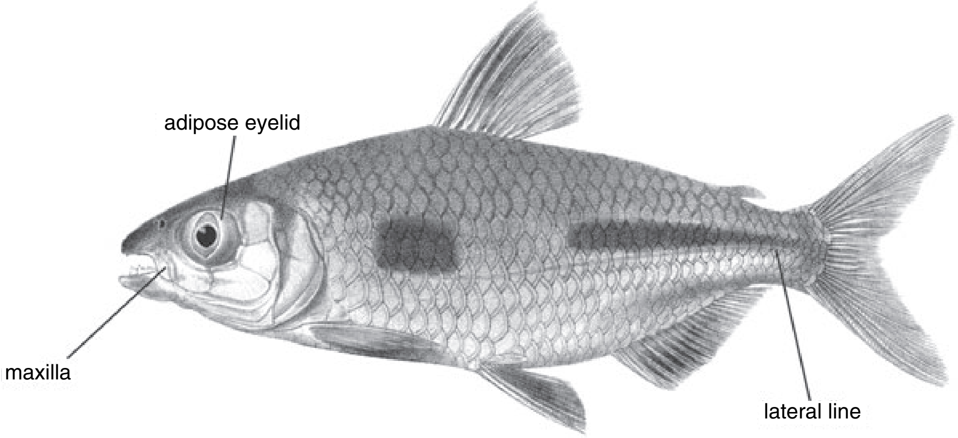

Figure 20. *Bryconaethiops boulengeri*, showing position of posterior margin of maxilla, position of laterosensory canal of lateral line, and well-developed adipose eyelid (taken from Boulenger, 1889: pl. 37, fig. 1).

The presence of a proportionally posteriorly more elongate maxilla in these basal lineages may reflect different underlying causes. The form of the maxilla in *Arnoldichthys* and *Chalceus* closely approximates the morphology of that bone in outgroup taxa. Within the context of the final phylogeny, the bauplan of the maxilla in *Arnoldichthys* and *Chalceus* represents the retention of the plesiomorphic morphology. In species of *Hydrocynus* (Fig. 3), in contrast, the overall form of the maxilla is notably modified and proportionally enlarged, with the overall mobility of the upper jaw on the mesethmoid dramatically increased. Associated with this restructuring of the upper jaw in *Hydrocynus* is the posterior extension of the maxilla to extend beyond the vertical through the lateral blade of the lateral ethmoid. This posterior extension is possibly a secondary condition in light of the degree of modification of the jaws in the genus, but alternatively may represent a modification of the morphology of the bone in *Arnoldichthys* and *Chalceus*.

Turning to the examined outgroups, we find in *Hemiodus* that the maxilla also falls short of the lateral ethmoid; however, the maxilla, and indeed the entire jaw system, is significantly modified across the Hemiodontidae relative to the morphology of that system in most characiforms, rendering homology comparisons of *Hemiodus* with the Alestidae for this body system tenuous at best. More significantly, the Hemiodontidae are hypothesized to be closely associated phylogenetically with groups other than the Alestidae (Buckup, 1998: 134). As such, any perceived similarities in the degree of extension of the maxilla between the Hemiodontidae and *Hydrocynus* are most parsimoniously hypothesized to be homoplastic. The opposite condition of a longer maxilla terminating posterior to the region through the vertical through the middle of the orbit was observed in *Charax*, *Hepsetus*, *Hoplias* and *Salminus* among examined outgroups, a modification apparently functionally correlated with the proportionally large gape of the mouth typical of all of those genera.

73. Presence or absence of process along posterodorsal margin of maxilla: (0) absent; (1) present (CI = 50; RI = 50)

Although various taxa in the Characidae and most examined species of the Alestidae have a slight irregularity of the posterodorsal margin of the maxilla in the region where it passes beyond the posterior terminus of the premaxilla, they lack a distinct posterior process on that portion. Such a process is, however, present in *Micralestes lualabae* Poll and all examined species of *Hydrocynus*.

According to Brewster (1986: fig. 5; process not labelled), who previously reported on the presence of the process in the species of *Hydrocynus*, the structure serves as an area of attachment for some dorsomedial fibres of the adductor mandibulae muscles. In *M. lualabae* there occurs a somewhat similar, albeit distinctly more triangular, process that is positioned in the same general region of the maxilla. Despite the differences between the *Hydrocynus* and *Micralestes* in the overall form and, to a degree, relative position of these structures on the maxilla (along the lateral margin in *Hydrocynus* and slightly more medially positioned in *M. lualabae*) we conservatively code these structures as homologues for the purposes of the analysis. The processes on the maxilla in these two genera are considered homoplastic under the overall most parsimonious hypothesis of relationships.

74. Profile of posterodorsal portion of maxilla in lateral view: (0) relatively straight or slightly convex; (1) distinctly convex (CI = 100; RI = 100)

In most examined characiforms the posterodorsal profile of the maxilla is either relatively straight (e.g. *Brycon*; see Weitzman, 1962: fig. 8) or slightly curved posteriorly (*Salminus*), albeit sometimes with a posterodorsal enlargement of the distal portion of the bone (e.g. *Hoplias*; see Roberts, 1969: fig. 3). A subunit of the Alestidae (*Alestes*, *Brycinus* and *Bryconaethiops*) has, however, a distinctive morphology, in which the posterior portion of the maxilla has an abrupt realignment of the distal portion of the ossification (Figs 17–20). As a consequence of this restructuring, the posterior portion of the maxilla is distinctly more ventrally aligned in *Alestes*, *Brycinus* and *Bryconaethiops* than it is in other alestids and examined outgroup taxa. This restructuring, furthermore, results in a distinct convex curvature of the posterior border of the maxilla in *Alestes*, *Brycinus* and *Bryconaethiops* when examined from a lateral view; a derived form of that ossification.

Hydrocynus has a distinct overall morphology of the maxilla, in particular the presence of a distinct posterodorsal process on the bone (see character 73) that makes it impossible to unambiguously code this character in that genus. *Hydrocynus* is consequently coded as unknown for this feature.

75. Canal running through maxilla: (0) absent or relatively short and limited to ascending process of maxilla; (1) more highly developed, with at least part of the canal system extending onto lamellar portion of maxilla and often to posterior margin of ossification (CI = 25; RI = 25)

The presence of a canal running through the anterior part of the maxilla to the distal one-third of that bone was described within the Characiformes by Menezes (1976: 6–7) in the Neotropical genera *Acestrorhynchus*, *Cynopotamus* and their relatives. As noted by Menezes (1976: 67) based on information provided by S. H. Weitzman, the canal does not serve a sensory role, but is rather a conduit for nerves and blood vessels. In many characiforms, particularly groups such as the Alestidae in which the posterior portion of the maxilla has an overall lamellar form, the canal system within the main body of the maxilla often assumes a relatively elaborate pattern. In most members of the Alestidae this system extends posterolaterally from the anterior portion of the ascending process of the maxilla, sometimes with one or more openings to varying degrees onto the lamellar portion of the bone. Within the Alestidae, a less extensive system limited to the ascending process of the maxilla occurs in *Clupeocharax* and *Tricuspidalestes*, with *Lepidarchus*, in turn, totally lacking a canal. A limited or absent canal system characterizes *Hemiodus* and *Xenocharax* among the examined outgroups.

76. Ridge on lateral surface of maxilla: (0) absent; (1) present (CI = 33; RI = 83)

The lateral surface of the maxilla in the majority of taxa examined in this study lacks a distinct ridge on its lamellar portion in the region where the ascending process merges into the main body of the ossification. This generality applies even in instances where the dorsal portion in that region is somewhat more laterally positioned than the posteroventral lamellar portion. A ridge on the dorsolateral surface aligned with the axis of that portion of the maxilla is, in contrast, present in a subset of the Alestidae (see Appendix 2). When present, the ridge clearly demarcates the main lamellar portion of the bone from the transversely thicker dorsal portion that is continuous anteriorly with the ascending process. This ridge lies proximate and dorsomedial to the posterior portion of the pedicle of the premaxilla.

77. Wavy ridges on lateral surface of maxilla: (0) absent; (1) present (CI = 100; RI = 100)

Most characids and alestids have a smooth lateral surface of the lamellar portion of the maxilla, as is the case in the South American genus *Brycon* (Weitzman, 1962: fig. 8) or have various degrees of irregularity. When present, such surface irregularities are associated with superficial portions of the canal system that often penetrate the surface to varying degrees (see discussion of canal system in character 75).

Arnoldichthys is unique among taxa examined in this study in having a series of wave-like ridges on the lateral surface of the maxilla, with most ridges aligned parallel to the long axis of the bone. *Hydrocynus* is the only other member of the Alestidae with modifications on the maxilla that are somewhat reminiscent of the wavy ridges that characterize that bone in *Arnoldichthys*. The elaborate pattern of ridges in the lamellar portion of the maxilla in *Hydrocynus* differs, however, in position and alignment from the wavy ridges on that bone characteristic of *Arnoldichthys*. Furthermore, the surface structures on the maxilla of *Hydrocynus* are directly associated with the series of small canals that penetrate that bone, as is the case in some outgroups but not *Arnoldichthys*. Thus, the structures in *Hydrocynus* are considered to be nonhomologous with the wavy ridges present in *Arnoldichthys*.

78. Teeth on maxilla: (0) absent; (1) present (CI = 25; RI = 81)

The possession of one to many teeth on the maxilla is a common feature among characiforms, whereas the maxilla is edentulous across the Alestidae (Figs 17, 18), other than in the basal genus *Chalceus* (Fig. 16). Although the species of *Bryconops* examined as part of the outgroup in this study lacks teeth on the maxilla, maxillary dentition is present in some of its congeners (Machado-Allison *et al*., 1993: figs 9, 12, 16). Teeth on the maxilla were also absent in the serrasalmines *Serrasalmus* and *Piaractus mesopotamicus* (Holmberg) (although present in *P. brachypomus* (Cuvier); see Machado-Allison, 1982: 29, fig. 22a) and *Crenuchus* among examined outgroups. The absence of maxillary dentition is also a synapomorphy for the clade consisting of the Neotropical families Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae (Castro & Vari, 2004: 20). That Neotropical clade is, however, hypothesized to be phylogenetically distant from the Alestidae (Buckup, 1998) and also lacks the other hypothesized synapomorphies for the Alestidae.

79. Relative size of anterior teeth on maxilla: (0) teeth approximately of equal size; (1) first tooth distinctly larger than remaining teeth in series (CI = 100; RI = 100)

Chalceus erythrurus Cope, *C. macrolepidotus* and *C. spilogyros* Zanata & Toledo-Piza demonstrate a pronounced disparity in the size of the first tooth on the maxilla relative to that of the second and subsequent teeth (Fig. 16). This difference in tooth size is an unusual situation among characiforms bearing teeth on the maxilla and such a disparity is thus considered derived.

Enlargement of the first tooth on the premaxilla relative to the other teeth on that bone also occurs in at least some species of *Pseudochalceus* (Schultz, 1966: 27; Géry, 1972a: 937, fig. 2b; 1972b: 28, fig. 7a), a genus of the Characidae endemic to drainage systems of the western slopes of the Andean Cordilleras of Colombia and Ecuador. The phylogenetic placement of *Pseudochalceus* is uncertain (Lima *et al*., 2003: 155), but an enlarged first tooth on the premaxilla is absent in *Hollandichthys multifasciatus* (Eigenmann & Norris) (see Géry, 1972b: 34, fig. 7b), an externally very similar Neotropical taxon that some previous authors (Schultz, 1966; Géry, 1972a, b) synonymized into *Pseudochalceus*, albeit without a thorough phylogenetic analysis.

Nonetheless, in light of the inconsistent presence of the enlargement of the first tooth on the maxilla in the assemblage apparently formed by *Hollandichthys* and *Pseudochalceus* and given the absence in those two genera of the other externally obvious derived characters common to *Chalceus* and the African members of the Alestidae we consider that the presence of an enlarged first tooth on the maxilla in *Chalceus* and *Pseudochalceus* represents a homoplasy.

The absence of dentition on the maxilla in the African components of the Alestidae along with *Crenuchus*, *Bryconops*, *Piaractus* and *Serrasalmus* in the outgroups made it impossible to code this character for those taxa.

80. Form and area of attachment of primordial ligament: (0) ligament relatively narrow and attaching to posteromedial portion of ascending process of maxilla; (1) ligament broad, robust, and attaching to the posterior half of maxilla; (2) ligament relatively narrow and attaching to posterolateral surface of ascending process of maxilla (CI = 50; RI = 91)

Characiforms demonstrate a broad range of modifications of the primordial ligament (*sensu* Winterbottom, 1974: 232; the articular-maxillary ligament of Alexander, 1964: 183). These differences involve both the overall form of the ligament and details of its areas of attachment dorsally to the maxilla and ventrally to the lower jaw and sometimes to the anteroventral components of the suspensorium. As would be expected, the unique overall morphology of the jaws that is characteristic of most members of the Alestidae is paralleled by distinctive changes both in the form of the primordial ligament and in its area of attachment to the maxilla.

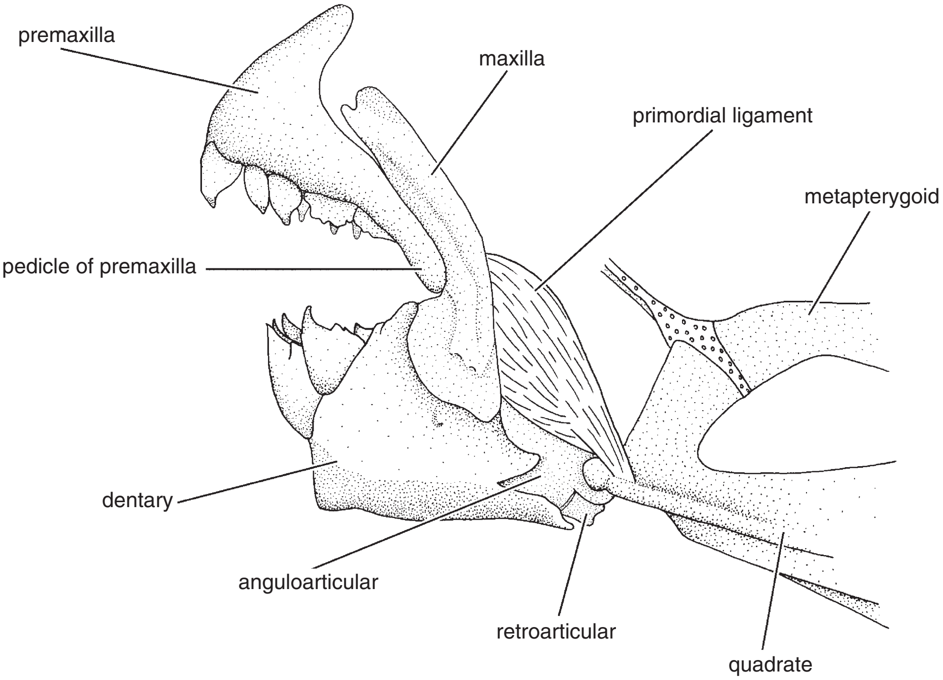

Figure 21. Form of primordial ligament and adjoining bones of *Bryconaethiops microstoma*, USNM 339722, 54.9 mm SL; left side, lateral view.

The common condition of the primordial ligament among the examined outgroup taxa is a relatively narrow connective tissue band attaching to the posteromedial portion of the ascending process of the maxilla, approximately at the level of the horizontal through the area of contact of the anterior surface of the maxilla with the posteroventral corner of the premaxilla. In addition, outgroup characids have a second ligament joining the medial surface of the posterior portion of the maxilla to the posterodorsal border of the dentary. These two ligaments in concert reduce the degree of mobility of the maxilla relative to the lower jaw.

All members of the Alestidae other than *Arnoldichthys*, *Chalceus*, *Clupeocharax*, *Hydrocynus*, *Lepidarchus* and *Tricuspidalestes* have the primordial ligament proportionally more robust than is the condition present in the examined outgroups; a modification reflected in a broader attachment area of the ligament on the maxilla (Fig. 21). In addition, whereas outgroups to the Alestidae have the primordial ligament attaching onto the posteromedial surface of the maxilla, in all members of that family with the exception of these six genera the ligament instead attaches onto a broad area on the posterior half of the maxilla.

Most alestids and outgroups have the area of attachment of the primordial ligament at the level of the posterior limit of the premaxilla. The increased proportional length of the premaxilla resulting from presence of a premaxillary pedicle in nearly all examined alestids shifts the region of attachment of the ligament on the maxilla in those taxa to a more posteroventral position than that typical among characids. This posterior shift of the attachment site furthermore results in a primordial ligament that is distinctly proportionally shorter than is the connective tissue band present in outgroups. Perhaps as a consequence of the resultant close, well-developed connection of the posterior portion of the maxilla to the lateral surface of the anguloarticular, the posterior ligament or mass of connective tissue joining the medial face of the maxilla to the lower jaw is less developed in most alestids than it is in examined Neotropical outgroups.

Arnoldichthys and *Chalceus*, the basal genera in the Alestidae under the final most parsimonious hypothesis of relationships, share the form and area of attachment of the primordial ligament with outgroup characiforms; an apparent retention of the hypothesized plesiomorphic condition under the final phylogenetic scheme arrived at in this study.

In the case of *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes*, the genera attaining the smallest body size within the Alestidae and which are deeply internested in the final phylogeny for the family, the primordial ligament, although more developed than the form of the ligament present in members of the outgroup of that body size, is not as proportionally massively developed as it is in the vast majority of alestids. More significantly, the area of attachment of the primordial ligament on the maxilla in these three genera is on the posteromedial surface of the ossification, a condition comparable to that present in outgroups and contrasting with the situation common to most alestids. Given its area of attachment we code the form of the ligament in *Clupeocharax*, *Lepidarchus* and *Tricuspidalestes* as state 0 for this character, notwithstanding its somewhat greater proportional size.

As noted in preceding character discussions, the species of *Hydrocynus* have the entire upper jaw and its association with the mesethmoid significantly modified. Associated with that restructuring of the jaw is a major revamping of the morphology of the primordial ligament. *Hydrocynus* has a strong, but relatively narrow, primordial ligament (the maxillary-mandibular ligament of Brewster, 1986: 172). This ligament attaches to the anterolateral surface of the ascending process of the maxilla within a small, laterally positioned depression on the anterolateral surface of the maxilla (see also Brewster, 1986: 171, Fig. 5). This morphology of the ligament and its area of attachment are unique to *Hydrocynus* among examined characiforms and this arrangement was proposed by Brewster (1986: 189) to be a synapomorphy for the species of the genus; a hypothesis congruent with our conclusions.

As a consequence of the pronounced modifications of the upper jaw in the outgroup genus *Serrasalmus* it was impossible to unequivocally code this character for that genus and it is coded as unknown.

81. Presence or absence of supramaxilla: (0) absent; (1) present (CI = 100; RI = 100)

According to Fink & Fink (1996: 230), the absence of a supramaxilla, an autogenous ossification situated along the dorsal margin of the maxilla, is a synapomorphy of the Ostariophysi. A supramaxilla has, however, been reported within the Characiformes in *Agoniates ladigesi* Géry by Géry (1962: 278, fig. 7), and in *Chalceus* and *Chilodus* by Roberts (1969: 416). The presence of a supramaxilla was also proposed as a synapomorphy for the members of the Neotropical family Chilodontidae by Vari (1983: 10, fig. 1). In his analysis, Vari reported that he observed a supramaxilla among examined characiforms only in the characid *Chalceus macrolepidotus* outside of the Chilodontidae.

Observations on *Agoniates* by Castro (1984: 80) and in the present study indicate that the genus lacks a supramaxilla, contrary to Géry (1962) who reported the presence of that ossification in the genus. There occur, however, longitudinal striae on the lateral surface of the maxilla of *Agoniates* that might be erroneously interpreted as the division between a maxilla and supramaxilla. Although Zarske & Géry (1997: 174) cite these striae on the maxilla as a 'suture with the former supramaxilla', they provide no evidence, ontogenetic or otherwise, to support the hypothesis of a secondary fusion of the maxilla with a previously autogenous supramaxilla in *Agoniates*.

A supramaxilla is present (Fig. 16) in all five species of *Chalceus* recognized in the most recent revision of that genus (Zanata & Toledo-Piza, 2004: 105) and is general in the Chilodontidae (Vari, 1983: 10). Phylogenetic information (Vari, 1983; Buckup, 1998; Castro & Vari, 2004; this paper) indicates, however, that the Chilodontidae is more closely related to the families Anostomidae, Curimatidae and Prochilodontidae than it is to *Chalceus*. Therefore, the presence of a supramaxilla in the Chilodontidae and *Chalceus* is hypothesized to represent independent acquisitions and possession of the bone is synapomorphic for the species of *Chalceus*.

LOWER JAW

82. Form of dentary symphysis: (0) without bony interdigitating articulations anteriorly; (1) with bony interdigitating symphyseal processes anteriorly (CI = 33; RI = 0)

In various characiforms the contralateral dentaries are joined at the dentary symphysis by a complex, interdigitating, hinge-like complex (Fig. 22) permitting lateral movement of the posterior portions of the lower jaw. This form of dentary symphysis is absent, however, in basal characiform lineages such as the Distichodontidae (represented by *Xenocharax* among the outgroups in this study), Citharinidae, and various more derived characiforms (e.g. *Spintherobolus*, Weitzman & Malabarba, 1999: 11).

Although the highly modified dentaries of the genera *Belonophago*, *Eugnatichthys*, *Mesoborus*, *Microstomatichthyoborus*, *Paraphago* and *Phago* that constitute a clade within the Distichodontidae (Vari, 1979: 268) are conjoined via interdigitations, the processes in these six distichodontid genera are less elaborate than those present in either the Characidae and Alestidae. More significantly, the interdigitations in these distichodontids are positioned at the rear of the expanded area of contact of the dentaries, rather than being situated anteriorly at the symphysis of the lower jaw. These interdigitations consequently serve to immovably conjoin the contralateral dentaries; a much different arrangement in terms of both position and function than the hinge-like symphysis at the anterior to the dentary that is present in many groups in the Characidae and nearly all members of the Alestidae.

A hinge-like dentary symphyseal joint is also absent in other families positioned towards the base of the characiform phylogeny under the hypothesis ad-

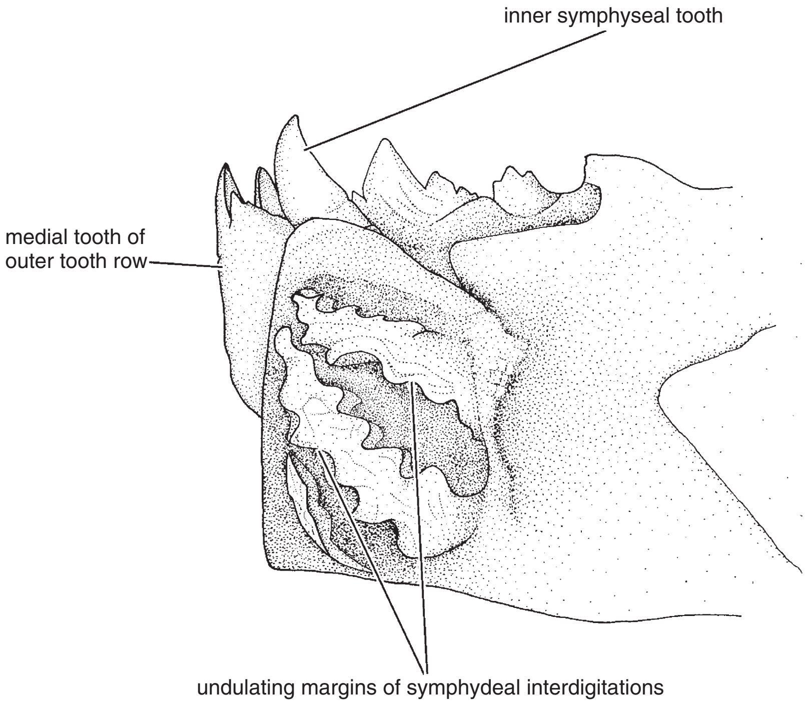

Figure 22. Anterior portion of lower jaw of *Bryconaethiops microstoma*, USNM 339722, 55.1 mm SL; left side, medial view.

vanced by Buckup (1998): the Curimatidae, Prochilodontidae, Chilodontidae and Anostomidae. The lack of a symphyseal dentary hinge is thus hypothesized to be plesiomorphic among characiforms. By contrast, in various characids and all alestids with the exception of *Lepidarchus*, the contralateral dentaries are joined anteriorly via a mobile, interdigitating, hinge-like joint. The particularly complex lower jaw hinge joint characteristic of larger specimens of *Hydrocynus* was illustrated by Eastman (1917: A–C in pl. 84) and was the subject of discussions by Gregory & Conrad (1937: figs 1–3, 6, 7; 1938: figs 19–22).

In the case of the diminutive alestid genus *Lepidarchus*, the extent of symphyseal contact of the contralateral dentaries is significantly smaller than in other alestids and lacks any indication of interdigitating processes joining the dentaries. This makes *Lepidarchus* the only genus in the Alestidae lacking these processes. Among our examined outgroup taxa, we found that dentary interdigitations are also absent in *Hemiodus* and *Xenocharax*.

83. Form of interdigitating processes in symphyseal dentary processes: (0) relatively simple with smooth margins; (1) more complex with undulating subprocesses and scalloped margins (CI = 20; RI = 80)

Although the presence of a hinge formed by interdigitating bony processes at the dentary symphysis occurs within various lineages within the Characiformes including the Alestidae (see character 82), most taxa within the order with such modifications retain relatively simple symphyseal processes with smooth distal margins. In a subset of the Alestidae (*Alestes*, *Brachypetersius altus*, *Brycinus*, *Bryconaethiops*, *Bryconalestes* and *Phenacogrammus urotaenia* (Boulenger) the components of the symphyseal processes are elaborated into an undulating wavy pattern (Fig. 22) that is clearly reflected in the scalloped margin of the hinge elements. In light of the lack of comparable undulations in the hinge elements in all examined outgroup taxa other than in the distantly related Neotropical serrasalmine *Piaractus*, the condition in the alestids listed above is considered a further derived state of the dentary interdigitations. It was impossible to code this character for taxa among alestids (*Lepidarchus*) and outgroups (*Hemiodus*, *Xenocharax*) that lack symphyseal interdigitations joining the contralateral dentaries.

84. Number of dentary teeth: (0) more than four; (1) four (CI = 20; RI = 86)

Although characiforms demonstrate a notable degree of variation in the overall number of teeth on the dentary, outgroups to the Alestidae typically have relatively higher number of teeth (5–43 in the coded outgroup taxa) than do the majority of the members of that family, most members of which have only four, a count that is the apparently primitive condition within the Alestidae.

Exceptions to this generalization within the Alestidae are *Brachypetersius gabonensis* with seven teeth on the dentary, and *B. notospilus* and *Hemmigrammopetersius intermedius* (Blache & Miton) with five. Among the species of relatively smaller body size, *Virilia pabrensis* has five teeth whereas *Clupeocharax* has 12, *Lepidarchus* has 11 and *Tricuspidalestes* has eight. These are apparent reversals to higher numbers of teeth within the context of the final phylogeny. The basal alestid genera *Arnoldichthys* and *Chalceus* also differs from many other members of the Alestidae in having 7–10 and 7–18 teeth on the dentary, respectively.

Although our examined cleared and stained specimens of *Hydrocynus* have six teeth on each dentary making a total of 12 in the lower jaws, Brewster (1986: 193, 196, 198, 201) reported a lower limit of eight teeth in the lower jaw for each species of that genus that she recognized in her study. Such counts, which presumably indicate the presence of only four teeth on each dentary, occur, however, in only 13 of the 278 specimens of *Hydrocynus* reported in Brewster (1986). All other examined specimens cited by Brewster and examined in this study had higher tooth counts that ranged up to a total of 13 teeth in the two jaws in some specimens; this count reflected the presence of at least six teeth on one dentary, presuming a somewhat even distribution of dentition on each part of the lower jaw. As a consequence, we code *Hydrocynus* as having four or more teeth on each dentary (state 0).

The single available cleared and stained specimen of *Ladigesia* from which we could confidently acquire tooth counts had five teeth on one dentary and four on the other; variation rendered unequivocal coding of this feature based solely on that specimen impossible. Géry (1968: 80), however, reported the presence of five teeth in the lower jaw of *Ladigesia*. In light of that information we code *Ladigesia* as has having five dentary teeth. The condition for this character for *Hemiodus* in the outgroup was coded as unknown because of its absence of dentary dentition.

85. Change in relative size of teeth on dentary: (0) dentary teeth approximately of same size along entire series or gradually becoming smaller posteriorly; (1) dentary teeth abruptly becoming smaller posteriorly (CI = 33; RI = 76)

In the majority of taxa examined in this study the posterior teeth on the dentary are either approximately the same size as the anterior teeth, or the teeth in that series gradually decrease in size posteriorly. The possession of posterior teeth that are abruptly smaller relative to the more anterior teeth is unique to a group of characids (*Astyanax*, *Charax*, *Brycon*, *Bryconops*, *Tetragonopterus* and *Triportheus*) among examined taxa.

A distinct disparity occurs between the teeth on the anterior portion of the dentary of *Hoplias* and those on the more posterior regions of that bone. The teeth of disparate size in that genus are, however, components of two different rows of dentition overlapping, in part, towards the posterior limit of the larger tooth series, a condition nonhomologous with that present in the noted characids. The absence of teeth in the lower jaw of *Hemiodus* made it impossible to code that genus for this character.

86. Form of second dentary tooth and relationship of second and third dentary teeth: (0) second and third dentary teeth not overlapping, or if overlapping, the second tooth lacks posterolateral margin inserting into distinct depression on anteromedial surface of third tooth; (1) posterolateral portion of second dentary tooth distinctly overlapping anteromedial portion of third tooth, with portion of second tooth typically inserting into distinct depression on anteromedial surface of third tooth (CI = 50; RI = 94)

Alestes, *Brycinus*, *Bryconaethiops* and *Bryconalestes* have a unique form of enlargement of the second dentary tooth (Fig. 23), with the ossified basal portion of the exposed portion of the fully developed tooth posteriorly expanded within the oral cavity. As a consequence of this modification, the posterolateral region of the basal portion of the second dentary tooth extends to varying degrees posteriorly to overlap the anteromedial portion of the third tooth in that series. This expanded portion of the second tooth, furthermore, typically inserts into a distinct depression on the basal portion on the third tooth in the region where these two teeth overlap.

The sequential dentary teeth in *Alestes macrophthalmus* demonstrate a greater degree of separation than is typical of either congeners or the species of *Brycinus*, *Bryconaethiops* and *Bryconalestes*. As a consequence, although *Alestes macrophthalmus* has a form of the second and third teeth comparable to those present in other taxa, it lacks a distinct overlap of these teeth. Nonetheless, because of the overall similarities of the modifications of these teeth in *A. macrophthalmus* with the condition in its congeners and closely related taxa, we code this species as having the same condition as those taxa. No modifications of the second and third dentary comparable to those present in *Alestes*, *Brycinus*, *Bryconaethiops*, *Bryconalestes* were found in the other examined taxa and we consequently consider those elaborations to be derived.

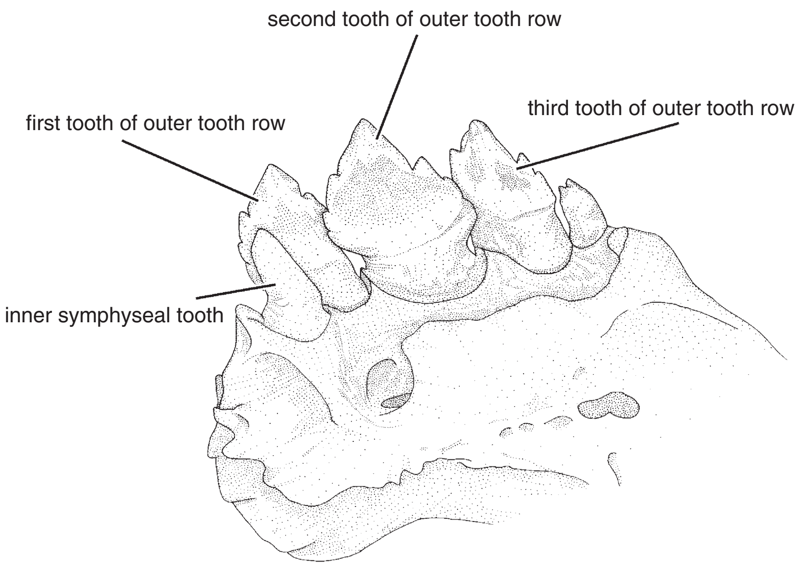

Figure 23. Dentary teeth of *Bryconaethiops microstoma*, USNM 339722, 55.1 mm; inner view.

Our observations of *Petersius conserialis* were limited to entire specimens; a restriction that complicated the coding of this character. Despite that operational limitation, it is clear from our observations that in *P. conserialis* there is a distinct overlap of the posterolateral portion of the second dentary tooth over the anteromedial portion of third tooth in that series, the derived condition. We were unable to determine whether the posterolateral portion of second tooth inserts into a distinct depression on the anteromedial surface of third tooth in these whole specimens and conservatively code this character are unknown for the genus.

If we look at examined outgroup characiforms, we find that the assemblage in which an overlap of the teeth on the dentary is developed to its greatest degree is various members of the Serrasalminae. In *Piaractus* and *Serrasalmus*, the two serrasalmines included in the outgroup analysis, we find, however, that the overlap between the dentary dentition differs from that present in the Alestidae in that the posterior margin of each tooth overlaps the anterior margin of the outer surface of the next tooth in the series (see Machado-Allison, 1983: fig. 5b). As a consequence, the region of overlap between successive teeth as one moves posteriorly along the jaw is on the outer surface of the tooth series in serrasalmines; this arrangement contrasts with that in the Alestidae, in which the region of overlap is positioned along the buccal surface of the dentary tooth series. It was impossible to code the condition of this character in *Hemiodus* because of the lack of dentary dentition in that genus.

87. Form and spacing of dentary teeth: (0) not as in state 1; (1) anterior dentary teeth tri- to pentacuspid and relatively elongate, with borders of teeth, including margins of cusps, running in parallel and with margins of adjoining teeth distinctly separated from each other (CI = 50; RI = 80)

Tooth morphology varies dramatically among different groups of characiforms. The form and spacing of the dentary dentition in *Arnoldichthys* and *Chalceus* is quite distinct from the robust, typically distally expanded teeth found in nearly all other members of the Alestidae and examined outgroup characids. In both *Arnoldichthys* and *Chalceus* the borders of the teeth, including the margins of the outermost cusps, are straight and run in parallel with the margins of the adjoining teeth clearly separated from each other. No comparable combination of form and spacing was observed in other examined characiform groups and the condition characteristic of those genera is consequently considered derived. It was impossible to code this character for *Hemiodus* in light of its absence of dentary dentition.

88. Presence or absence of inner row tooth proximate to dentary symphysis: (0) absent; (1) present (CI = 100; RI = 68)

Characiforms demonstrate a considerable degree of variation in the presence or absence of an inner row of teeth on the dentary and in the degree of development of such teeth, when present. Inner dentary tooth rows of varying degrees of development occur in several Neotropical characiforms (e.g. Lebiasinidae, Weitzman, 1964: 143), various groups in the Alestidae (Poll, 1957: 95) and the Distichodontidae (Vari, 1979: 275–277). When present, the inner dentary row can be represented by a complete row of numerous small teeth or one relatively large unicuspid tooth followed by a diastema and then a posterior row of small teeth. Alternatively, there may be only one tooth positioned proximate to the dentary symphysis (Figs 22, 23) or a posteriorly positioned row of small teeth aligned along the posterior margin of the primary tooth replacement trench of the dentary. Only one of these variants, the presence or absence of a relatively large tooth proximate to the dentary symphysis, is pertinent to the relationships within and of the Alestidae and is coded herein (Appendix 2).

Although the presence or absence of a tooth proximate to the dentary symphysis and internal to the outer tooth row underpins the limits of diverse genera within the African components of the Alestidae (e.g. Paugy, 1990a), the final most parsimonious hypothesis of relationships indicates that such a tooth was acquired and lost several times in the evolution of that family. Furthermore and more significantly, the presence or absence of this symphyseal tooth is in many instances intraspecifically variable. This is aptly demonstrated by the sample of *Brachypetersius gabonensis* analysed herein in which eight specimens have inner symphyseal teeth whereas 12 lack those structures. As a consequence we code the character as '?' for that species.

Such variation in the possession of the symphyseal tooth was reported by Amiet & Nzeyimana (1990: 8) in other species of the Alestidae. In the case of *Phenacogrammus major*, those authors report that only 35% of the examined specimens of that species have the inner dentary teeth present; in *Hemmigrammopetersius pulcher* (Boulenger) they found the inner dentary teeth to be present in only one of 13 examined specimens.

Intraspecific variability concerning the presence vs. absence of the symphyseal dentary teeth raises questions as to the utility of the feature for phylogenetic analyses. Under the final most parsimonious hypothesis of relationships, this character stands, however, as the unique synapomorphy for only a single minor clade within the Alestidae formed by *Alestopetersius* and *Duboisialestes*.

89. Relative size of tooth of inner dentary tooth row:
(0) tooth, when present, large and approximately same height as, or higher than, dorsal limit of symphyseal tooth of outer dentary tooth row; (1) tooth, when present, small and falling distinctly short of dorsal limit of symphyseal tooth of outer row and of approximately same size as lateral cusp of symphyseal tooth (CI = 25; RI = 78)

When present, the single tooth of the inner tooth series of the dentary within the Alestidae assumes one of two relative sizes, being either proportionally large (Figs 22, 23) or small. In those alestid species achieving only relatively small body size, the inner row teeth, when present, are typically proportionally small (Appendix 2). The single exception to this correlation between body size and the relative size of the inner row teeth among examined members of the Alestidae involves *Bryconalestes intermedius*, a species of relatively large body size compared to closely related species but with proportionally small teeth on the inner tooth series of the dentary. Among examined outgroups a relatively small symphyseal tooth also occurs in the Neotropical species *Brycon falcatus* Müller & Troschel. It was impossible to code this feature for the series of ingroup and outgroup taxa that lack an inner row of teeth on the dentary.

90. Replacement tooth trench or crypt in dentary:
(0) present; (1) absent (CI = 50; RI = 0)

The replacement teeth of the dentary in the vast majority of characiforms develop within a replacement trench or crypt situated within the dentary and then shift ontogenetically into their final functional position (see Roberts, 1967a: figs 3, 4). This general characiform condition is similarly present in the vast majority of alestids, whereas *Lepidarchus* (Roberts, 1966: 213) and *Clupeocharax* lack these trenches. The replacement teeth of the lower jaw in these genera develop in the soft tissues overlying the dentary in the region posteroventral to the base of the row of functional dentary teeth rather than in the trenches.

91. Orientation of developing dentary replacement teeth and structure, when present, of replacement tooth cavity in dentary: (0) with replacement teeth approximately in same alignment as functional dentary teeth and with continuous trench or crypt in dentary containing all replacement teeth for outer functional tooth row;
(1) with replacement teeth aligned at distinct angle relative to functional dentary teeth and with replacement teeth enclosed within individual cavities within dentary (CI = 100; RI = 100)

The typical characiform condition is for the replacement teeth of the outer dentary tooth row to develop in proximity to each other, either in a dorsally open replacement tooth trench or in a crypt within the dentary that is pierced dorsally to varying degrees by one or more openings (the gubernacula of Shellis & Berkovitz, 1976: 72). In some characiforms, often those of smaller body size (see character 90), the teeth may alternatively develop in the fleshy covering of the inner surface of the dentary.

The developing replacement teeth among characiforms nearly universally demonstrate approximately the same orientation within the dentary trench or crypt that they assume when functional. In the species of *Hydrocynus*, however, the dramatically enlarged lower jaw teeth typical of the genus (Fig. 3) are isolated in individual cavities within the dentary (the replacement cavities of Brewster, 1986: 171), with both the cavities and the contained teeth distinctly posteriorly angled relative to the approximately vertical orientation of the functional teeth in the closed lower jaw (see Fig. 3, also Eastman, 1917: A, B in pl. 84; Gregory & Conrad, 1937, fig. 1; Gayet *et al.*, 2003: fig. 9B).

Although some other characiforms have the dentary replacement teeth positioned such that their tips are clearly posteriorly directed (e.g. Cynodontidae, Toledo-Piza, 2000: 35; Hepsetidae) or posteromedially directed (Ctenoluciidae), the teeth in these outgroups are all situated within a continuous, undivided replacement tooth trench. The combination of the posterior orientation of the replacement teeth within the dentary replacement trench and the subdivision of the primitively continuous trench into a series of individual chambers for each replacement tooth is unique to the species of *Hydrocynus* among characiforms. Brewster (1986: 189) appropriately utilized the presence of the series of replacement cavities within the dentary as a synapomorphy for the species of *Hydrocynus*; however, here we incorporate that feature into a more encompassing character detailed above.

Various outgroup taxa with a dentary replacement tooth crypt have a series of openings (gubernacula) between the chamber within that bone and the oral surface of the lower jaw, but in nearly all such instances these apertures enter into a single cavity within the dentary. The single observed exception to that generalization involves the Neotropical genus *Charax*, all members of which have individual dentary replacement tooth cavities. Such individual cavities are, however, restricted to the anterior portion of the dentary, a condition that is significantly different from the morphology of the chambers present in *Hydrocynus*, which has separate replacement cavities along much of the length of the dentary. Furthermore, the replacement tooth cavities and their contained teeth in *Charax* retain the same orientation as that of the functional teeth in the dentary (i.e. nearly vertical). That alignment differs considerably from the condition in *Hydrocynus* in which the replacement teeth (and trenches) lie at a distinct posterior angle relative to the axis of the functional teeth.

The result is a replacement tooth system in the dentary of *Charax* that differs in numerous, often significant, details from the morphology of the replacement tooth cavities in *Hydrocynus.* The two systems are thus hypothesized to be nonhomologous. *Clupeocharax* and *Lepidarchus* could not be coded for this feature as a consequence of the lack of dentary replacement tooth trenches in those genera.

92. Site of attachment on dentary of main portion of tendon from adductor mandibulae muscle: (0) located midway along horizontal length of lower jaw, distant from posterior wall of replacement tooth trench, and close to ventral margin of dentary; (1) located on posterior wall of replacement tooth trench and distinctly dorsal to ventral margin of dentary (CI = 100; RI = 100)
The tendon extending anteriorly from the adductor mandibulae (*sensu* Winterbottom, 1974) is typically subdivided anteriorly into two sections among examined characiforms. These subunits are a lateral component inserting on the coronomeckelian bone and a more anteroventrally directed and typically larger medial, tendonous band attaching to the medial surface of the dentary. This morphology of the tendon from the adductor mandibulae occurs among the examined taxa in both outgroup characids and in many alestids. In the anteroposteriorly foreshortened lower jaw that is characteristic of the assemblage consisting of *Alestes*, *Brycinus* and *Bryconaethiops*, the area of attachment of the medial band of the tendon is shifted dorsally onto the posterior surface of the replacement tooth trench. The insertion site of the tendon is, furthermore, within a variably developed pocket on the posterior wall of the replacement trench. These modifications of the site of attachment of the tendon from the adductor mandibulae are unique to *Alestes*, *Brycinus* and *Bryconaethiops* among examined characiforms.

93. Position of articulation between angulo-articular and quadrate: (0) situated posterior to vertical through ventral tip of lateral process of lateral ethmoid; (1) situated anterior to, or along, vertical through ventral tip of lateral process of lateral ethmoid (CI = 33; RI = 91)
The position of the articulation between the quadrate and lower jaw relative to the vertical extending through the tip of the lateral process of the lateral ethmoid varies within characiforms, with the relative location of the articulation typically correlated with the overall length of the lower jaw and relative position of the mouth (superior, terminal, or inferior). In basal groups within the Characiformes, the articulation between the angulo-articular and quadrate is often situated distinctly posterior to the vertical through the tip of the lateral process of the lateral ethmoid (e.g. *Xenocharax*).

The common condition within the Alestidae, with the exception of *Arnoldichthys*, *Chalceus*, *Hydrocynus* and *Lepidarchus*, is for the articulation between the quadrate and lower jaw to be positioned anterior to, or along, the vertical through the tip of the lateral process of the lateral ethmoid. *Arnoldichthys* and *Chalceus*, the basal genera in the Alestidae, share the posterior position of the articulation common to many outgroups and given their phylogenetic placement in the final phylogeny, it is most parsimonious to assume that these genera retain the generalized outgroup condition. In *Hydrocynus* and *Lepidarchus*, the lower jaw is proportionally longer than that present in other alestids, with the elongation of the jaws apparently accommodated, at least in part, by the posterior shift of the point of articulation of the quadrate with the angulo-articular in each genus. Proportional elongation of the lower jaw does not invariably result in a shift of this point of articulation of the quadrate and angulo-articular to a relatively more posterior portion within the Alestidae.

Clupeocharax and *Tricuspidalestes*, although both possessing proportionally long dentaries relative to those in other members of the Alestidae other than *Hydrocynus* and *Lepidarchus* (see above), nonetheless, still retain the anterior position of the articulation between the lower jaw and quadrate relative to the lateral process of the lateral ethmoid. The only taxon among examined outgroups with an anterior position of the articulation was *Triportheus*.

PALATINE ARCH

94. Presence or absence of ossified palatine: (0) present; (1) absent (CI = 100; RI = 100)

An ossified palatine is nearly universally present across the Characiformes. All examined cleared and stained specimens of *Lepidarchus*, in contrast, lack an ossified palatine although they do possess a distinct cartilage body at the anterior terminus of the ectopterygoid that is presumably homologous with the ossified palatine located in that position in other characiforms.

In his description of the osteology of *Lepidarchus adonis*, Roberts (1966: fig. 5) illustrated an ossified palatine in a specimen of the genus of an unspecified size. Roberts (1966: 212) did, however, note that the osteological description was based on three cleared and stained paratypes of *L. adonis*, with the largest paratype of the species cited by Roberts (1966: 210) as being 20.4 mm SL, approximately the same size as the largest of the cleared and stained specimens examined for this study (19.1 mm SL). Even if an ossified palatine is present in specimens of *Lepidarchus* of a larger size than those examined in this study, the bone in that genus clearly ossifies relatively late in ontogeny compared to the situation in cleared and stained specimens of other alestids, a derived condition in its own right. An osteological examination of additional specimens of *L. adonis* is necessary to resolve the apparent inconsistency between the lack of an ossified palatine in the material of the genus examined in this study and the reported presence of such an ossification in *Lepidarchus* by Roberts (1966).

95. Form of posterolateral margin of palatine: (0) without posteroventral process extending along anterodorsal portion of ectopterygoid; (1) with posteroventral process extending along anterodorsal portion of ectopterygoid (CI = 50; RI = 50)

The presence of a posteroventral process of the palatine extending along the anterodorsal portion of the ectopterygoid was limited to *Micralestes acutidens*, *M. elongatus* and *M. lualabae* among taxa examined in this study. It was impossible to code the condition of this character for *Lepidarchus* because of the absence of an ossified palatine in that genus.

96. Area of articulation of palatine on neurocranium: (0) palatine articulates with lateral margin of vomer; (1) palatine articulates with anterolateral margin of vomer and posterolateral margin of mesethmoid (CI = 100; RI = 100)

Outgroups to the Alestidae have the cartilaginous anteromedial articular portion of the palatine articulating with a corresponding articular surface on the anterolateral surface of the vomer. All examined members of the Alestidae, with the exception of *Arnoldichthys*, *Chalceus* and *Hydrocynus*, have the articulation of the palatine with the neurocranium situated proximate to a cartilage body that is positioned further anteriorly at the lateral margin of the region of articulation between the vomer and mesethmoid. This anterior position of the area of articulation of the palatine on the neurocranium is considered derived in light of its absence in outgroups. *Lepidarchus* lacks an ossified palatine and as a consequence it was impossible to code this character for that genus.

97. Relative extent of area of contact of ectopterygoid with palatine: (0) broad, with anterior portion of ectopterygoid as wide as proximate portion of palatine; (1) narrow, with anterior portion of ectopterygoid usually half as wide as proximate portion of palatine (CI = 33; RI = 87)

Typically, in examined outgroups to the Alestidae the anterior portion of the ectopterygoid is relatively broad and as wide as the proximate posterior portion of the palatine. In members of the Alestidae, with the exception of *Clupeocharax* and *Tricuspidalestes,* the anterior portion of the ectopterygoid is proportionally narrower, with its area of attachment with the palatine limited to the ventrolateral half of the proximate

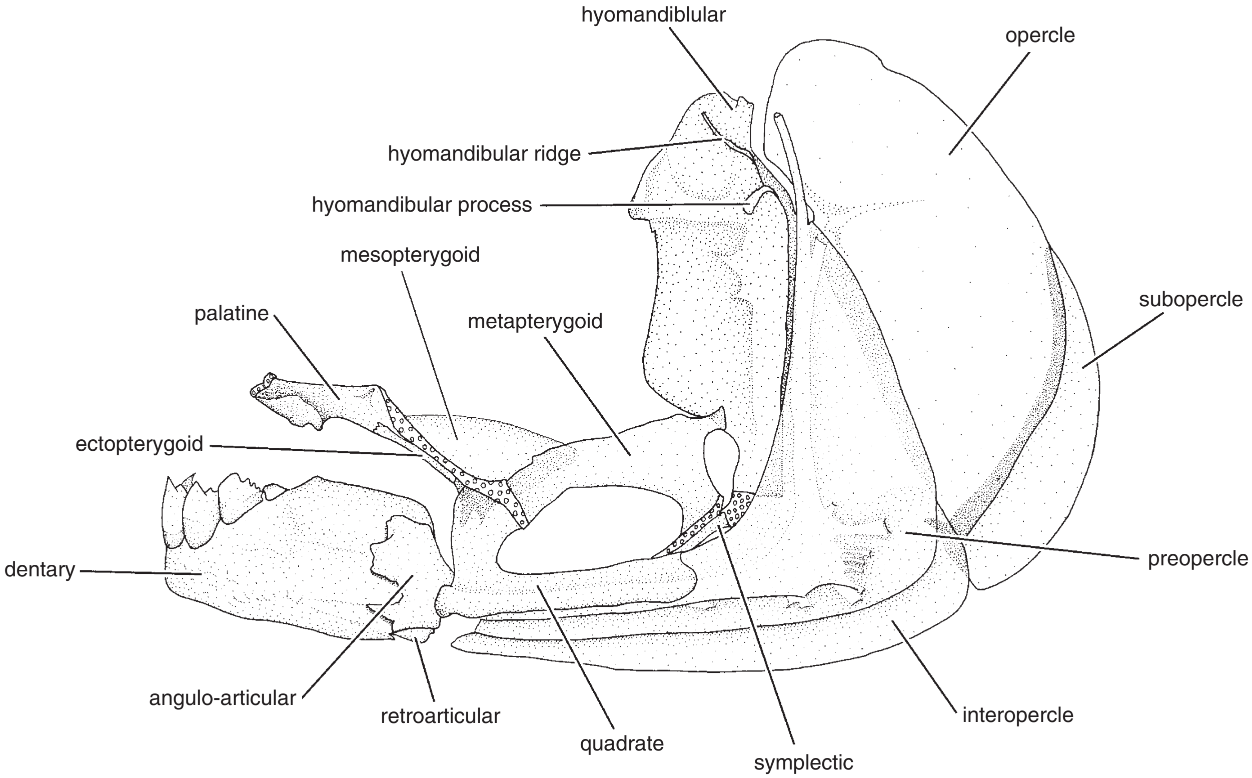

Figure 24. Lower jaw, suspensorium, and opercular apparatus of *Brycinus nurse*, USNM 339724, 104.4 mm SL; left side, lateral view.

portion of the ectopterygoid (Fig. 24). By contrast, in both *Clupeocharax* and *Tricuspidalestes*, there are broad areas of contact of the ectopterygoid with the palatine, notwithstanding the fact that the palatine itself is proportionally narrower in these genera than it is in other examined alestids. Nonetheless, the ectopterygoid in *Clupeocharax* and *Tricuspidalestes* is proportionally wider than is the form of the bone present in other alestids and the condition in both of these two genera is thus coded as state 0.

Coding of the state of the ectopterygoid–palatine articulation in the diminutive alestid *Lepidarchus* is complicated by the lack of an ossified palatine in all examined cleared and stained specimens of that genus (see discussion in character 94). Although this makes a direct comparison of the proportional width of the anterior portion of the ectopterygoid with that of the palatine in *Lepidarchus* impossible, the anterior portion of the ectopterygoid present in that genus is clearly proportionally quite narrow. The ectopterygoid is furthermore comparable in overall form to the ossification present in other alestids, in which the anterior portion of the bone is narrower than the palatine. We consequently code *Lepidarchus* as having the derived condition of the ectopterygoid typical of most alestids (state 1).

An ectopterygoid that is narrower anteriorly than the rear portion of the palatine was found in *Crenuchus* and some, but not all, of the examined species of *Triportheus* among examined Neotropical characiform outgroups. Although the ectopterygoid in both *Crenuchus* and *Triportheus* lacks an anterior margin completely overlapping the posterior margin of the palatine, as is the case in many characiforms, that ossification is, nonetheless, wider anteriorly than the condition nearly universal within the Alestidae. The condition in *Crenuchus* and *Triportheus* is thus coded as state 0 for this character.

98. Size and form of ectopterygoid: (0) ectopterygoid not as in state (1); (1) ectopterygoid relatively short but transversely wide with overall ovoid form, and falling short of anterodorsal margin of palatine (CI = 100; RI = 100)

In her discussion of the ectopterygoid of *Hydrocynus*, Brewster (1986: 175, 190) noted that this ossification in that genus was a relatively short, disk-shaped bone. In her analysis she utilized its shortness, but not its shape, as a synapomorphy for the species of the genus (relative shortness but not shape of the bone illustrated by Brewster, 1986: fig. 8).

We concur with Brewster that the shortening of the ectopterygoid is a derived condition within the context of our outgroup studies, but also discovered that varying levels of reduction of the ossification occur across the more encompassing samples of the Alestidae examined in this study. This variation makes it impossible to unambiguously define character states of the ectopterygoid based solely on its relative length. Our analysis indicates, nonetheless, that the combination of a short, relatively wide ectopterygoid with an overall somewhat ovoid form is unique to *Hydrocynus* among examined taxa and such a form of the bone is thus hypothesized to be synapomorphic for the members of the genus.

99. Presence or absence of ligamentous attachment of ectopterygoid to neurocranium: (0) present; (1) absent (CI = 100; RI = 100)
Diverse examined outgroup characiforms have a connective tissue band attaching the ectopterygoid to the ventrolateral portions of either the vomer or mesethmoid. All of the examined members of the Alestidae lack such a ligamentous attachment of the ectopterygoid to the ventral region of the anterior portion of the neurocranium; a hypothesized derived condition.

100. Area of attachment on neurocranium of ligament extending from anterodorsal portion of suspensorium to anteroventral portion of neurocranium: (0) attachment located on ventral surface of main body of vomer and distinctly medial to lateral margin of that bone; (1) attachment located more anteriorly than in state 0 and situated in region of lateral margin of vomer along area of articulation of vomer and mesethmoid (CI = 100; RI = 100)
Many characiforms have a ligament arising from the anterodorsal portion of the mesopterygoid or jointly from the mesopterygoid plus ectopterygoid. This ligament extends anterodorsally to an attachment on the ventral portion of the main body of the vomer at a location that is distinctly separated from both the anterior and lateral margins of that bone. In all members of the Alestidae, with the exception of *Arnoldichthys* and *Chalceus*, this ligament has a distinctly more anterolaterally positioned area of attachment onto the cranium either on the lateral margin of the region of articulation between the vomer and mesethmoid or solely on the mesethmoid. In *Arnoldichthys* and *Chalceus* the area of attachment of the ligament on the cranium is comparable to that present in examined outgroups (state 0), a condition that within the context of the final phylogeny presumably reflects the retention of the plesiomorphic condition.

In the species of *Hydrocynus*, alternatively, the mesopterygoid is posteriorly positioned relative to its location in other alestids (see Brewster, 1986: fig. 8; the endopterygoid of that author). A possible consequence of this posterior shift is the absence in the examined species of *Hydrocynus* of a continuous ligament extending anteriorly from the mesopterygoid to the vomer and/or mesethmoid. Species of *Hydrocynus* have instead a complex of ligaments in this region between the mesopterygoid and neurocranium.

The first of these is a prominent connective tissue band extending from the mesopterygoid to the medial surface of the palatine. The second extends from the palatine to the lateral margin of the vomer in the area of the articulation of the vomer and mesethmoid. This second band retains the same orientation as the ligament between the mesopterygoid and neurocranium that is present in all other alestids other than *Arnoldichthys* and *Chalceus*. Because of the locations of these two ligaments and the area of attachment of the connective tissue bands on the neurocranium, these ligaments in *Hydrocynus* are considered in sum to represent the homologue to the single ligament present in that region in most other members of the Alestidae. *Hydrocynus* is consequently coded as having state 1 for this character.

101. Area of attachment on suspensorium of ligament extending from anterodorsal portion of suspensorium to anteroventral portion of neurocranium: (0) attachment onto anterodorsal margin of mesopterygoid or of mesopterygoid and ectopterygoid; (1) attachment primarily onto medial region of anterodorsal portion of palatine, with small area of attachment on anterodorsal portion of mesopterygoid (CI = 100; RI = 100)
In the majority of alestids and also typically among examined outgroups, the ligament extending from the anterodorsal region of the suspensorium to the anteroventral portion of the neurocranium arises (1) from the suspensorium along the anterodorsal region of the mesopterygoid, or (2) in common from the proximate dorsal surfaces of the mesopterygoid plus ectopterygoid. In the species of *Hydrocynus*, the ligament instead arises primarily from the dorsomedial margin of the palatine, albeit with a limited amount of associated connective tissue extending posteriorly from the main body of the ligament to the anterodorsal margin of the somewhat posteriorly repositioned mesopterygoid (see Brewster, 1986: fig. 8; the endopterygoid of that figure). Although the ligament in *Hydrocynus* attaches primarily to the palatine rather than to the mesopterygoid or to the mesopterygoid plus ectopterygoid as is the case in outgroups, this connective tissue band in *Hydrocynus* is considered homologous with that present in other alestids

because of its position, function and similar area of attachment anteriorly to the anteroventral portion of the neurocranium.

102. Form of metapterygoid-quadrate fenestra and degree of contribution of symplectic to border of that opening: (0) not as in state 1; (1) metapterygoid-quadrate fenestra longitudinally elongate with longest axis aligned along horizontal axis of body and with extensive gap between posteroventral process of posterior portion of metapterygoid and posterodorsal process of quadrate, and with dorsal border of symplectic consequently forming major portion of posteroventral border of fenestra (CI = 50; RI = 95)

The metapterygoid-quadrate fenestra, a typically large aperture within the central portion of the suspensorium of characiforms, assumes a number of shapes across the order but often has a rounded overall form. In the majority of examined characiform taxa the fenestra is bordered solely by the metapterygoid and quadrate as a consequence of the proximity of the anteroventral terminus of the posterior portion of the metapterygoid and the posterodorsal process of the quadrate, hence the name of the opening.

In the Alestidae, with the exception of *Chalceus* and *Hydrocynus*, the metapterygoid-quadrate fenestra is anteroposteriorly elongate (Fig. 24) relative to its form in outgroups. More significantly, most alestids have the terminus of the anteroventral portion of the metapterygoid along the posteroventral margin of the fenestra located some distance from the posterodorsal process of the quadrate. As a consequence of the resultant separation of those proximate processes of the quadrate and metapterygoid, the symplectic now forms a significant portion of the posteroventral border of the fenestra. An anteroposteriorly elongate fenestra was previously reported by Lucena (1993) for *Alestes leuciscus* and *Hemmigrammopetersius rhodesiensis*.

Chalceus has a form of the metapterygoid-quadrate fenestra that is comparable to that in the examined outgroups. This represents a presumed retention of the plesiomorphic condition under the final most parsimonious hypothesis of relationships. In the case of the species of *Hydrocynus* the overall form of the suspensorium is apparently altered as part of the series of modifications associated with the dramatically restructured jaws, in particular the proportionally elongate lower jaw. This may account for the realignment of the longest axis of the fenestra in that genus to a posterodorsal orientation. Nonetheless, the overall form of the fenestra in *Hydrocynus* is rotund rather than distinctly anteroposteriorly elongate (see Brewster, 1986: fig. 8) and as such we code the genus as having state 0 for this character.

Looking at the outgroups we find that various aspects of the complex form of the metapterygoid-quadrate fenestra characteristic of nearly all members of the Alestidae occur in some nonalestid taxa, but also that none of these outgroups demonstrate the combination of all of the attributes of state 1. Although a horizontally elongate fenestra is present in the Hemiodontidae, the members of that family lack the pronounced gap between the processes of the metapterygoid and quadrate, resulting in the symplectic delimiting a significant portion of the border of the fenestra. The fenestra in *Triportheus*, although somewhat elongate, is, however, posterodorsally inclined contrary to being horizontally aligned as is the case in most alestids. Furthermore, the contribution of the symplectic to the border of the fenestra is correlated with the vertical expansion of the posterior portion of the symplectic in the species of *Triportheus*, a different condition than that which is present in any species of the Alestidae.

MANDIBULAR ARCH

103. Presence or absence of ridge on lateral surface of hyomandibular: (0) lateral surface of dorsal portion of hyomandibular unelaborated; (1) lateral surface of dorsal portion of hyomandibular with ridge or distinct lateral process (CI = 20; RI = 80)

The lateral surface of the hyomandibular lacks distinct processes in the majority of characiforms. Nearly all alestids, in contrast, have a distinct ridge or process in the region between the area proximate to the dorsal articular surface of the hyomandibular and the posterior margin of that ossification in the vicinity of the articular condyle for the opercle (Fig. 24).

The elaboration of that region of the hyomandibular among alestids takes a variety of forms that range from a relatively elongate ridge, through a shorter ridge, to a relatively small, discrete process. Regardless of their form, these elaborations of the hyomandibular all function as an attachment area for a portion of the adductor mandibulae muscle. The effective continuum in the degree of development of these elaborations on the lateral surface of the hyomandibular makes it impossible to unambiguously parse this variation into more than one character. We consequently code only the presence or absence of some such elaborations on that region of the hyomandibular regardless of the degrees of development of the structures.

Although common to the majority of alestids, such processes on the hyomandibular are, however, absent in *Bathyaethiops*, *Chalceus*, *Hydrocynus* (see also comments in the next paragraph), *Ladigesia* and *Lepidarchus*. *Chalceus*, the basal lineage of the Alestidae under the final most parsimonious hypothesis of relationships, shares the condition of the hyomandibular common to many outgroups and the lack of the process on the bone in that genus apparently represents the retention of the plesiomorphic outgroup condition. The absence of the process on the hyomandibular in *Bathyaethiops*, *Ladigesia* and *Lepidarchus* is hypothesized to be a secondary loss of the structure within the context of the overall most parsimonious hypothesis of relationships. This loss is perhaps correlated with the relatively diminutive body size of these three taxa and the correlated reduction in the degree of ossification of many components of the skeleton.

Further comment is appropriate as to the condition of this portion of the hyomandibular in *Hydrocynus*. Although the species of *Hydrocynus* have a distinct spine on the lateral surface of the hyomandibular (see character 104 and Brewster, 1986: fig. 8), it is located distinctly anterior to the position of the ridge or associated process present in that region in most other members of the Alestidae. This difference in position casts doubt on the homology of the spine in *Hydrocynus* vs. the structures present in that region of the hyomandibular in many other alestids and we consequently code the character as '?' for *Hydrocynus*. Hyomandibular ridges comparable to those present in most alestids are present in *Xenocharax* and *Crenuchus* in the examined outgroups.

104. Presence or absence of hyomandibular spine:
(0) absent; (1) present (CI = 100; RI = 100)
In her discussion of the hyomandibular, Brewster (1986: 174, 189, fig. 8; synapomorphy 17) noted that all species of *Hydrocynus* possess a distinct, laterally directed process located on the dorsolateral portion of the hyomandibular. She termed this structure the hyomandibular spine and identified it as a synapomorphy for the species of the genus. Our observations confirm both the unique nature of this process among examined taxa and its derived nature (see also comments in character 103).

105. Presence or absence of process on ridge on lateral surface of hyomandibular: (0) absent; (1) present (CI = 20; RI = 55)
A diversity of species in the Alestidae have a distinct ridge on the lateral surface of the dorsal portion of the hyomandibular (see character 103). In a subset of these taxa (various species of *Brycinus*, *Phenacogrammus* and *Nannopetersius*, see Appendix 2) the ridge bears a laterally directed process (Fig. 24) extending distinctly beyond the margin of the main body of the ridge at a level somewhat dorsal to the horizontal through the articular condyle of the opercle. The process on the lateral surface of the hyomandibular that serves as an area of attachment for various connective tissue bands was not present in any other examined taxa and its presence is consequently hypothesized to be derived.

PREOPERCLE AND SUPRAPREOPERCLE

106. Presence or absence of ossified portion of laterosensory canal dorsal to main body of preopercle:
(0) present; (1) absent (CI = 33; RI = 60)
Numerous characiforms have an ossified tube, the suprapreopercle, extending between the dorsal limit of the laterosensory canal segment within the main body of the preopercle and the laterosensory canal system in the neurocranium. Within the examined members of the Alestidae, this tube either assumes the form of an ossification which is independent of (*Arnoldichthys*) or continuous with (most other examined alestids) the main portion of the preopercle. Such an extension of the laterosensory canal system as an ossified tube above the main body of the preopercle is absent in *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*. This absence of the ossified suprapreopercle is hypothesized to be derived within the context of the overall most parsimonious hypothesis of relationships.

A tubular ossification in the region usually occupied by the suprapreopercle is absent in *Crenuchus* and *Hoplias* among outgroups examined for this analysis, albeit with the suprapreopercle also absent in various other characiforms. *Hoplias* has, however, a laminar bone in the region between the preopercle and lateral margin of the neurocranium that Roberts (1969: fig. 3) homologized with the suprapreopercle. This laminar ossification in *Hoplias*, however, lacks a laterosensory canal system and is of a totally different overall morphology than the form of the suprapreopercle of other components of the Otophysi. As such, the homology of the laminar ossification in *Hoplias* with the tubular suprapreopercle present in some other characiforms is questionable.

107. Position of suprapreopercle relative to opercle:
(0) suprapreopercle not extending over anterodorsal portion of opercle; (1) suprapreopercle extending over anterodorsal portion of opercle (CI = 50; RI = 90)
In various examined outgroups, the suprapreopercle, when present, passes anterior to the anterodorsal margin of the opercle. In *Brycon pesu*, *Hemiodus* and *Hepsetus* and in the Alestidae, however, the dorsal portion of the preopercular canal or suprapreopercle, when present, extends over the anterodorsal portion of the opercle (Fig. 24). This character cannot be coded within the Alestidae for *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, all of which lack a continuation of the preopercular laterosensory canal

system beyond the dorsal margin of the main body of that bone. Among outgroups, this character could not be coded for *Crenuchus* that lacks a suprapreopercle and for *Hoplias* that has a bone of uncertain homology and without a sensory canal segment situated dorsal to the preopercle (see comments in character 106).

108. Position of laterosensory canal segment in vertical arm of preopercle: (0) canal segment distinctly separated from anterior margin of vertical arm of preopercle and from posterior margin of hyomandibular and not overlapped by posterior margin of third and fourth infraorbitals even when those ossifications are well-developed; (1) canal segment located proximate to, or along, anterior margin of vertical arm of preopercle and near to, or sometimes overlapping posterior margin of hyomandibular and overlapped by posterior margins of third and fourth infraorbitals other than when these latter ossifications are proportionally reduced (CI = 25; RI = 82)

In all examined taxa of the Alestidae, with the exception of *Chalceus*, the laterosensory canal segment in the preopercle is more anteroventrally angled than is the case with that system in most examined outgroups. This realignment of the canal within the Alestidae is reflected both in the reduction in the distance between the anterior margin of the vertical arm of the preopercle and the anterior margin of the canal and in the decreased separation of the canal from the posterior margin of the hyomandibular. Associated with the anterior shift of this portion of the laterosensory canal in the preopercle of these taxa is an increased degree of overlap of the canal laterally by the posterior portions of the third and fourth infraorbitals in all of those groups which have those bones fully developed.

Although the majority of taxa in the Alestidae, other than *Chalceus*, clearly demonstrate state 1, the evaluation of the state of the character in a subset of the Alestidae is complicated by restructurings in the form of the anterior margin of the dorsal portion of the preopercle and/or by the variation in the degree of the posterior development of the third and fourth infraorbitals. These complications are discussed in the following paragraphs.

In *Clupeocharax* and *Lepidarchus*, the third and fourth infraorbitals are proportionally posteriorly less developed than is the case for those ossifications in their proximate groups under the final phylogeny. As a consequence, these infraorbitals fail to overlap the laterosensory canal segment running through the vertical portion of the preopercle. The orientation of the laterosensory canal segment in the vertical portion of the preopercle in *Clupeocharax* and *Lepidarchus*, nonetheless, corresponds to that of most other examined taxa in the Alestidae and these two genera are consequently coded as having state 1.

Ladigesia, another diminutive alestid characterized by proportionally small third and fourth infraorbitals, also possesses the derived anteroventral orientation of the canal in the preopercle. In addition, although smaller individuals of *Ladigesia* lack the overlap of the preopercular canal by the posterior portions of the infraorbitals, at least the posterior portion of the third infraorbital in the largest cleared and stained specimen does overlap the canal. *Ladigesia* is consequently coded as having state 1.

In species of *Hydrocynus* the overall form of the preopercle is highly modified relative to the morphology of that bone characteristic of most other alestids, with the restructuring probably associated with the dramatically modified jaws of the genus. Notwithstanding the alterations of the preopercle as a whole, the species of *Hydrocynus* demonstrate the basic alestid form of the position of the laterosensory canal in the vertical portion of the preopercle and also have an overlap of that canal segment by the third and fourth infraorbitals. *Hydrocynus* is consequently coded as having state 1 for this character. Looking at the outgroups, we find that *Hemiodus*, *Hoplias* and *Triportheus* also have forms of the laterosensory canal segment in the vertical arm of the preopercle that are herein considered equivalent to state 1.

HYOID ARCH

109. Presence or absence of basihyal tooth plate: (0) anterior portion of basihyal partially covered dorsally by basihyal tooth plate, an independent plate-like ossification; (1) anterior portion of basihyal not overlapped dorsally by basihyal tooth plate (CI = 50; RI = 88)

The basihyal tooth plate is a plate-like ossification overlying the cartilage continuous with and located anterior to the ossified portion of the basihyal. This tooth plate, when present, extends posteriorly to overlap at least the anterior region of the ossified portion of the basihyal (e.g. Prochilodontidae, Vari, 1983: fig. 22).

The possession of a basihyal tooth plate is broadly distributed across the Characiformes and is present in all examined species of the Alestidae (the condition could not be determined in *Petersius*). A basihyal tooth plate is present in *Hepsetus*, *Triportheus*, *Xenocharax* and *Hoplias* among outgroups in this study [NB: although Roberts (1969: 421, fig. 35) reported that *Hoplias* has an anteriorly expanded basihyal with a broadly rounded margin, our specimens demonstrate two components in what that author evidently identified as a single bone, a ventrally positioned slightly anteriorly expanded basihyal and a dorsally situated, distinctly anteriorly expanded basihyal tooth plate].

110. Presence or absence of fossa on anterior ceratohyal receiving the head of the third branchiostegal ray: (0) absent; (1) present (CI = 100; RI = 100)
Brewster (1986: 178) noted that the head of the third branchiostegal ray in the species of *Hydrocynus* articulates with the anterior ceratohyal (= the anterohyal of that author) via a distinct fossa that is situated on the lateral surface of the anterior ceratohyal. This fossa was illustrated, although not labelled, by Brewster (1986: fig. 12) for *H. forskahlii*. Our analysis found that the presence of this form of fossa on the anterior ceratohyal is unique to the species of *Hydrocynus* not only within the Alestidae but also among examined outgroups; the presence of that depression is consequently considered to be derived.

111. Presence or absence of foramen on the posterodorsal portion of the anterior ceratohyal: (0) absent; (1) present (CI = 100; RI = 100)
In the majority of the examined characiforms the anterior portion of the hyoid arch has an anteriorly positioned foramen delimited anteriorly by the ventrohyal and posteriorly by the dorsohyal. The aperture is the anterior limit of a canal that continues posteriorly as a passage through the body of the dorsohyal and into the posterior ceratohyal where it exits the bone by way of a prominent opening. This combined canal system extending through these bones apparently serves for the passage of blood vessels and/or nerves.

Among some of the characids examined in this study (*Astyanax*, *Charax*, *Cheirodon* and *Tetragonopterus*), the apparently primitively present middorsal portion of the anterior ceratohyal appears to be variably eliminated with a consequent exposure of the dorsal portion of the canal, a unique and apparently derived condition. The presence of this additional foramen on the dorsal surface of the anterohyal was previously proposed as a potential synapomorphy for at least a component of the Tetragonopterinae (*Astyanax*, *Bryconamericus*, *Piabina* and *Creagrutus*) by Castro (1984: 98). That polarity hypothesis is congruent with the conclusions of this study.

112. Number of branchiostegal rays: (0) five; (1) four; (2) three (CI = 50; RI = 50)
In his survey of branchiostegal rays across a vast expanse of fish groups, McAllister (1968: 68, 176) noted that there was a range of three to five rays within the Characiformes (the Characoidei of McAllister, 1968) and proposed that a higher number was the plesiomorphic condition within the order. Roberts (1969: 422) reported that the majority of characiforms have four branchiostegal rays on each side, a value confirmed in most of the outgroup taxa examined in this study.

Outgroup comparisons in the present study have, however, found five rays to be present in *Crenuchus*, *Hemiodus*, *Hepsetus*, *Hoplias* and *Piaractus*, and that number has also been reported among Neotropical characiforms for *Characidium fasciatum* Reinhardt (Buckup, 1992: 1069), *Thoracocharax* (Weitzman, 1960: 241) and the members of the Cynodontidae (Toledo-Piza, 2000: 32).

The vast majority of examined species of the Alestidae have four branchiostegal rays on each side with three rays present within that family solely in *Ladigesia*, an apparent autapomorphy for the genus within the context of the overall most parsimonious hypothesis of relationships arrived at herein. This reduction in the number of branchiostegal rays was utilized, with qualifications, by Géry (1968: 81) to distinguish *Ladigesia* from other alestids.

113. Degree of development of lateral lamellae of urohyal: (0) lamellae reduced or absent; (1) lamellae present and well-developed (CI = 14; RI = 25)
In most of the examined species within the Alestidae and outgroups the main body of the urohyal is tripartite in cross-section, with one dorsally directed medial wing and a ventrolaterally directed process on each side. Within the Alestidae these ventrolateral processes of the urohyal are proportionally distinctly reduced in *Clupeocharax*, *Lepidarchus*, *Phenacogrammus major* and *Tricuspidalestes* relative to their degree of development in other members of the family. Looking at the examined outgroups, we find that in both *Crenuchus* and *Hepsetus* the ventrolateral process on each side of the urohyal is absent and that in *Charax*, *Astyanax* and *Tetragonopterus* these processes are significantly reduced.

WEBERIAN APPARATUS

114. Position of anterior tip of transverse process of third vertebra: (0) falling short of, or just extending past, posteroventral margin of scaphium; (1) extending distinctly over scaphium, or if transverse process more anterodorsally orientated, then positioned along vertical running through main body of scaphium (CI = 20; RI = 88)
Fink & Fink (1981: 329) and Vari (1995: 27) discussed the presence and phylogenetic utility in various groups within the Characiformes of the elongate anterodorsal process on the third vertebra that is usually termed the transverse process of the third neural arch. This process projects lateral to the ascending process of the intercalarium in most characiforms, but

varies within the Alestidae in the relative position of its anterior terminus.

In most outgroup taxa, along with some members of the Alestidae (*Alestes*, *Arnoldichthys*, *Brycinus*, *Bryconaethiops* [with the exception of *B. boulengeri*], *Chalceus* and *Hydrocynus*), the transverse process of the third vertebra is proportionally smaller than in the other examined characiforms; as a consequence, the anterior tip falls short of, or barely reaches, the posteroventral margin of the scaphium. In the remaining examined alestids (see Appendix 2) along with *Bryconops*, *Crenuchus* and *Triportheus* among examined outgroups, the process is proportionally longer. Depending on its alignment it either distinctly overlaps the lateral surface of the scaphium (when it is more anteriorly directed) or extends to a point along a vertical distinctly anterior to the posterior margin of the scaphium (when it is more anterodorsally orientated and overlaps the lateral surface of the claustrum).

RIBS AND PARAPOPHYSES

Roberts (1969: 426) described a medially directed process on the first rib in the region proximate to the base of the fifth vertebra in *Acestrorhynchus*, *Alestes baremoze*, *Brycon meeki* and *Piaractus*. Examination of these taxa, along with the others included in this study, demonstrates that the form, position and orientation of processes on the basal region of the first rib vary among these taxa and actually represent independent modifications that are more appropriately analysed separately. These are discussed in characters 115 and 116.

115. Medially directed, elongate process arising distinct distance from base of first rib: (0) absent; (1) present (CI = 20; RI = 60)

An elongate, somewhat finger-like, medially directed process arising from the base of the first rib a discrete distance from the head of the rib (Fig. 25) and entirely situated below the body of the rib was observed only in *Arnoldichthys*, *Chalceus* and *Lepidarchus* among examined taxa of the Alestidae. A comparable process is also present in *Brycon falcatus*, *B. pesu*, *Crenuchus* and *Hemiodus* among examined outgroups. The distal portion of this process serves as an attachment area for a medially directed ligament. This process differs in form, position and alignment from the process of the first rib described in character 116 and the processes in these two characters are thus considered nonhomologous.

In *Triportheus*, along with phylogenetically allied genera not included in this analysis, there is a finger-like process on the upper portion of the first rib. However, it arises from a posteromedially directed, triangular process extending from the main body of the rib rather than arising directly from the main body of the rib as is the case in the taxa listed above. Furthermore, the process is directed anteromedially rather than medially, as is the structure present in *Arnoldichthys*, *Chalceus* and *Lepidarchus*. It is thus considered nonhomologous with the process found in these three alestid genera.

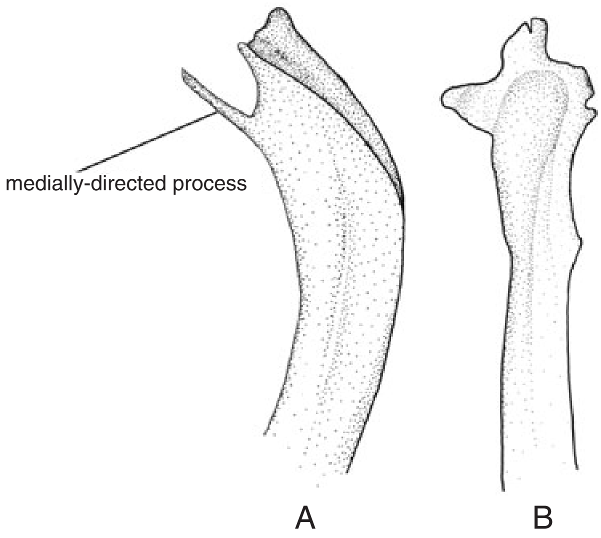

Figure 25. Medially-directed, elongate process extending from base of first rib of *Chalceus spilogyros*, MZUSP76069, 122.7 mm SL; (A) lateral and (B) dorsal views.

116. Presence or absence of posteriorly directed projection near base of first rib: (0) absent; (1) present (CI = 20; RI = 73)

A different form of the process present on the first rib in character 115 is found in all examined members of the Alestidae (with the exception of *Arnoldichthys*, *Chalceus* and *Lepidarchus*) and in *Astyanax*, *Cheirodon*, *Serrasalmus*, *Piaractus*, *Tetragonopterus* and *Xenocharax* among examined outgroup taxa. The process is a triangular structure arising closer to the head of the rib than that described in character 115. It is, furthermore, posteromedially rather than medially directed (Fig. 26) and serves as the area of attachment on the rib for ligaments extending to the base of the immediately posterior rib and its parapophysis. This is in contrast to the process described in character 115, which serves as an attachment area for a medially directed ligament. It is noteworthy that in most examined representatives of the Alestidae, this process is relatively small whereas in the outgroup genera *Piaractus* and *Serrasalmus* it is robust. This

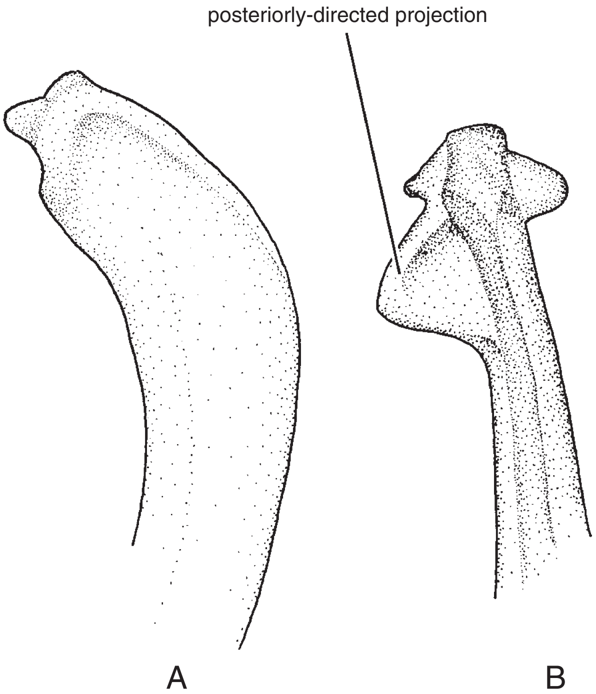

Figure 26. Posteriorly-directed process extending from near base of first rib of *Brycinus nurse*, USNM 339724, 107.4 mm SL; (A) lateral and (B) dorsal views.

difference parallels the apparent homoplasy of the structures between these taxa that derives from the overall most parsimonious hypothesis of relationships. *Triportheus* was not coded for this character for the reasons discussed in character 115.

117. Presence or absence of medially directed process on base of second rib: (0) absent; (1) present (CI = 33; RI = 66)
The medial surface of the second rib is usually unmodified in characiforms. However, *Chalceus* and *Lepidarchus* in the Alestidae and *Hemiodus* (family Hemiodontidae) within the outgroup have a medially directed, variably elongate process on the second rib that is similar in form to, albeit in some instances not as highly developed as, the process on the corresponding region of the first rib. A similar, medially directed process on the second rib is also present in *Cynodon* and *Hydrolycus* of the Neotropical family Cynodontidae (Toledo-Piza, 2000: 44), taxa that are not included in the outgroup for this analysis.

Both the Hemiodontidae and Cynodontidae are distant phylogenetically from the Alestidae (Buckup, 1998: 134; Lucena & Menezes, 1998: 263) and the modifications of the second rib in those New World taxa are obviously homoplastic relative to the occurrence of these structures in *Chalceus* and *Lepidarchus* of the Alestidae. Outgroup comparisons have demonstrated that the Neotropical serrasalmines *Piaractus* and *Serrasalmus* also possess distinct processes situated proximate to the base of the second rib. The modifications of the rib in these serrasalmines are, however, strong triangular structures arising proximate to the base of the rib and are distinctly posteriorly orientated, a considerably different morphology from the form of the elaboration of the second rib described above for *Chalceus* and *Lepidarchus*.

118. Presence or absence of medial process on central portion of body of first rib: (0) absent; (1) present (CI = 100; RI = 100)
Tricuspidalestes is unique within the Alestidae in possessing a distinct, triangular, medially directed process arising from the central portion of the body of the first rib. Although processes arising from this portion have also been reported in the Characidiinae (Buckup, 1993a: 239) and a subunit of the Distichodontidae (Vari, 1979: 309), those taxa are distant phylogenetically from the Alestidae (Vari, 1979; Buckup, 1998). The elaborations of the first rib in these taxa are herein hypothesized to be homoplastic relative to the process in that position present in *Tricuspidalestes*.

119. Presence or absence of posteriorly directed process on posterodorsal margin of upper portions of first through eighth ribs: (0) absent; (1) present (CI = 100; RI = 100)
Nearly all alestids, and indeed all characiforms, have an unelaborated posterodorsal margin of the upper portion of the first through eighth ribs in the region, where the body of the rib curves ventrally. The only exception to that generalization encountered during this study was *Micralestes lualabae*, in which the first through eighth ribs each bear a variously developed, posteriorly directed process that apparently serves as the point of attachment on each rib for various ligamentous bands. This feature, although uninformative as to higher level relationships in this analysis, may nonetheless prove phylogenetically useful at the intrageneric level when the character is examined across a larger number of *Micralestes* species than were available for this study.

120. Form of parapophyses of fifth and subsequent vertebrae: (0) parapophyses not elongate and with anterior limit situated posterior to anterior limit of centrum; (1) parapophyses elongate and with anterior limit extending distinctly anterior to anterior limit of centrum (CI = 50; RI = 66)
Most members of the Alestidae have a moderately developed parapophysis associated with each rib. In

that typical condition, the anterior limit of the parapophysis falls short of the anterior limit of both the articular surface of the associated rib and of the associated centrum. This condition also occurs among outgroups examined in this study and is illustrated for *Brycon meeki* by Weitzman (1962: fig. 14d).

In *Alestes baremoze*, *A. dentex*, and the species of *Hydrocynus* examined in this study, the parapophysis of each precaudal vertebra is instead longitudinally elongate, extending anteriorly beyond the anterior limit of its associated centrum. In most of the vertebrae it also extends distinctly forward of the anterior limit of the head of the rib. This disparity in the degree of anterior development is less apparent, albeit present, in the more posterior ribs.

In *Alestes baremoze*, *A. dentex* and the species of *Hydrocynus* we examined, the ligaments arise from the posterior border of each rib, extending posteriorly to attach primarily to the anteriorly expanded portion of the parapophysis of the following vertebra and to a lesser extent to the anterior portion of the base of the rib associated with the following parapophysis. The species of *Hydrocynus* have elongate parapophyses present on a higher number of vertebrae than is the case in *A. baremoze* and *A. dentex*, a feature correlated with the higher number of intermediate vertebrae in *Hydrocynus* (see discussion in character 121). Both *Alestes* and *Hydrocynus* are, however, coded as state 1 for this character in the matrix because of their common possession of elongate parapophyses.

An anterior elongation of the parapophysis was reported for the Neotropical characiform family Cynodontinae by Toledo-Piza (2000: 44). This elongation, although similar to the condition observed in the Alestidae in terms of the degree of anterior development, has in addition an articulation between the anterior portion of the parapophysis and the posteroventral border of the anterior vertebra, a contact absent in the Alestidae. Furthermore, and more significantly, the elongated parapophysis in the Cynodontinae is situated further dorsally on the centrum than is the structure present in *Alestes* and *Hydrocynus*.

Such differences cast significant doubt as to the homology of the elaborations of the vertebrae in these Old vs. New World characiforms. These reservations are reinforced by the results of Lucena & Menezes (1998: 263), who advanced synapomorphies in support of the hypothesis that the phylogenetic relationships of the Cynodontinae lie with the subfamily Roestinae and family Acestrorhynchidae, both of which are also endemic to the New World. Thus, the elongation of the parapophyses present in *Alestes* and *Hydrocynus* is considered homoplastic relative to the elaboration of those structures in the Cynodontinae.

INTERMEDIATE-TYPE VERTEBRAE

121. Number of intermediate-type vertebrae: (0) less than ten; (1) more than ten (CI = 100; RI = 100)
Characiforms have varying numbers of intermediate-type vertebrae (*sensu* Weitzman, 1962: 38) in which the haemal arch and eventually the components of the haemal spine progressively increase in both completeness and length posteriorly, but in which the arch, nonetheless, does not terminate distally in a single spine. A range of 2-8 such vertebrae occurs in all members of the Alestidae other than for *Hydrocynus brevis* and *H. forskahlii*, where there are 12 intermediate-type vertebrae with 11 and 12 transitional ribs, respectively.

Brewster (1986: 192) proposed that the presence of 8–11 pairs of transitional ribs associated with the intermediate-type vertebrae was a synapomorphy that supported a clade consisting of *Hydrocynus* and *Alestes*. Murray & Stewart (2002: 1893) followed Brewster's delimitation of the feature. The examination of a diversity of alestids in this study has revealed a continuum in the range of transitional ribs within the family, a situation preventing the delimitation of discrete character states based on the number of such ribs. There is, however, a gap between the maximum of eight intermediate vertebrae in some, but not all, *Alestes* species which is the highest value encountered in the Alestidae outside of *Hydrocynus*, and the presence of 12 such vertebrae in the examined species of *Hydrocynus*. In light of that gap we cast the character in terms of the number of intermediate vertebrae.

SUPRANEURALS

122. Presence or absence of supraneural anterior to neural spine associated with fourth vertebrae: (0) present; (1) absent (CI = 14; RI = 82)
Many characiforms, including members of the basal family Distichodontidae represented in this study by *Xenocharax*, have a varyingly shaped supraneural in the space between the rear of the neural complex of the Weberian apparatus and the neural spine of the fourth vertebra (supraneural shown but not labelled in various species of the Neotropical family Cynodontidae by Toledo-Piza, 2000: figs 14–16). This supraneural is varyingly present in the Alestidae (see Appendix 2). Although many of the alestid taxa lacking this ossification are of relatively small body size as adults, the absence of this supraneural does not invariably correlate with a reduction in overall body size across the Alestidae in so far as the ossification is absent in some alestids attaining relatively large body size. This supraneural is also absent in *Astyanax*, *Charax*, *Cheirodon*, *Crenuchus*, *Hoplias* and *Tetragonopterus* among examined outgroups and has been apparently lost independently in various clades among characiforms.

INTERMUSCULAR BONES

123. Position of first intermuscular bones: (0) located posterior to transverse plane through Weberian apparatus; (1) located more anteriorly and proximate to rear of neurocranium (CI = 16; RI = 61)

The series of dorsolaterally located intermuscular bones (epineurals; see Patterson & Johnson, 1995) in most groups of characiforms commences anteriorly at the transverse plane through the Weberian apparatus and projects posteriorly in the myocommata of the epaxial muscles (Lucena & Menezes, 1998: 263). In other species of characiforms, the anterior portion of the first epineural is positioned immediately posterior to the neurocranium in the area proximate to the rear of the epiotic and pterotic and distinctly anterior to the Weberian apparatus. Within the Alestidae, an anteriorly positioned first epineural occurs in *Alestes*, *Chalceus*, *Brycinus macrolepidotus*, *Hydrocynus*, *Micralestes elongatus* and *M. lualabae*; in the remaining alestids the anteriormost epineurals are situated more posteriorly.

Anteriorly positioned epineurals were also observed in *Triportheus* among outgroup taxa included in the present study. Elsewhere within the Characiformes, a pronounced anterior position of the forward-most epineurals was reported for the Neotropical families Acestrorhynchidae and Cynodontidae (with the exception of *Roestes*) by Lucena & Menezes (1998: 263), who utilized that feature as a synapomorphy for that pair of families. Weitzman (1954: 224) reported an anterior position of the epineurals in the genera *Thoracocharax* and *Carnegiella* of the Neotropical Gasteropelecinae. Although the phylogenetic placement within the Characiformes of many of these outgroups characterized by anteriorly positioned epineurals is uncertain, the available evidence fails to indicate a close association of any of these taxa with the Alestidae.

Although the available cleared and stained specimens of *Lepidarchus* fail to demonstrate any ossified intermuscular epineurals, the presence, but not the anterior limit of the distribution, of those bones was reported for that genus by Roberts (1966: 213). In the absence of information to the contrary we code *Lepidarchus* as having the condition typical for closely related species that is also general for most characiforms.

DORSAL FIN AND DORSAL-FIN RADIALS

124. Presence or absence of small ossification associated with first proximal dorsal-fin radial: (0) present; (1) absent (CI = 20; RI = 63)

The moderately to well-developed first dorsal-fin rays present in many characiforms are preceded in many instances by a small, variably ray-like ossification or sometimes ossifications. Such elements protrude to differing degrees from the middorsal surface of the body and are associated with the dorsal margin of the first proximal dorsal-fin radial. In some characiforms one of these autogenous ossifications is restructured into a distinct, variably mobile procumbent spine (Stethaprioninae, Reis, 1989: figs 7–11; Curimatidae, Vari, 1992: fig. 3; Castro & Vari., 2004: fig. 23).

An autogenous ossification anterior to the first unbranched dorsal-fin ray is the common condition among Neotropical characiforms that typically also have two well-developed unbranched rays associated with the first proximal dorsal-fin radial. In the Alestidae the small ossification anterior to the first distinct unbranched fin ray is, alternatively, absent – an apparently derived condition. This structure is also lacking in several examined outgroup taxa (*Charax*, *Bryconops*, *Serrasalmus*, *Triportheus*). Various taxa in the Neotropical Serrasalminae have a distinct anterior process of the proximal radial (see illustration of *Tometes* in Jégu, Santos & Belmont-Jégu, 2002: fig. 14c); however, this process is integral to the proximal radial rather than being an autogenous ossification associated with it, as is the structure described in this character.

125. Number of dorsal-fin proximal radials: (0) 12 or more; (1) 11; (2) ten; (3) nine; (4) eight (CI = 33; RI = 77)

In examined species of the Alestidae there is a constant count of nine proximal dorsal-fin radials, with the exception of *Lepidarchus*, where there are ten, and *Arnoldichthys* and *Chalceus*, where there are 11. The examined outgroup characiforms have some variation in the number of proximal radials, differences reflecting the total number of dorsal-fin rays. Dorsal fins with a high number of proximal radials were observed in *Xenocharax* (17), *Crenuchus* (18), *Hoplias* (13), *Serrasalmus* (16) and *Piaractus* (14). *Hepsetus*, in contrast, has the lowest number of these elements (8) among examined taxa. The most common condition in the members of the Characidae examined in this study is the presence of ten radials.

126. Number of fin rays supported by posteriormost proximal radial of dorsal fin: (0) two; (1) one (CI = 25; RI = 81)

In *Xenocharax*, *Hemiodus* and all members of the Alestidae with the exception of *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, two rays are supported by the posteriormost proximal radial of the dorsal fin. In the majority of examined characiform outgroups, in contrast, only one ray is supported by this radial (see Weitzman, 1962: fig. 16, for this condition in *Brycon meeki*). All of the five examined, cleared and stained specimens of the outgroup genus *Crenuchus* have a posteriormost radial supporting only one ray and we consequently code the genus as having that value. Buckup (1998: 132), however, reported intraspecific variation in this feature within *Crenuchus*.

PECTORAL GIRDLE AND FIN

127. Presence or absence of extrascapular: (0) present; (1) absent (CI = 100; RI = 100)
The extrascapular, a laminar ossification of the lateral surface of the head bearing a segment of the laterosensory canal system (e.g. *Brycon meeki*, Weitzman, 1962: fig. 18), was reported by Roberts (1966: 212, fig. 7) as lacking in *Lepidarchus adonis*. Our studies confirmed that observation and demonstrated that the extrascapular is furthermore also absent in *Ladigesia* and *Tricuspidalestes*. A small, round ossification within the region primitively occupied by the extrascapular is present on only one side of the head in one of the two examined cleared and stained specimens of *Tricuspidalestes*. In addition to being asymmetrically present, the overall size of that ossification in that specimen is proportionally significantly smaller than is the extrascapular in the other alestids retaining that bone. The ossification in that individual of *Tricuspidalestes*, furthermore, lacks any indication of the laterosensory canal segment that typically transverses the extrascapular in characiforms. As such, the homology of this ossification is questionable and *Tricuspidalestes* is coded as lacking the extrascapular (state 1).

128. Separation or fusion of post-temporal and supracleithrum: (0) separate; (1) fused (CI = 100; RI = 100)
Lepidarchus is unique within the Alestidae in possessing a single, dorsoventrally elongate ossification comparable in overall profile to the separate post-temporal and supracleithrum characterizing all other members of the family. We consequently consider the single bone present in *Lepidarchus* to represent a fusion of the post-temporal and supracleithrum. Although Roberts (1966: fig. 7) illustrated a post-temporal that is autogenous from the supracleithrum in *Lepidarchus*, we were unable to identify that condition in any of the examined cleared and stained specimens of the genus.

Within the Characiformes, fusion also occurs in the Gasteropelecidae (Weitzman, 1960: 217) and the Characidae (the genus *Engraulisoma*; Castro, 1984: 122). Neither the Gasteropelecidae nor *Engraulisoma* are hypothesized to be closely related to *Lepidarchus* on the basis of available evidence and the fusion of these bones is considered autapomorphic for the latter genus in the Alestidae.

129. Size and form of post-temporal: (0) moderate sized and ventrally expanded, usually with included laterosensory canal segment; (1) very slender throughout and relatively short, without ventral expansion or included laterosensory canal segment (CI = 100; RI = 100)
In nearly all alestids, and all examined outgroup characiforms, the post-temporal is a triangular, ventrally wider ossification including a segment of the laterosensory canal. Uniquely in *Ladigesia*, it is a proportionally vertically shorter and ventrally narrower, splint-like ossification lacking an included laterosensory canal segment.

We are unable to code the condition of the post-temporal in *Lepidarchus* since it is impossible to determine the extent to which it may have contributed to the hypothesized fused post-temporal and supracleithrum characteristic of that genus (see previous character). There is no indication of a laterosensory canal segment in the composite post-temporal/supracleithrum of *Lepidarchus*. The absence of that passage parallels the lack of the canal in *Ladigesia*, which is its hypothesized sister group within the final most parsimonious hypothesis of relationships.

130. Presence or absence of medially directed, spine-like process on post-temporal: (0) present; (1) absent (CI = 20; RI = 55)
Weitzman (1962: 42) noted that the ventromedial surface of the post-temporal of *Brycon meeki* bears a small spine-like process extending towards the intercalar (the opisthotic of Weitzman). Such a process was also reported for *Hydrocynus* by Brewster (1986: 179). In most alestids and other characiforms this process (Fig. 27) serves as the attachment area for a ligament extending medially to insert on the intercalar. Weitzman (1964: 147) noted that the post-temporal in the Pyrrhulinae lacks a medial process and the absence of that structure was also reported for the Characidiinae by Buckup (1993a: 237).

The medial spine-like process of the post-temporal was found to be absent in some of the species in the Alestidae achieving only small body size as adults (Appendix 2). In nearly all of these species, however, there is a process of comparable shape extending medially from the main body of the supracleithrum, serving as the area of attachment on the pectoral girdle for the ligament extending laterally from the intercalar (see character 131).

In some taxa in the Alestidae (*Alestopetersius*, *Bryconalestes*, *Duboisialestes*, *Nannopetersius* and some species of both *Micralestes* and *Phenacogrammus*) spine-like medial processes are present on the medial surfaces of both the post-temporal and supracleithrum. In this condition, the proximate surfaces of the

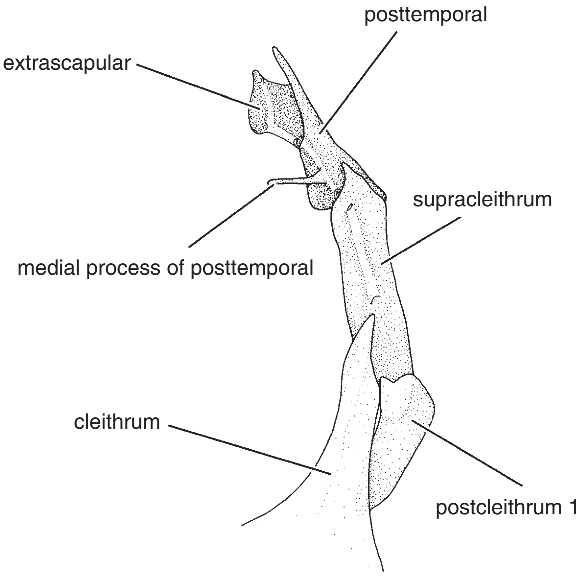

Figure 27. Dorsal portion of pectoral girdle of *Hydrocynus forskahlii*, USNM 339724, 120.0 mm SL; right side, medial view, showing spine-like process on medial surface of post-temporal.

processes of these two bones are in, or nearly in, contact and the ligament originating from the intercalar attaches onto the distal portions of the medial processes of both the post-temporal and supracleithrum. Only *Ladigesia* and *Lepidarchus* among examined alestids lack spine-like, medial processes on both the post-temporal and supracleithrum. The absence of these processes in both *Ladigesia* and *Lepidarchus* directly correlates with their lack of the intercalar (see character 42) and of the ligament that extends between the intercalar and the pectoral girdle in most characiforms.

131. Presence or absence of spine-like, medially directed process on medial surface of supracleithrum: (0) absent; (1) present (CI = 16; RI = 79)

As discussed in character 130, in a subset of the species in the Alestidae (Appendix 2) there is a medial process of the supracleithrum (Fig. 28) that partially, or entirely, serves as the area of attachment on the pectoral girdle for the ligament originating on the intercalar (see also character 42). The medial process of the supracleithrum in *Clupeocharax* and *Tricuspidalestes* is less developed than in other taxa with that structure. Nonetheless, these genera are coded as having state 1 for this character in light of the presence of at least a partial medial process on the supracleithrum. The only examined outgroup characiform in which we found a medial process of the supracleithrum associated with the absence of a comparable medial process on the post-temporal was the Neotropical genus *Characidium*.

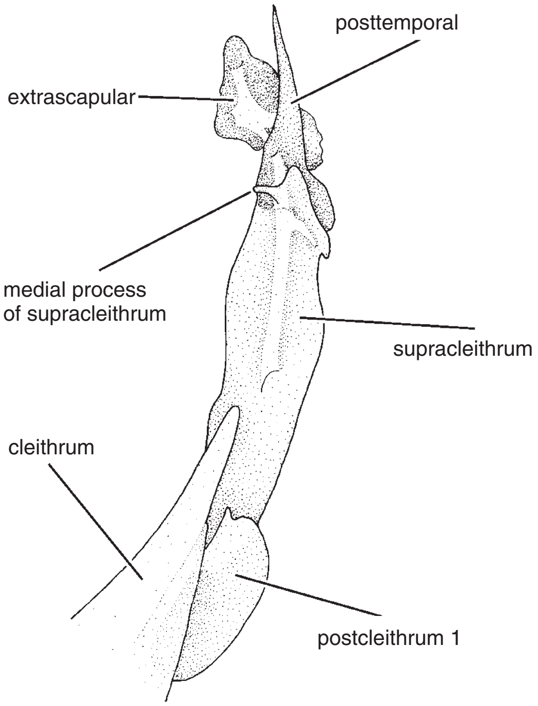

Figure 28. Dorsal portion of pectoral girdle of *Bryconalestes longipinnis*, USNM 193937, 76.2 mm SL; right side, medial view, showing spine-like process on medial surface of supracleithrum.

Postcleithra. Most characiforms typically have three postcleithra (e.g. *Brycon meeki*, Weitzman, 1962: figs 18, 19), which demonstrate various patterns of reduction and fusion within that order. We treat the presence or absence of each element as an independent feature under the next three characters.

132. Presence or absence of postcleithrum 1: (0) present; (1) absent (CI = 100; RI = 100)

The absence of postcleithrum 1 is unique to *Lepidarchus* among examined members of the Alestidae and outgroup taxa. It is absent elsewhere in the Characiformes in *Nannocharax* and *Hemigrammocharax* within the Distichodontidae (Vari, 1979: 311), the Chilodontidae (Vari, 1983: 36, fig. 30), in *Synaptolaemus* and *Sartor* within the Anostomidae (Winterbottom, 1980: 46), and in the subfamily Gasteropelecinae of the Characidae (Weitzman, 1960: 241). It is also reduced or absent in the Characidiinae (Buckup, 1993b: 315). The hypotheses of higher level phylogenetic relationships involving these outgroups (Vari, 1979, 1983; Winterbottom, 1980; Buckup, 1998) indicate that none of the outgroup taxa lacking postcleithrum 1 are closely related to the Alestidae and the loss of that ossification in those nonalestids is consequently considered homoplastic with respect to its absence in *Lepidarchus*.

133. Presence or absence of postcleithrum 2: (0) present; (1) absent (CI = 33; RI = 0)
Postcleithrum 2 is uniquely absent in *Rhabdalestes rhodesiensis* (Ricardo-Bertram) among examined alestids, although this feature is potentially informative with regard to phylogenetic relationships once more species of the genus are examined. Postcleithrum 2 has been reported to be absent among New World characiforms in some species of *Boulengerella* (Vari, 1995: 26), *Ctenolucius* (Vari, 1995: 26), *Engraulisoma* (Castro, 1984: 52), the Gasteropelecinae (Weitzman, 1960), *Gilbertolus*, *Gnathocharax* and the Cynodontinae (Toledo-Piza, 1997: 113, 114) and in *Triportheus* and *Lignobrycon* (M.C. de S.L. Malabarba, 1998: 76). Among African characiforms, postcleithrum 2 is absent in the putatively monotypic family Hepsetidae (Roberts, 1969: 426). None of these outgroup taxa share the derived features characteristic of the Alestidae and at least *Boulengerella*, *Ctenolucius* and *Hepsetus* are more closely related to groups other than the Alestidae (Vari, 1995; Buckup, 1998). The loss of postcleithrum 2 is consequently considered homoplastic in those outgroups vs. *Rhabdalestes rhodesiensis*.

134. Presence or absence of postcleithrum 3: (0) present; (1) absent (CI = 20; RI = 0)
Postcleithrum 3 is absent in *Clupeocharax*, *Hemmigrammopetersius barnardi* (Herre) and *Rhabdalestes rhodesiensis* among examined taxa in the Alestidae. Elsewhere in the Characiformes the ossification has also been reported as absent in the African family Hepsetidae (Roberts, 1969: 426) and in the Neotropical taxa *Ctenolucius* (Vari, 1995: 26), *Gilbertolus*, *Gnathocharax* and the Cynodontinae (Toledo-Piza, 1997: 113, 114), the Gasteropelecinae (Weitzman, 1960), *Chilodus* (Vari, Castro & Raredon 1995: 9), *Engraulisoma* (Castro, 1984: 52) and *Triportheus* and *Lignobrycon* (M.C. de S.L. Malabarba, 1998: 76). None of these taxa share the derived features characteristic of the Alestidae and many share derived features with other groups in the Characiformes (Vari, 1995; Buckup, 1998; Lucena & Menezes, 1998). The loss of postcleithrum 3 is consequently considered homoplastic in those outgroups vs. the absence of the structure in *Clupeocharax*, *H. barnardi* and *R. rhodesiensis*.

135. Form of postcleithrum 3 when present: (0) with lamella; (1) without lamella (CI = 14; RI = 76)
Many of the examined taxa within the Alestidae and outgroups have a relatively rod-like form of postcleithrum 3 (e.g. *Brycon meeki*, Weitzman, 1962: fig. 19). Some components of the Alestidae (Appendix 2) instead have a distinct lamellar process located on the posterior margin of the rod-like process of that bone in the region proximate to the second postcleithrum. A third postcleithrum is absent within the Alestidae in *Clupeocharax*, *H. barnardi*, *Hepsetus* and *R. rhodesiensis*, with that absence making it impossible to code this character for those taxa. Among examined outgroup taxa it was impossible to code this feature for *Crenuchus*, *Triportheus* and *Xenocharax* in which postcleithra 2 and 3 are apparently fused into a single bone.

136. Presence or absence of narrow ring-like process of scapula forming anterior border of scapular foramen: (0) present; (1) absent (CI = 50; RI = 91)
The anterior portion of the scapula in many characiforms has a narrow ring of bone delimiting the anterior portion of the scapular foramen that separates that aperture from a more anteriorly positioned opening bordered by the scapula, coracoid and cleithrum. A well-developed ring-like process of the scapula occurs in the majority of the species of the Alestidae, whereas this structure ranges from being significantly reduced to effectively absent in *Alestopetersius*, *Bathyaethiops*, *Brachypetersius*, *Clupeocharax*, *Duboisialestes*, *Nannopetersius* and *Phenacogrammus*.

Although many of the species of the Alestidae without this ring-like process of the scapula are of relatively small body size, there is no absolute correlation between absence and size. For example, the process is present in *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, all of which are of smaller body size than are the alestid species lacking that structure. Indeed, in *Lepidarchus*, a species of diminutive size, the width of the process is proportionally significantly expanded. The consequent reduction in the relative size of the aperture in the centre of the scapular foramen is an apparent autapomorphic condition of *Lepidarchus*. The only other examined characiform with a somewhat comparable reduction in the extent of the scapular foramen is the Neotropical genus *Triportheus*, a group of somewhat uncertain phylogenetic position, which is apparently not closely related to the Alestidae. This region of the pectoral girdle is highly modified in *Hoplias,* making it impossible to code the state of the character for that genus.

137. Degree of development of dorsal process on base of first branched pectoral-fin ray: (0) similar to that of remaining branched rays; (1) distinctly greater than that of remaining branched rays, with process overlapping base of unbranched ray to varying degrees from medial view (CI = 20; RI = 80)
In most of the examined outgroup taxa and the majority of examined alestids there is a distinct process

formed by a dorsal expansion on the basal portion of the first branched pectoral-fin ray. As such, the overall morphology of that portion of the first branched ray differs from comparable portions of the remaining branched rays, all of which lack that expansion.

In a subset of the Alestidae consisting of species typically of small body size (Appendix 2), the basal portion of the first branched ray lacks a dorsal expansion and is similar in form and degree of development to the following rays. The process of the first branched ray in *Virilia* and *Hemmigrammopetersius* is less developed than it is in many members of the Alestidae. However, it is more highly developed than the corresponding structure in those genera coded as lacking the process. *Virilia* and *Hemmigrammopetersius* are thus coded as demonstrating the presence of the process (state 1). An absence of the enlarged process on the basal portion of the first branched ray was also observed in *Astyanax*, *Charax*, *Cheirodon*, *Crenuchus*, *Triportheus* and *Xenocharax* among examined outgroups.

Processes are present on the dorsal regions of the basal portions of many of the branched rays in *Hoplias*, but with the process on the first ray of the series not distinctly larger than it is in the following rays. Furthermore, these processes have an anteromedial orientation, rather than dorsal orientation reported above for many characiforms. In light of these differences, the enlargement on the first branched ray in *Hoplias* is considered nonequivalent to that present in many species of the Alestidae.

PELVIC BONE AND FIN

138. Number of unbranched plus branched pelvic-fin rays: (0) 11; (1) nine; (2) eight; (3) seven (CI = 27; RI = 73)

The number of pelvic-fin rays varies within the Characiformes, with a count among examined taxa ranging from seven in *Cheirodon*, *Serrasalmus* and *Triportheus* to 11 in *Hemiodus* and *Xenocharax*. A more restricted range of variation characterizes both the Alestidae and Characidae. As previously noted by Weitzman (1962: 45) and Menezes (1976: 11), most characids have eight; some have fewer.

Two major components within the Alestidae are delimited by the number of pelvic-fin rays. The first group, with nine, consists of *Alestes*, *Brycinus*, *Bryconaethiops*, *Chalceus* (with the exception of *C. guaporensis*), *Hydrocynus* and *Petersius*. The second group, with eight, consists of *Arnoldichthys*, *Bryconalestes*, *C. guaporensis*, *Micralestes*, *Rhabdalestes,* plus various other genera of the Alestidae that typically achieve only small body size (Appendix 2).

Intraspecific variation in the number of pelvic-fin rays occurs periodically across the Characiformes. In the Alestidae, eight of the specimens of *Alestopetersius hilgendorfi* (Boulenger) examined in this study had eight rays in each fin, three specimens had eight rays on one side and nine on the other and only one specimen had nine rays in both fins. In light of the more common presence of eight rays in this sample, we code *A. hilgendorfi* as having that count.

139. Form of pelvic bone: (0) distinctly bifurcated anteriorly; (1) not distinctly bifurcated anteriorly (CI = 50; RI = 66)

Among the taxa examined in this study, a distinctly anteriorly bifurcated pelvic bone was limited to the examined species of *Bryconaethiops* (Fig. 29; see also comments below) and *Xenocharax*. Both genera have a deep incision on the anterior margin of the ossification, apparently resulting from the anterior extension of the medial margin of the pelvic bone.

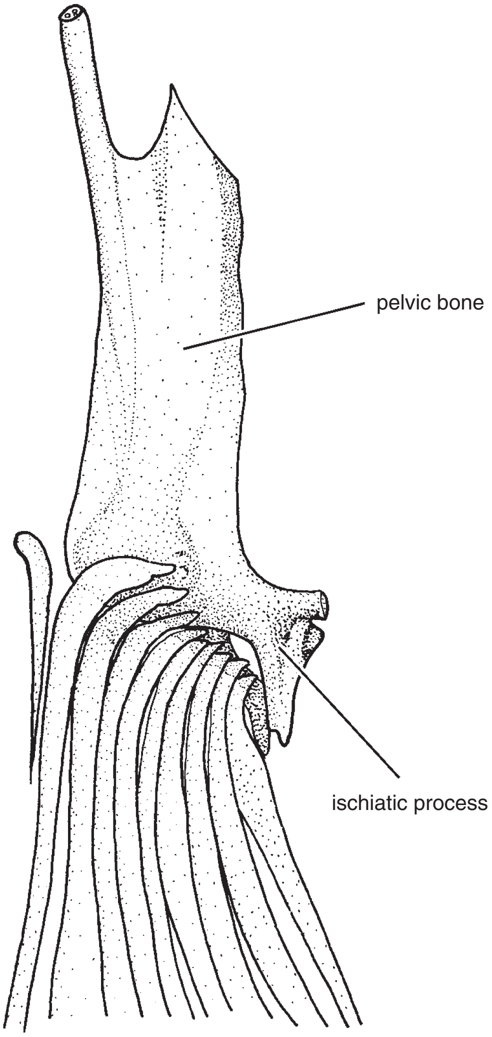

Figure 29. Pelvic bone of *Bryconaethiops microstoma*, USNM 339722, 55.1 mm SL; dorsal view.

Although *Bryconaethiops* and *Xenocharax* differ in aspects of the morphology of the anterior portion of the pelvic bone, these differences do not support an a priori hypothesis that the bifurcation is a consequence of different developmental processes. We thus code these occurrences of a bifurcate pelvic bone in *Bryconaethiops* and *Xenocharax* as the same feature, albeit one that obviously arose independently in these genera in light of the significant phylogenetic distances between the Alestidae and Distichodontidae (Vari, 1979; Buckup, 1998; this study).

It is noteworthy that whereas one cleared and stained specimen of *B. microstoma* demonstrated the strong bifurcation of the pelvic bone present in all of the examined cleared and stained individuals of congeneric species, a second specimen of approximately comparable size lacked such a bifurcation. We tentatively code the bifurcation of the pelvic fin as being present in *B. microstoma* because of its occurrence in the first specimen and in all examined congeners. Examination of other, preferably larger, specimens of *B. microstoma* is a prerequisite for the resolution of the question of the condition of the pelvic bone typical for this species.

The ambiguous distribution of the anterior bifurcation of the pelvic bone within the Characiformes was discussed by Buckup (1998: 132). Although he indicated in his matrix that *Crenuchus* has such a bifurcation, the cleared and stained specimens of that genus examined in this study lack such a morphology.

140. Degree of development of rod-shaped portion of lateral surface of pelvic bone: (0) terminates anteriorly at limit of lamellar portion of pelvic bone; (1) extends distinctly anterior to lamellar portion of pelvic bone (CI = 33; RI = 33)

Weitzman (1962: 42: fig. 21) noted that the anterior portion of the pelvic bone of *Brycon meeki* is a flat plate with a rod-shaped process extending along its lateral border. A restriction of this process to the region posterior to the anterior limit of the laminar portion of the pelvic bone was the most common condition among the taxa examined in this study. *Alestes baremoze* and *A. dentex* in the Alestidae and *Hoplias* and *Triportheus* among the examined outgroups share an extension of the rod-shaped portion of the pelvic bone anterior to the margin of the lamellar portion of the bone.

The condition of the anterior portion of the pelvic bone in the Neotropical genus *Serrasalmus* appears superficially comparable to the morphology of that bone in these alestids and outgroups. The pelvic bone in *Serrasalmus* is, however, proportionally significantly reduced in multiple aspects, and retains only residual portions of the lamellar regions present on that bone in other characiforms. As a consequence, the apparent rod-shaped structure on the anterior portion of the pelvic bone in *Serrasalmus* primarily reflects the reduction of the lamellar portion of the pelvic bone rather than the development of a rod-like extension. That condition is nonhomologous with the morphology of the bone present in *A. baremoze* and *A. dentex* that retains both a distinct lamellar component and an anterior rod-shaped extension.

A pelvic bone with a rod-shaped process extending anteriorly beyond the laminar portion of the bone was interpreted as a synapomorphy for the Neotropical characiform genera *Lignobrycon* and *Triportheus* by M.C. de S.L. Malabarba (1998: 77, fig. 12) and the presence of that condition in these taxa was confirmed in this study. The outgroup taxon *Xenocharax* was coded as '?' in the matrix for this character, since the pronounced bifurcate condition of the pelvic bone in the genus makes it impossible to evaluate whether the rod-shaped process is present.

141. Separation and mode of contact of medial portions of ischiatic processes on contralateral pelvic bones: (0) processes positioned relatively distant from each other and connected by cartilage and ligaments along relatively narrow region, or if in direct contact, then area of contact of process limited and not in form of broad, smooth surface; (1) processes positioned close to each other with distinct area of direct contact via wide smooth flat surface on each process (CI = 50; RI = 50)

In most alestids and examined outgroup characiforms, the medial margin of the ischiatic process of the pelvic bone is relatively convex and either lacks direct contact with its counterpart or has at most a limited degree of such contact. Instead, the contralateral pelvic bones are joined via ligaments running between the ischiatic processes. *Alestes baremoze* and *A. dentex* differ from the generalized characiform condition in having a direct articulation of the contralateral pelvic bones via a distinct, wide, smooth articular surface on the medial surface of each ischiatic process. The Neotropical outgroup *Triportheus* is the only other examined taxon with a morphology of the ischiatic processes reminiscent of the form of those structures present in *A. baremoze* and *A. dentex*, albeit with some differences in the form of the articular surfaces. Nonetheless, we herein code the two examined species of *Alestes* and *Triportheus* as having the same condition in light of their common possession of the distinct articular surfaces on the ischiatic processes.

ANAL FIN AND ANAL-FIN RADIALS

142. Number of unbranched anal-fin rays: (0) two; (1) three; (2) four or five (CI = 66; RI = 92)

The majority of the examined species in the Alestidae have three unbranched anal-fin rays, a condition shared by *Crenuchus*, *Hepsetus* and *Hoplias* among examined outgroups. Most examined outgroup taxa have four, with five present in the examined representatives of the Tetragonopterinae and Cheirodontinae. Two genera of diminutive body size within the Alestidae, *Ladigesia* and *Lepidarchus*, have only two unbranched anal-fin rays, whereas the basal African alestid *Arnoldichthys* has four. *Bathyaethiops* demonstrates intraspecific variation in the number of unbranched anal-fin rays. Observations on two cleared and stained specimens and two whole specimens of the genus examined via radiographs found that three unbranched rays were present in two of the specimens and four in two other individuals, albeit with the anterior ray being proportionally very small when four were present. Because of this equivocal information, *Bathyaethiops* is coded as '?' for this character.

143. Form of basal portion of first proximal radial of anal fin: (0) without dorsally directed process on anterior surface; (1) with dorsally directed process on anterior surface (CI = 100; RI = 100)

The basal portion of the first proximal radial of the anal fin demonstrates various modifications both within the Alestidae and among examined outgroup characiforms. Nonetheless, the presence of a distinct, dorsally directed, pointed process arising from an anteroposteriorly expanded flange of the basal portion of the first proximal radial (see Brewster, 1986: fig. 23; Murray & Stewart, 2002: 1883) is unique to *Alestes* among examined taxa.

144. Form of proximal radials of anal fin: (0) main body cylindrical or with varyingly developed lateral expansion in addition to anteroposterior expansion; (1) with anteroposterior but no lateral expansion (CI = 33; RI = 84)

The morphology of the proximal radials of the anal fin, in particular the anterior components of that series, demonstrates a broad range across the Characiformes. In many taxa (e.g. the characid genus *Brycon*) the proximal radials are rod-like, whereas in others they have plate-like extensions arising from their anterior, posterior and lateral margins.

In combination, these processes extending from the main body of the proximal radial produce an ossification with a cross-sectional form in the shape of a cross. The latter morphology is present in the majority of the examined taxa in the Alestidae, whereas in a subset of small body size (see Appendix 2) the lateral processes on these elements are absent. These taxa consequently have overall transversely flattened plate-like, vertically elongate, proximal radials with a slight lateral thickening of the element along the shaft-like central portion of the bone. *Ladigesia*, although of small body size has, however, definite lateral flanges on the central shaft of these radials, albeit with a more posterolateral orientation than that found in the other alestids, in which they have a lateral orientation. Only *Cheirodon* has state 1 for this character among outgroups examined in this study.

145. Relative length of posterior proximal radials of anal fin: (0) gradually decreasing in length posteriorly; (1) abruptly decreasing in length approximately at centre of base of anal fin (CI = 100; RI = 100)

In her analysis of the phylogenetic relationships of a component of *Alestes*, Brewster (1986: 190, fig. 23) proposed that possession of very short, posterior, proximal anal-fin radials in conjunction with the more anterior inclination of these elements relative to the orientation of their serial homologues in the remainder of the fin was a synapomorphy for a clade consisting of *Alestes ansorgii* Boulenger, *A. baremoze*, *A. dentex*, *A. liebrechtsii*, *A. macrophthalmus* and *A. stuhlmanni* Pfeffer.

Murray & Stewart (2002: 1893) utilized Brewster's definition of this character in their analysis of a subset of the Alestidae. Such modifications of the length and orientation of these anal-fin radials accommodate the posterior extension of the swimbladder in these species of *Alestes* beyond its typical termination of that structure at the anteriormost proximal radial (see character 200).

Our observations indicate that these modifications of the radials, albeit indeed derived, are more appropriately subdivided into two characters, given their occurrence at different levels of inclusiveness among alestids. Although the posterior proximal radials are inclined anteriorly, the pronounced reduction in relative size occurring in *A. baremoze* and *A. dentex* is absent in *A. macrophthalmus* [NB: some of the *Alestes* species reported in Brewster (1986) were not incorporated in this study]. These characters are: (1) the pronounced reduction in the relative length of the posterior proximal radials relative to the more anterior components of that series (this character); and (2) the shift in the relative alignment of the posterior proximal radials (character 146).

146. Orientation of posterior proximal anal-fin radials: (0) approximately parallel to, or only slightly anteriorly inclined relative to, orientation of anterior proximal radials; (1) distinctly more anteriorly inclined relative to orientation of anterior proximal radials (CI = 100; RI = 100)

The proximal radials of the anal fin in characiforms typically demonstrate approximately the same alignment along the length of the fin. In *Alestes baremoze*, *A. dentex* (see Brewster, 1986: fig. 23) and *A. macrophthalmus*, by contrast, the posterior proximal radials of the anal fin are distinctly more anteroventrally angled than their more posteriorly positioned serial homologues.

147. Anal-fin stay: (0) totally cartilaginous or represented by small plate-like bone; (1) represented by elongate bone similar in overall form to adjoining proximal radial (CI = 25; RI = 78)
Brachypetersius gabonensis, *Brycinus*, *Bryconalestes* and *Petersius conserialis* have a distinctly elongated, well-ossified anal-fin stay (*sensu* Weitzman, 1962: fig. 17) that has an overall morphology similar to that of the anteriorly adjoining proximal anal-fin radial. All the remaining taxa observed in this study have instead a small, plate-like, cartilaginous or ossified anal-fin stay similar in form to that illustrated by Weitzman (1962: fig. 17) for *Brycon meeki*.

CAUDAL VERTEBRAE AND CAUDAL FIN

148. Number of epural bones: (0) one or two; (1) three (CI = 50; RI = 91)
Characiforms have a range of 1-3 epurals, with these bones, together with the urostyle and the posteriormost neural spines serving to support the dorsal procurrent rays of the caudal fin. Roberts (1969: 428) proposed that possession of three epurals was probably plesiomorphic within the Characiformes (his Characoidei), and suggested that the evolutionary trend within the order was a reduction from a primitive count of three epurals. Subsequent studies have shown that basal characiforms, including *Xenocharax* included herein as an outgroup, rather have two epurals. Similarly, the majority of examined outgroup Neotropical characiforms (Appendix 2) have two, whereas all members of the Alestidae have three, possession of which number was proposed by Murray & Stewart (2002: 1893) as a synapomorphy for the Alestidae, a family that those authors limited to African taxa.

Two specimens of *Rhabdalestes septentrionalis* were examined, either as a cleared and stained preparation or via radiography. The first had three epurals, the count typical for most other alestids, the second only two. In the latter, each epural had anomalous overall morphologies relative to the form of those bones in all other examined alestids and the condition in that specimen is considered aberrant. We consequently code *R. septentrionalis* as having three epurals. Within examined outgroup taxa, three epurals are present in *Crenuchus*, *Hemiodus* and *Hepsetus*.

Although common across the Alestidae, the final most parsimonious hypothesis of relationships indicated that the presence of three epurals, rather than being a synapomorphy for the Alestidae, is derived at a more inclusive phylogenetic level within the Characiformes. This conclusion differs from that of Murray & Stewart (2002), who proposed it as a synapomorphy for the African component of the Alestidae. Those authors, however, utilized different outgroup taxa in their analysis.

149. Number of uroneural bones: (0) one pair; (1) two pairs (CI = 16; RI = 14)
Two pairs of uroneurals are present in all African components of the Alestidae, with the exception of *Arnoldichthys* and *Lepidarchus,* both of which retain only one pair. Two pairs of uroneurals are also present in most, but not all, species of *Chalceus* (but see next paragraph) and various outgroups.

Two specimens of *Chalceus erythrurus* were cleared and counterstained; the first had one pair of uroneurals and the second two pairs. This variation renders it impossible to code this feature for this species. The single cleared and stained specimen of *C. spilogyros* had one pair of uroneurals of a form notably atypical relative to that characteristic of its congeners. The unusual value of one uroneural in *C. spilogyros*, in conjunction with the anomalous morphology of that ossification in the single cleared and stained specimen of the species relative to the uroneurals of other species of *Chalceus*, raises questions as to whether the condition in this individual is anomalous. In light of that uncertainty we find it impossible to determine the condition of the uroneurals for that species.

150. Presence or absence of bony caudal-fin stays: (0) absent; (1) present (CI = 50; RI = 96)
Roberts (1969: 429, fig. 57) noted that the caudal-fin skeleton of members of the Neotropical characiform family Ctenoluciidae incorporated vertical, plate-like bones positioned anterior to the bases of both the dorsal and ventral procurrent rays. That author identified potentially homologous, albeit proportionally smaller, ossifications in the African genus *Hydrocynus* (Roberts, 1969: fig. 60; Brewster, 1986: fig. 20).

In comparative studies associated with a phylogenetic study of the Ctenoluciidae, Vari (1995: 32) confirmed that bony stays (elongate, approximately horizontally orientated, laminar, median ossifications) were widely distributed in the Alestidae (the African Characidae of that author), being present in *Alestes lateralis* Boulenger, *A. nurse* (Rüppell), *Brycinus longipinnis* (Günther), *Bryconaethiops*, *Micralestes acutidens*, *Petersius intermedius* Blache & Miton, *Phenacogrammus interruptus* (Boulenger) and *P. pabrensis*. He noted that bony stays are absent in *Lepi-*

darchus adonis and were apparently lacking in *Brycinus macrolepidotus*, based on a radiograph of a sample of that species. According to Vari (1995) the possession of bony stays might define a presumably monophyletic subunit of the Alestidae. More recently, Murray & Stewart (2002: 1893) proposed that the possession of bony caudal-fin stays was a synapomorphy for the Alestidae, a family that they limited to African taxa.

Buckup (1998: 132) defined the bony stay as a large, laminar structure present at the base of both the dorsal and ventral origins of the caudal fin and restricted its presence in his study to the New World family Ctenoluciidae. This action highlights the problems inherent within the unequivocal definition of these structures. Although the degree of development of bony stays in many species of the Alestidae falls short of the proportional size of these ossifications in the Ctenoluciidae, some taxa in the Alestidae (e.g. various species of *Micralestes* and *Bryconaethiops*) have well-developed laminar ossifications that approximate the location and proportional degree of development of the bony stays that are present in some members of the Ctenoluciidae. This complicates the definition of bony stays so as to exclude the ossifications present in some components of the Alestidae. Nonetheless, the occurrence of bony stays in units of the Alestidae is homoplastic with respect to the presence of apparently homologous bones in the Ctenoluciidae, based on recent hypotheses of relationships of the latter family (Vari, 1995; Buckup, 1998).

Caudal-fin bony stays with some degree of development positioned anterior to and overlapping the anteriormost dorsal and ventral procurrent caudal-fin rays (Fig. 30) were observed to be present across the Alestidae other than in the basal genera *Arnoldichthys* and *Chalceus* on the one hand and a subgroup of the family consisting primarily of species of smaller body size on the other (Appendix 2). The coding for *Arnoldichthys* was, however, problematic in that one of the two cleared and stained specimens lacked any ossifications in the region occupied by bony stays in many other genera in the Alestidae. In the second, meanwhile, possible bony stays, albeit smaller than those in

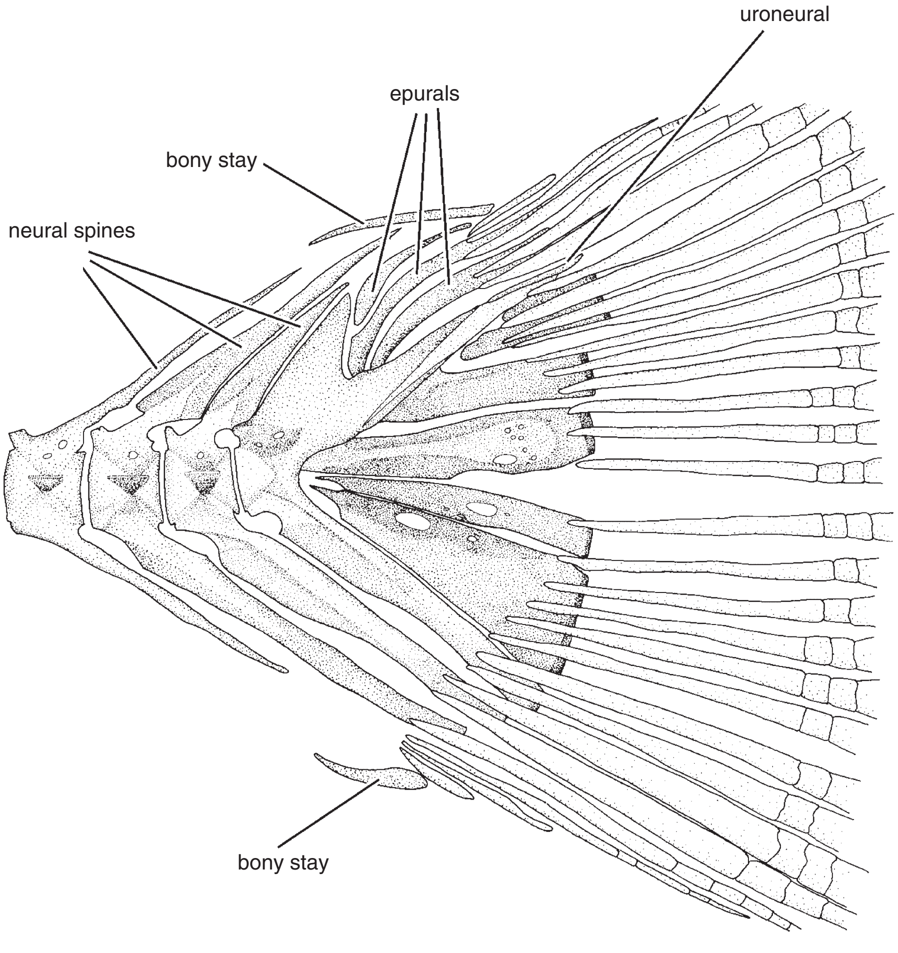

Figure 30. Caudal skeleton of *Brycinus macrolepidotus*, MZUSP 60303, 58.6 mm SL; lateral view, anterior to left.

many alestids, were present. The relatively thick scales characteristic of *Arnoldichthys* made it impossible to resolve the question of the presence or absence of the stays in other specimens of the genus via radiographs and we consequently code the condition as '?' for this character. The coding of *Petersius* as having the stays was based on radiographs of the three available whole specimens.

According to Vari (1995: 32) the homology of the bony stays is uncertain. Roberts (1969: 429) suggested that in the Ctenoluciidae these bones are apparently of dermal origin, given the absence of cartilage along their margins; he proposed that such stays may have 'originated from fusion of anterior procurrent rays.' Vari (1995) confirmed that an absence of cartilage associated with bony stays characterizes larger cleared and stained material of the Ctenoluciidae. He noted, however, that small specimens of *Boulengerella* have splint-like, unpaired, Alcian blue-staining structures positioned in the areas occupied by the bony stays in adults of the genus. No indication of cartilage was found to be associated with the bony stays in those members of the Alestidae with such ossifications.

Various of the examined outgroup characids (e.g. *Astyanax*, *Tetragonopterus*) have a small, medial ossification anterior to the series of dorsal procurrent rays. In addition to being smaller and of a different shape than the dorsal bony stay present in that general region in many alestids, this ossification in these outgroup taxa is located distinctly anterior (e.g. dorsally proximate to the anterior limit of the epurals). This outgroup structure is thus considered nonhomologous with the bony stay of alestids. Contrary to Murray & Stewart (2002: 1893) who reported that the stays were uniquely absent in *Brycinus sadleri* among the alestids that they examined in their study, we found those ossifications to be invariantly present in the examined cleared and stained specimens of that species.

LATEROSENSORY SYSTEM ON HEAD AND BODY

151. Presence or absence of laterosensory canal segment in fourth infraorbital: (0) present; (1) absent (CI = 100; RI = 100)

A laterosensory canal segment transversing the fourth infraorbital is nearly universally present among characiforms possessing that ossification (Figs 1, 2, 4). *Tricuspidalestes* is unique within the Alestidae in lacking such a canal in its relatively large, lamellar fourth infraorbital. Although a canal segment is also absent in some of the species of smaller body size in the Distichodontidae (see Daget, 1965: fig. 7), those taxa are more closely related to other members of the family retaining that structure (Vari, 1989).

Serrasalmus and *Charax* among examined outgroups have only a single ossification in the area primitively occupied by the third and fourth infraorbitals. Although the exact homology of this large ossification is uncertain, it most likely represents a fusion of these infraorbitals. An elongate laterosensory canal segment is furthermore present along the entire expanse of the likely composite bone. These taxa are thus coded as having a laterosensory canal in the fourth infraorbital. It was impossible to code *Ladigesia* and *Lepidarchus* for this feature because of the absence of a fourth infraorbital.

152. Presence or absence of laterosensory canal segment in fifth infraorbital: (0) present; (1) absent (CI = 100; RI = 100)

A laterosensory canal segment is typically present in the fifth infraorbital in those characiforms retaining that ossification (Figs 1, 2, 4). *Tricuspidalestes* is unique in the Alestidae in lacking a laterosensory canal in the fifth infraorbital, an ossification that is, furthermore, somewhat reduced in proportional overall size in that genus. It was impossible to code *Ladigesia* and *Lepidarchus* for this feature because of the lack of a fifth infraorbital in those genera.

153. Complexity of laterosensory canal system in sixth infraorbital: (0) with two branches dorsally and overall system tripartite; (1) with anterodorsal branch absent and single remaining laterosensory canal segment extending from fifth infraorbital to neurocranium (CI = 20; RI = 86)

A tripartite laterosensory canal system running through the sixth infraorbital is common to a diversity of characiforms (e.g. *Alestes baremoze*; *Brycinus macrolepidotus*, Fig. 1A; *Brycon meeki*, Weitzman, 1962: fig. 8; *Hydrocynus forskahlii*, Brewster, 1986: fig. 7) and is also present in numerous alestids and outgroup characiforms examined in this study. A subgroup of the Alestidae (Appendix 2) lacks the anterodorsal portion of the canal system that transverses that portion of the sixth infraorbital in most characiforms. As a consequence, the canal system in that ossification is reduced to a single tube communicating with the fifth infraorbital ventrally and the neurocranium dorsally. A simple canal system in the sixth infraorbital (state 1) also occurs in *Astyanax*, *Charax*, *Cheirodon*, *Crenuchus* and *Serrasalmus* among examined characiform outgroups. The condition of the laterosensory canal system in the sixth infraorbital could not be coded within the Alestidae for *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, all of which lack that ossification.

154. Connection between posterior component of sensory canal in sixth infraorbital and laterosensory canals on neurocranium: (0) through pore located on pterotic or between junction of pterotic and frontal; (1) through more anteriorly located pore located in frontal (CI = 16; RI = 28)

In most of the species examined in this study, the laterosensory canal in the sixth infraorbital bifurcates dorsally, with the anterior branch of the system, when present (see character 153), usually exiting laterally as a pore on the infraorbital without any communication with the laterosensory canal system in the neurocranium (see also comments below with respect to the condition of the canal in *Hepsetus* and in the members of the Distichodontidae).

The posterior branch of the laterosensory canal in the sixth infraorbital typically communicates in either of two distinct methods with the canal system extending through the neurocranium in the frontal and pterotic. The most common condition within examined characiforms, in general, and alestids, in particular, has the pore in the canal system situated approximately along the area of contact between the frontal and pterotic, with this opening located proximate to the pore in the posterodorsal portion of the sixth infraorbital.

A different arrangement was observed in *Alestes baremoze*, *A. dentex*, *Hydrocynus forskahlii* (but not *H. brevis*) and all *Micralestes* species with the exception of *M. elongatus* in the Alestidae and *Brycon pesu* in the outgroup. These taxa have in common a more anteriorly positioned pore in the laterosensory canal system of the neurocranium that is situated entirely within the frontal bone. The condition in *A. macrophthalmus* was coded as '?' for this character in the analysis as a consequence of the incongruent presence of state 0 on one side of the single cleared and stained specimen and state 1 on the other. It was impossible to code this character for *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* because of the absence of an ossified sixth infraorbital in those genera and the consequent absence of a corresponding pore in the neurocranium.

The overall form of the laterosensory canal system in the region where the sixth infraorbital, frontal and pterotic come together in the members of the Distichodontidae differs significantly from the arrangement of that system present in most other characiforms. *Xenocharax* lacks a direct communication between the laterosensory canal segment in the frontal and the canal segment in the pterotic. Continuity between the laterosensory systems of the pterotic and frontal is achieved via the canal system in the sixth infraorbital (Daget, 1960: fig. 7), a situation that is carried further in other members of the Distichodontidae (Vari, 1979: figs 22–25).

Although the condition in the Distichodontidae has the posterior branch of the laterosensory canal connecting with the pterotic, the revamping of the laterosensory canal system in that region of the neurocranium is so pronounced as to render that condition not directly homologous with the canal system present in the Alestidae or most other examined characiforms. We consequently code the feature in *Xenocharax* as '–' for this character. Similarly, *Hepsetus* lacks direct communication between the laterosensory canal systems in the frontal and pterotic, with continuity between those systems achieved through the system in the intervening sixth infraorbital in larger examined cleared and stained specimens (smaller specimens lack a canal segment within the sixth infraorbital communicating with the canal segment in the frontal). We also code *Hepsetus* as '–' for this feature.

155. Form of epiphyseal branch of supraorbital canal: (0) relatively elongate and simple; (1) short, with two or three short branches arising from main body of supraorbital canal (CI = 50; RI = 75)

The epiphyseal branch of the supraorbital canal is typically aligned with the medial epiphyseal process of each frontal. It extends to the margin of the frontoparietal fontanel when that medial opening is present (e.g. *Brycon meeki*, Weitzman, 1962: fig. 9) but falls short of the joint between the contralateral frontals when the opening is absent. *Alestes* and *Hydrocynus* are unique among taxa examined in this study in having the epiphyseal branch of the supraorbital canal distinctly shortened relative to the typical condition, with two or three short side branches extending dorsally from the main canal (see Brewster, 1986: fig. 1A). Although there is a presumed homology between one of these short canals and the shortened version of the epiphyseal canal that is present in other alestids (and most characiforms), the others canals apparently represent *de novo* structures.

156. Degree of development of parietal branch of supraorbital laterosensory canal: (0) extending from main supraorbital canal across posterior portion of frontal and into parietal; (1) either absent or distinctly shortened and falling short of parietal (CI = 50; RI = 92)

In the majority of examined species of the Alestidae, the parietal branch of the supraorbital laterosensory canal extends posteriorly to the rear of the frontal and continues into the parietal, a type of system common across the Characiformes. In the species within the Alestidae with state 1 (Appendix 2), the posterior section of the canal is instead completely absent or in the case of *Phenacogrammus urotaenia* is represented solely by a very short canal segment. Looking at examined outgroups, we find that the canal is also short in *Hepsetus*.

Among other characiforms, a reduction of the parietal branch of the supraorbital laterosensory canal also characterizes the Ctenoluciidae (Vari, 1995: 16, fig. 5) and is present within the Lebiasinidae (Weitzman, 1964: fig. 2; Vari, 1995: 16) and Characidiinae (Buckup, 1993b: 312). These outgroups, however, are not hypothesized to be closely related to the Alestidae (Vari, 1995; Buckup, 1998) and the reduction of the extent of the canal in these various Neotropical taxa is hypothesized to be homoplastic relative to the presence of a similar feature in some species of the Alestidae.

In their discussion of miniaturization in fishes, Weitzman & Vari (1988: 445) cited a reduction in the degree of development of the laterosensory canal system on the head and body as an apparently paedomorphic trend characteristic of such miniatures. Although the group within the Alestidae characterized by the reduction of this portion of the laterosensory canal includes taxa of small body size (e.g. *Lepidarchus adonis*, 15.5–18.1 mm SL), it also encompasses species distinctly larger as adults than those forms that are usually considered to be miniatures (e.g. *Phenacogrammus aurantiacus* (Pellegrin), 67.0 mm SL).

157. Presence or absence of laterosensory canal in parietal: (0) present, extending from suture between frontal and parietal to posterior portion of parietal; (1) absent (CI = 25; RI = 81)

In characiforms, the parietal branch of the supraorbital canal typically continues from the frontal into the parietal and to the rear of that bone (e.g. *Brycon meeki*, Weitzman, 1962: fig. 9). Taxa that lack the posterior portion of the parietal branch of the supraorbital canal within the frontal also lack the component of the canal in the parietal. The parietal canal is absent in *Alestopetersius*, *Bathyaethiops*, *Brachypetersius altus*, *Clupeocharax*, *Duboisialestes*, *Hemmigrammopetersius barnardi, Ladigesia*, *Lepidarchus*, *Nannopetersius*, *Phenacogrammus*, *Tricuspidalestes* within the Alestidae and in *Cheirodon* and *Hepsetus* in outgroups examined in this study and various other characiforms of small body size (see Weitzman & Fink, 1985: figs 51–55).

158. Presence or absence of supratemporal laterosensory canal: (0) present and running parallel and proximate to posterior margin of parietal, contacting extrascapular laterosensory canal; (1) absent (CI = 100; RI = 100)

The supratemporal laterosensory canal segment is present in many characiforms (e.g. *Brycon meeki*, Weitzman, 1962: fig. 9) and in all examined species of the Alestidae with the exception of *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, all of which are taxa of relatively small body size. Among outgroup characiforms, albeit those not included in the analysis, the canal segment is absent in some species in the New World Lebiasinidae (Weitzman, 1964: fig. 2) and the canal is shortened, albeit still present, in some members of the South American family Ctenoluciidae (Vari, 1995: 17, fig. 5) and various characiforms of small body size (see Weitzman & Fink, 1985: figs 51–55).

159. Presence or absence of laterosensory canal segment in pterotic: (0) present, contacting extrascapular canal posteriorly, preopercular canal ventrally and canals in frontal and/or sixth infraorbital anteriorly; (1) absent (CI = 100; RI = 100)

A laterosensory canal segment in the pterotic is widely distributed across the Characiformes (e.g. *Brycon meeki*, Weitzman, 1962: fig. 9) but is absent within the Alestidae in *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, all of which are species of relatively small body size. The absence of the canal segment in the pterotic is unique to these taxa among the groups examined in this study.

Elsewhere in the Characiformes a reduction or absence of this canal segment also occurs in some members of the African family Distichodontidae, in which the posterior extension of the sixth infraorbital (dermosphenotic) results in a reduction in the canal-bearing portion of the pterotic (Vari, 1979). Within that family, a subunit of *Neolebias* encompassing some of the smallest species in that genus also lacks a canal segment within the pterotic (Vari, 1979: 328). That absence of the canal is considered homoplastic to the absence of the system in *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* within present hypotheses of higher-level relationships within the Characiformes (Vari, 1979; Buckup, 1998; this study).

160. Presence or absence of laterosensory canal segment in post-temporal: (0) present, extending between laterosensory canal segments in extrascapular and supracleithrum; (1) absent (CI = 100; RI = 100)

The laterosensory canal segment within the post-temporal is absent within the Alestidae in *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*. In the case of *Lepidarchus*, the post-temporal is apparently fused with the supracleithrum (see character 128), without any indication of a laterosensory canal segment in the resultant complex ossification. The condition in that genus is consequently coded as the absence of the canal segment. *Clupeocharax* is coded as questionable since one of the two examined cleared and stained specimens of the genus retained a canal in the post-temporal while the other did not. Although all examined outgroup taxa in this study retain the canal segment in the post-temporal, that structure is also absent elsewhere in the Characiformes in the Neotropical family Chilodontidae (Vari, 1983: 34–35, figs 30, 31), a family that is more closely related to the Neotropical families Anostomidae, Curimatidae and Prochilodontidae (Vari, 1983) than it is to the Alestidae.

161. Presence or absence of laterosensory canal segment in supracleithrum: (0) present; (1) absent (CI = 100; RI = 100)
Lepidarchus has a single ossification in the dorsal portion of the pectoral girdle that, based on its location and overall form, apparently represents a fused post-temporal plus supracleithrum (see character 128). This composite bone lacks any indication of the laterosensory canal segment in the supracleithrum present in all other outgroup characiforms in this study, albeit also absent in some Neotropical characids (e.g. various glandulocaudines, see Weitzman & Fink, 1985: figs 52–54).

162. Degree of development of lateral line: (0) complete and extending to rear of caudal peduncle, or if reduced then absent on only few terminal scales of lateral line series; (1) distinctly reduced, with number of scales that lack laterosensory canal and associated pores greater than number of scales that have them (CI = 20; RI = 63)
A reduction in the extent of the poring of the lateral line occurs independently in a variety of characiforms, with the tendency for such reductions to be more typical of, albeit not exclusive to, species of small to diminutive body size. In species of the Alestidae of smaller body size (Appendix 2), the degree of poring is often, but not always, reduced, with the extent of the reduction resulting in the presence of only 1–15 pored scales along the lateral-line series (possession of one pored scale limited to *Lepidarchus*, whereas the other species have five or more).

These scale counts, even at the higher end of this range, represent less than one-half of the total longitudinal number of scales in any particular species. Alternatively, in *Bathyaethiops*, *Brachypetersius gabonensis*, *Duboisialestes*, *Rhabdalestes eburneensis* (Daget) and *R. septentrionalis* the reduction in the poring of the lateral line is limited to the 3–6 posteriormost scales in that series. In these species, however, there is pronounced variation in the degree of incompleteness of the poring, not only among specimens of a species from a single population sample, but also, on occasion, on both sides of a single individual. In light of that variation, we limit the utilization of the reduction of the pored lateral line scales to those species with a distinctly shortened lateral line, as evidenced by having a higher number of scales with the pores absent rather than present. Among examined outgroups, the presence of lateral-line poring reduced to such a degree was restricted to *Crenuchus* and *Cheirodon*.

163. Length of laterosensory canal system of lateral line: (0) lateral line not extending beyond posterior limit of caudal peduncle; (1) lateral line extending beyond posterior limit of caudal peduncle and onto middle rays of caudal fin (CI = 100; RI = 100)
In all alestids, the pored scales and the associated laterosensory canal system of the lateral line, when complete, terminate proximate to the base of the caudal-fin rays. In *Salminus*, *Triportheus* and all species of *Brycon* among the examined outgroups, the scales and associated laterosensory canal extend further posteriorly and distinctly overlap the membrane between the middle rays of the caudal fin. This character was not coded for those species with a reduction in the length of the pored portion of the lateral line discussed in character 162.

164. Relative position of laterosensory canal of lateral line on body: (0) lateral line located approximately along horizontal midline of body or only slightly ventral to that location and approximately at middle of caudal fin at hypural joint; (1) lateral line ventrally decurved and located approximately at level of base of second to sixth principal fin ray of lower caudal-fin lobe at point where lateral line crosses vertical through hypural joint (CI = 33; RI = 88)
Myers (1929: 4) remarked on the relatively ventral position of the lateral line in what he termed the ‘characin fishes of Africa’, an apparent reference to African component of the Alestidae of this study. All members of the Alestidae with the exception of *Arnoldichthys* and *Bryconaethiops* are characterized by the possession of a lateral line that, when present, is relatively ventrally positioned (e.g. *Brycinus grandisquamis* (Boulenger) (Fig. 19). This is best quantified by the position of the lateral line at the point where it crosses the vertical through the hypural joint.

In alestids other than *Arnoldichthys* and *Bryconaethiops* the lateral line at that point is located approximately along the horizontal intersecting the bases of the second through sixth rays on the lower lobe of the caudal fin. This ventral position of the lateral line on the posterior portion of the body is also reflected in the disparity in the relative number of scales above and below the lateral line on the narrowest portion of the caudal peduncle. Members of the Alestidae with a ventrally shifted lateral line usually have $^1/_2$ to $1^1/_2$ series of scales below the lateral line vs. $3^1/_2$ to $5^1/_2$ series of scales above the lateral line in that location. Examined outgroups, in contrast, have equivalent (e.g. *Hepsetus*, *Hoplias*, *Piaractus*, *Serrasalmus* and *Xenocharax*) numbers of scales above and below the lateral line; alternatively, if a difference occurs in the number of scales, then the disparity in the number of rows of scales dorsal and ventral to the lateral line is less pronounced than that typical of most taxa in the Alestidae.

Two exceptions to the aforementioned generalized, ventrally positioned lateral line, occur within the Alestidae, although they involve different conditions. All of the species of *Bryconaethiops* have an only slightly decurved lateral line (Fig. 20) that is symmetrically positioned along the caudal peduncle at the hypural joint (usually $2^1/_2$ scales below and $2^1/_2$ scales above the lateral line) and with the posteriormost pored lateral-line scales positioned over the middle caudal-fin rays. This arrangement closely approximates the alignment of the lateral line present in the outgroups and is coded as state 0.

Arnoldichthys spilopterus retains the overall ventral position of much of the lateral line system along the body that typifies most taxa within the Alestidae; however, contrary to other members of the family, the posterior portion of the lateral line in that species curves dorsally to the level of the middle of the posterior portion of the caudal peduncle and terminates posteriorly over the middle caudal-fin rays. A similar ventral curvature of the lateral line on the anterior but not posterior portion of the body occurs in the outgroup taxon *Triportheus*.

Despite the overall ventral curvature of most of the lateral line along most of its length in these two genera, both were coded as state 0 for the character in the analysis, given that the lateral line in each genus is situated at the level of the middle caudal-fin rays at the point where the lateral line crosses the hypural joint. This character could not be coded for the species that have the reduction in the length of the pored portion of the lateral line discussed in character 162, in which the poring of that system terminates anterior to the caudal peduncle.

165. Morphology of sensory canal on lateral-line scales in portion of scale proximate to region of overlap of sequential scales: (0) simple, with only short side branch terminating in pore; (1) highly divided, with branches extending dorsal and ventral to primary horizontal canal and with each branch terminating in pore (CI = 50; RI = 0)

Variation in the form of the laterosensory canal in the lateral line scales occurs in a variety of taxa within the Characiformes, but most members of the order have a simple canal system terminating posteriorly in a single pore in each scale. *Alestes macrophthalmus* has a form of the laterosensory canal system in the scales of the anterior one-third of the lateral line that is unique within the Alestidae (Fig. 31). In those scales the originally simple tube present in outgroups is significantly branched posteriorly and has up to ten lateral pores.

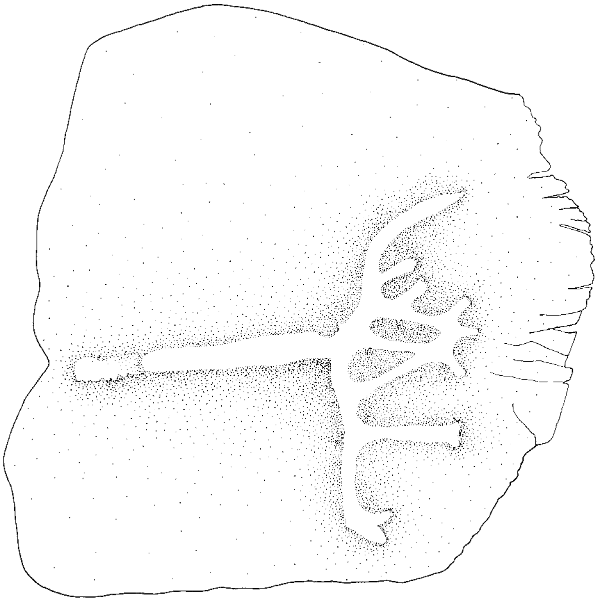

Figure 31. Lateral-line scale of *Alestes macrophthalmus*, USNM 42368, 176.3 mm SL; lateral view, anterior to left.

Although some other species in the Alestidae have usually ventrally directed side branches of the primary canal in the anterior scales of the lateral line series (e.g. *Alestes baremoze*, *A. dentex* and *Brycinus macrolepidotus*), none of these species have the branching patterns of the canals as complex as is the system that is characteristic of *A. macrophthalmus*. Among examined outgroup taxa, various species of the Neotropical genus *Brycon* (Zanata, 2000: fig. 56) are known to possess comparable modifications of the canal system in the anterior scales of the lateral line. This New World lineage is, however, distant phylogenetically from *A. macrophthalmus* (Zanata, 2000; this study). This character was not coded herein for *Lepidarchus*, which lacks nearly all scales on the body (see character 167).

166. Morphology of sensory canal segment of lateral-line scales in portion of scale distinctly posterior to limit of overlap of sequential scales: (0) simple, or with only single short side branch; (1) highly divided, with branches dorsal and ventral to primary horizontal canal arising distinctly posterior to limit of posterior margin of preceding scale and with each branch terminating in pore (CI = 100; RI = 100)

In the species of *Chalceus* the sensory canal in the anterior scales of the lateral line is elaborated into a

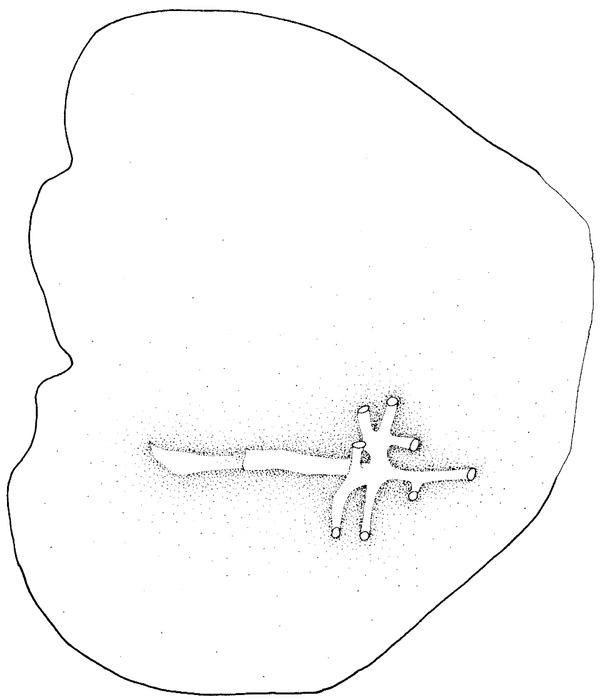

Figure 32. Lateral-line scale of *Chalceus macrolepidotus*, MZUSP 43291, 207.9 mm SL; lateral view, anterior to left.

complex series of branches, all terminating in a pore distally (Fig. 32). Although the complexity of the branching pattern and pores in these lateral line scales is at first reminiscent of that present in the scales of *Alestes macrophthalmus* (see previous character), the canal complex in the character in question is positioned distinctly further posteriorly on the body of the scale in *Chalceus* than it is in *A. macrophthalmus*. Given their positional nonequivalence, these modifications of the laterosensory canals in the scales of these two taxa are considered nonhomologous. The character was not coded for *Lepidarchus*, which lacks nearly all scales on the body (see character 167).

SCALES

167. Presence or absence of scales on body: (0) body entirely covered by scales, or scales missing only along dorsal midline; (1) dorsal region of body without scales over broad region from rear of head to posterior to dorsal-fin base; (2) body completely without scales except for one small, canal-bearing scale located at anterior limit of lateral line system on body and one scale situated anterior to base of anal fin (CI = 100; RI = 100)

Having the body totally covered by scales is the typical condition both across the Characiformes and among nearly all members of the Alestidae. As noted by Géry (1968: 78, fig. 5) the dorsal region of the body in *Ladigesia roloffi* Géry lacks scales over a broad region from the rear of the head to a point in front of adipose fin (see also Paugy, 1990b: fig. 20.39). *Ladigesia roloffi* lacks approximately three of the dorsal rows of scales anteriorly on each side of the body, with a progressive decrease posteriorly in the number of absent scale rows. *Lepidarchus adonis* is, in turn, effectively scaleless other than for the presence of one scale at the anterior limit of the lateral-line system on each side of the body and a second situated on each side of the anterior limit of the base of the anal fin (Roberts, 1966: 209). Roberts (1966: 211), however, reported a short bony canal 'apparently derived from two or three scales' immediately anterior to the anterodorsal corner of the pseudotympanum in *Lepidarchus*, a feature absent in the cleared and stained specimens of the species examined in this study, all of which have a single scale anteriorly.

Although the presence of scales over the entire body is a nearly universal attribute of characiforms, a reduction in extent of the scale cover on the body has occurred, apparently independently, in various groups within that order. The Argentinean characid genus *Gymnocharacinus* lacks scales almost completely (see Miquelarena & Arámburu, 1983: fig. 16). In the Neotropical characid subfamily Serrasalminae, the median scales along the predorsal line are absent, a feature that was proposed as a synapomorphy for that subfamily by Machado-Allison (1983: 161). Various other characids (e.g. some species of *Astyanax*) also lack median predorsal scales.

The reduction in the extent of the degree of scalation in those outgroup taxa (with the exception of *Gymnocharacinus*) is, however, less extensive than in *Lepidarchus* and *Ladigesia* and thus questionably homologous. Furthermore, available phylogenetic information fails to support a hypothesis of the homology of scale reduction *per se* across those taxa. Although the exact phylogenetic positions of *Astyanax, Gymnocharacinus* and the Serrasalminae are undetermined, all of these taxa lack the synapomorphies for the Alestidae. The reduction or absence of body scales in *Lepidarchus* and *Ladigesia* vs. *Gymnocharacinus*, the Serrasalminae and components of *Astyanax* is consequently considered to represent homoplastic losses.

168. Arrangement of scales along posterodorsal margin of head: (0) scales arranged along margin of supraoccipital spine; (1) scales cover supraoccipital spine and insert into groove along posterior margin of parietal bones (CI = 25; RI = 80)

In characiforms, the scales on the dorsal surface of the body behind the head are usually arranged along the margin of the median supraoccipital spine, extending varying distances posteriorly from the main body of the cranium. As a consequence, in most examined characiforms there is a rounded or parabolic anterior margin of the scale field on each side of the middorsal line (e.g. *Brycon argenteus* Meek & Hildebrand, Vari, 1995: fig. 11a). In *Arnoldichthys*, *Chalceus* and some species of *Brycinus* in the Alestidae and in *Brycon pesu*, *Hepsetus* (Vari, 1995: fig. 11c) and *Hoplias* in the outgroup, the dorsal scales of the anteriormost portion of the body dorsally overlap the supraoccipital spine and the anterior margins of the scale series insert into a variably developed, transversely relatively straight, groove positioned along the posterior margin of the parietal bones.

The presence of a scale field extending medially to cover the supraoccipital spine was reported among other characiforms by Vari (1995: 29, fig. 11) in the Neotropical families Lebiasinidae, Erythrinidae and Ctenoluciidae, a pattern interpreted by that author as derived. That hypothesis is in keeping with the results of this study. The condition of this character was not coded for *Lepidarchus* and *Ladigesia* in this study as a consequence of the lack of scales on the anterodorsal region of the body in those two genera.

169. Relative size of scales dorsal and ventral to lateral line: (0) scales approximately of the same size overall and gradually decreasing in relative size ventrally; (1) scales situated dorsal to lateral line much larger than those ventral to lateral line (CI = 50; RI = 80)

The nearly universal condition of the relative size of the body scales among characiforms is the absence of a pronounced difference in the relative size of the scales located dorsal and ventral to the lateral line. *Arnoldichthys* and *Chalceus* (Fig. 33) are apparently unique within the Characiformes in having the scales situated dorsal to the lateral line distinctly larger than those located ventral to the lateral line (see Poll, 1967a: fig. 10; Fowler, 1950: fig. 413a, for illustrations of the relative sizes of the scales on the body in *Arnoldichthys* and *Chalceus*, respectively). The disparity in the size of the scales situated dorsal and ventral to the lateral line was proposed as diagnostic for *Arnoldichthys* by Myers (1926: 174; 1929: 4), Hoedeman (1951: 6), Géry (1977: 50) and Paugy (1990a: 78; 1990b: 232), and was used to define *Chalceus* by Eigenmann (1912: 256, 372) and Géry (1977: 342). Coding of this character for *Lepidarchus* was impossible since the genus lacks most of the scales on the body (see character 167).

170. Relative size of scales along lateral line: (0) scales along lateral line gradually diminish in size towards caudal peduncle; (1) scales along lateral line other than on caudal peduncle alternatively large and small (CI = 50; RI = 80)

As discussed in character 169, in *Arnoldichthys* and *Chalceus* the scales dorsal to the lateral line are distinctly larger than those below it. Associated with that abrupt change in scale size at the level of the lateral line is a pattern of alternatively large and small scales (Fig. 33) that was not encountered elsewhere among characiforms. The larger of the lateral line scales are smaller than those located above it, with the small scales in this series approximately the same size as those situated ventral to the lateral line. Such disparity in size of the sequential lateral line scales disappears over the caudal peduncle, with the scales in that portion of the lateral line in both *Arnoldichthys* or *Chalceus* approximately the same size as those situated ventral to it.

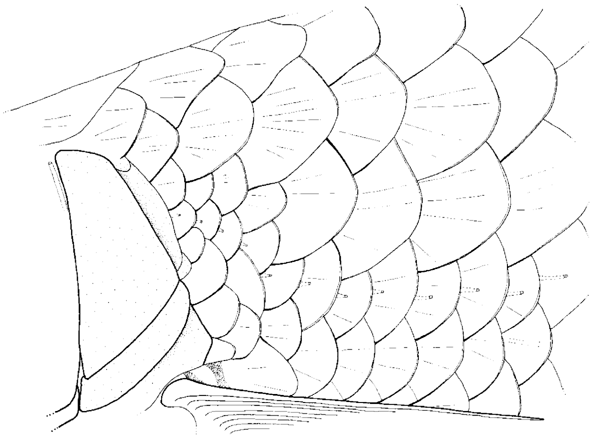

Figure 33. Posterior portion of head and anterior portion of lateral surface of body of *Chalceus erythrurus*, showing different sizes of scales dorsal and ventral to, and along, lateral line; MZUSP 75613, 92.4 mm SL; left side, lateral view.

Alternation of large and small lateral-line scales in *Arnoldichthys* and *Chalceus* results in an increase in the total number of scale series in the lateral line relative to the counts in the scale row immediately dorsal to the lateral line (e.g. 30 or 31 scales along the lateral line vs. 20–22 in the immediately dorsal row in *Arnoldichthys,* and 38–40 vs. 23–25, respectively, in *Chalceus macrolepidotus*; counts based on five specimens of each form). Such pronounced disparity in the number of scales in these adjoining rows of scales was noted for *Chalceus* by Géry (1977: 342), but was neither previously cited for *Arnoldichthys* nor observed in any other examined characiform. The condition of this character was not coded for *Lepidarchus* as a consequence of the lack of scales over most of the body in that genus (see character 167).

171. Circuli on exposed portion of scales: (0) distinct from state 1; (1) with overall posterior orientation and individual circuli relatively straight or slightly inclined towards horizontal midline of scale (CI = 16; RI = 75)

A pronounced degree of variation occurs in the pattern of circuli on the scales across the Characiformes.

Various authors (e.g. Cockerell, 1910) have utilized this information in an attempt to delimit groups within the order. The circuli among groups examined in this study range from totally absent or very reduced (e.g. *Brycon falcatus, Bryconops*, *Triportheus*, Cheirodontinae and Tetragonopterinae), to well-developed and continuous with the anterior portion of the scales (e.g. *Chalceus*, *Crenuchus*, *Hoplias*, *Salminus*, *Serrasalmus* and *Xenocharax*).

A notable degree of variation occurs in this system across the Alestidae. Most members of the family have poorly developed or absent circuli on the posterior portion of the scales. These conditions range from the apparent absence of circuli in most species of *Rhabdalestes* and *Phenacogrammus* to circuli that are represented by interrupted lines on the exposed portion of the scale in *Alestes*, *Bryconaethiops* and *Hydrocynus*.

It proved impossible to unambiguously parse much of the variation in the degree of development of the circuli into discrete characters. The only distinct, phylogenetically informative pattern that we were able to identify occurs in *Arnoldichthys*, *Brachypetersius gabonensis*, *Brycinus*, *Chalceus*, *Micralestes acutidens* and *M. occidentalis* (Günther) in the Alestidae and in *Crenuchus* and *Hoplias* among outgroups. In these taxa the posterior circuli have developed into obvious ridges (Fig. 34) on all scales sampled from the region between the lateral line and the insertion of the dorsal fin. Such ridges, rather than paralleling the contour of the posterior margin of the scale, are either orientated towards the posterior border of the scale (*Arnoldichthys*, *Brycinus bimaculatus*, *B. carolinae*, *B. kingsleyae*, *B. lateralis*, *B. leuciscus*, *B. macrolepidotus*, *B. nurse*, *Chalceus*) or are somewhat directed towards the horizontal midline of the scale (*Brachypetersius gabonensis*, *Brycinus sadleri*, *Micralestes acutidens*, *M. occidentalis*). It is impossible to determine the form of the circuli in *Lepidarchus* that possesses only a few, poorly developed scales (see character 167).

172. Position of scale radii: (0) radii usually restricted to posterior portion of scale; (1) radii originate on centre of scale and extend in various directions onto both anterior and posterior portions of scale (CI = 50; RI = 90)

In members of the Characiformes radii often originate on the central portion of the scale and extend in various directions to its margins. Within the Neotropical Characidae the most common condition is for the radii, when present, to originate in the central portion of the scale and to extend posteriorly, with the individual radii being orientated approximately in parallel to each other. In the case of the Neotropical serrasalmines *Piaractus* and *Serrasalmus*, the poorly developed radii are, nonetheless, posteriorly directed. In *Tetragonopterus* the radii are relatively reduced, being represented only by a vertical line separating the anterior and posterior portions of the scale.

Figure 34. Scale removed from area between dorsal fin and lateral line of *Brycinus macrolepidotus*, MZUSP 60303, 58.6 mm SL; lateral view, anterior to left.

Nearly all species of the Alestidae (Appendix 2) have well-developed radii originating on the central portion of the scale, extending radially in various directions, including anteriorly (Figs 33, 34). This arrangement differs from that present in the members of the Neotropical Characidae, in which anteriorly directed radii are usually absent (see Cockerell, 1910; pl. 1, figs 4–6) and such an overall pattern is absent in most other examined characiform taxa. Among examined outgroup taxa we discovered that a condition similar to the pattern characteristic of most members in the Alestidae also occurs in *Hepsetus*, *Hoplias* and *Triportheus*. No radii were observed in *Xenocharax* and that genus was coded as '–' in the matrix. It is impossible to determine the form of the radii in *Lepidarchus*, a genus retaining only a few, poorly developed scales (see character 167).

PIGMENTATION ON BODY AND FINS

173. Presence or absence of deep-lying midlateral stripe extending along body onto caudal peduncle: (0) absent; (1) present (CI = 14; RI = 68)

A dark midlateral stripe extending varying distances along the body and onto the caudal peduncle, but falling short of the base of the caudal-fin rays, is present within the Alestidae in *Brycinus lateralis*, *B. leuciscus*,

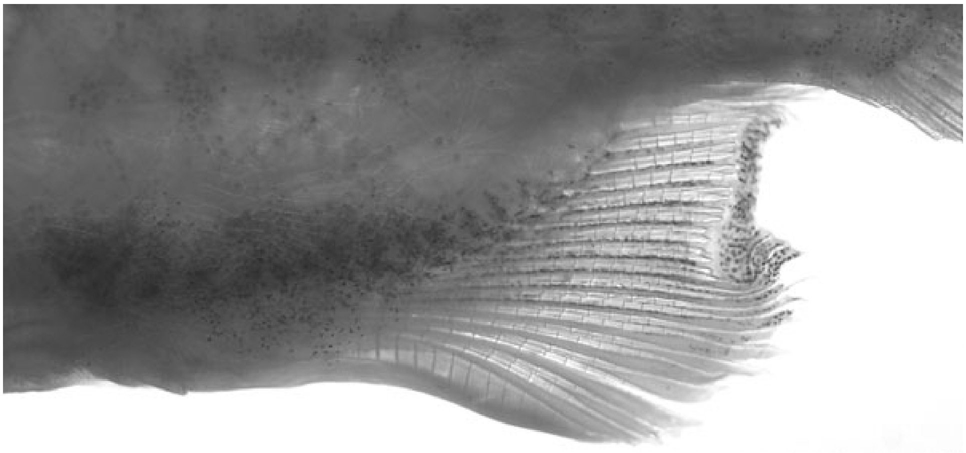

Figure 35. *Rhabdalestes eburneensis*, USNM 193974, male, 40.7 mm SL; anal fin and adjoining posterior portion of body, left side, lateral view.

B. sadleri, *Bryconaethiops microstoma*, *Chalceus epakros*, *C. guaporensis*, *Hemmigrammopetersius*, *Micralestes*, *Rhabdalestes* and *Virilia*. Examination of alcohol-preserved specimens of these taxa reveals that this dark stripe is formed by concentrations of large chromatophores that are positioned deep in the skin underlying the scales. Such a condition is present in *Astyanax* and *Bryconops* among the examined outgroups.

In *B. microstoma* this deep-lying midlateral stripe appears to be overlain by a second set of dark chromatophores situated within the skin underneath the surface of each scale in that region. This superficial dark pigmentation comes off with the scales. The presence of this more superficially positioned dark pigmentation represents an apparent autapomorphy for that species within the Alestidae.

The specimen of *Bryconaethiops macrops* cleared and stained in this study, and the only specimen examined herein, lacked dark pigmentation. Furthermore, the original description of the species (Boulenger, 1920: 15) is uninformative as to whether the species possesses a midlateral stripe. We consequently code the species as having state 0 for this character in the analysis.

Although *Brycinus carolinae* has a midlateral stripe, the dark chromatophores forming that stripe are restricted to the superficial skin layers and are lost with the removal of the scales overlying the stripe. This is a condition different than that in the chromatophores in the species with state 1 and *B. carolinae* is thus coded as state 0.

174. Presence or absence of band of dark chromatophores above anal fin: (0) absent; (1) present (CI = 50; RI = 91)
A longitudinal band of dark chromatophores located on the ventrolateral surface of the body wall above the anal-fin base occurs in all species of *Hemmigrammopetersius*, *Ladigesia*, *Micralestes*, *Rhabdalestes* (Fig. 35) and *Virilia*. In most examined specimens of these listed taxa other than *Ladigesia* (see below) the chromatophore field on the second series of scales above the anal fin originates anterior to the vertical through the base of the first anal-fin ray. This dark pigmentation continues directly posteriorly over the scale series situated immediately above the anal fin and terminates on the basal portion of the posterior anal-fin rays (e.g. *Rhabdalestes septentrionalis*, see Paugy, 1990b: 231, fig. 20.36; *H. barnardi*, see Skelton, 1993: 205; *H. intermedius*, see Géry, 1977: figure on p. 46). *Ladigesia* lacks the posterior portion of the stripe over the anal-fin rays but retains the remainder of the stripe in both sexes.

Looking at the other alestids, *Brycinus lateralis* and *B. sadleri* have a concentration of dark chromatophores on the ventrolateral portion of the body proximate to the base of the anal fin. The chromatophore field in these two species neither forms a discrete band nor extends to the anal-fin rays, a considerably different condition than that present in the taxa listed above and one that is thus considered nonhomologous with the pattern in the genera with state 1.

175. Extent of development of dark pigmentation on dorsal fin: (0) absent or limited to distal borders of fin rays; (1) present in two patches, one along margins of basal half of fin rays, the other covering distal portion of last unbranched and first through third or fourth branched rays and intervening membranes (CI = 100; RI = 100)
Micralestes acutidens and *M. occidentalis* have the distinctive pigmentation pattern described under state 1 that is absent in other examined species in the Alestidae. The dark pigmentation on the distal portion

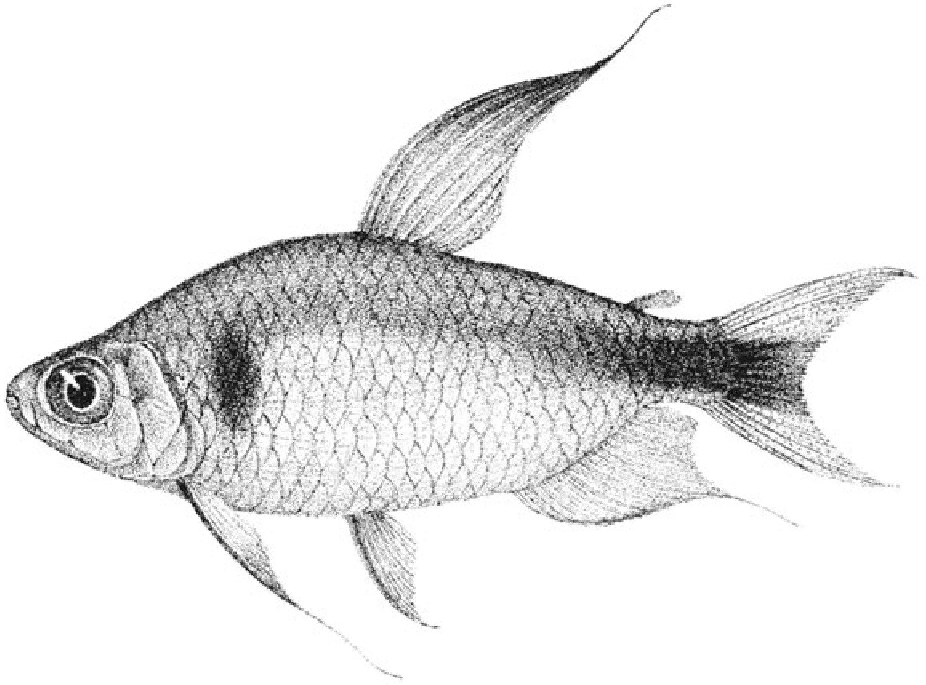

Figure 36. *Nanopetersius ansorgii*, showing elongation of fins (taken from Boulenger, 1912: pl. 17, fig. 2).

of the dorsal fin in some species of *Rhabdalestes* differs from that of the two species of *Micralestes* in being limited to the distal portion of the dorsal fin and is, furthermore, not accompanied by the more basal dark pigmentation that is present on the dorsal fin in *Micralestes acutidens* and *M. occidentalis*.

SEXUAL DIMORPHISM OF FINS

176. Sexual dimorphism in degree of development of first through third pectoral-fin rays: (0) absent; (1) present with first through third rays filamentous distally (CI = 100; RI = 100)

Nannopetersius ansorgii (Boulenger) is unique among the species examined in this study in having the first through third rays of the pectoral fin, most notably the second ray, elongate and extending beyond the primary margin of the fin (Fig. 36). Such an extension was, however, not illustrated by Poll (1967a: fig. 24) for the male lectotype of the species, raising the possibility that the presence of this feature is seasonably variable such are various other features in some characiforms.

177. Sexual dimorphism in degree of development of anterior branched dorsal-fin rays: (0) absent; (1) present (CI = 33; RI = 84)

Several subunits of the Alestidae demonstrate sexual dimorphism in the degree of development of the anterior branched dorsal-fin rays. In the males of *Alestopetersius*, *Bryconaethiops* (see, however, comments below), *Bryconalestes*, *Duboisialestes*, *Nannopetersius* and *Phenacogrammus*, the second through fourth or fifth branched dorsal-fin rays are distinctly elongate relative both to the posteriormost unbranched dorsal-fin rays and the remaining branched dorsal-fin rays (Fig. 36).

This elongation, absent in females of these taxa, is a function of the elongation of the portion of the rays situated distal to the branch between the two primary components of each ray. Although the examined specimens of *Alestopetersius* lack such a sexually dimorphic elongation of the anterior branched dorsal-fin rays, Poll (1967a: 77) followed by Paugy (1990b: 229, fig. 20.34) reported the elongation of these rays for the species of the genus included in this study.

Looking at other species in the Alestidae, we find that one species of *Bryconaethiops* (*B. yseuxi* Boulenger) was shown by Roberts & Stewart (1976: 273, pl. 6) to have a pronounced elongation of the apparently anterior rays of the dorsal fin; however, those authors did not explore the question of the presence or absence of that feature among its congeners. Although an elongation of the dorsal-fin rays was absent in the material of *Bryconaethiops* examined in this study, Géry (1977: 20) reported the presence of dorsal-fin filaments on unspecified rays in all species of *Bryconaethiops*. Teugels & Thys van den Audenaerde (1990): 210) in their description of the dorsal fin in

B. quinquesquamae similarly reported: 'third dorsal ray usually longest, becoming filamentous in largest specimens', with the elongate ray presumably being the first branched fin-ray (two unbranched dorsal-fin rays being present in the genus).

Boulenger (1920: 15, fig. 6) also reported the presence of such elongation of the dorsal-fin rays in *Bryconaethiops macrops*, while Poll (1967b: fig. 33) and De Vos *et al*. (2001: figs 22, 23) presented photos of male and female *B. microstoma* illustrating the distinct elongation of the anterior rays of the dorsal fin in males vs. females of that species. In light of this consistent information from the literature, we code all species of *Bryconaethiops* in this analysis as having state 1 for this character. Further analysis is, however, required to confirm that the elongation of the anterior dorsal-fin rays in the species of *Bryconaethiops* is equivalent to that state in the other taxa coded herein as having that character.

Although *Tricuspidalestes* has an elongation of some of the rays of the dorsal fin, the elongate fin-rays in that genus are apparently the last unbranched and perhaps first branched dorsal-fin rays (Matthes, 1964: Fig. A in pl. II; species identified therein as *Phenacogrammus caeruleus*). This condition is different from that present in the taxa coded as having state 1 for this character.

178. Sexually dimorphic elongation of pelvic-fin rays in males: (0) absent; (1) present (CI = 50; RI = 66)

Examined males of *Bryconalestes derhami* and *B. longipinnis* demonstrate a distinct elongation of the first branched pelvic-fin ray that in *B. longipinnis* extends posteriorly beyond the anal-fin origin. These species also have an elongation of the second branched ray, but with a less pronounced degree of development. Comparable modifications of these pelvic fin-rays were also reported to be present in *Bryconalestes intermedius* and *B. longipinnis* by Paugy (1986: 97, 99, 117) and were illustrated for *B. longipinnis* by Géry (1977: 41) (note that these authors assigned these species to *Brycinus*).

Although no identical elongations of these pelvic-fin rays were found in most other examined taxa in the Alestidae, an elongation of the first three branched pelvic-fin rays does occur in *Nannopetersius*, a condition subsuming the elongation of the first and second rays present in *Bryconalestes*. The elongations in the two genera are consequently coded as equivalent, although the greater number of elongate pelvic-fin rays in *Nannopetersius* may represent an autapomorphy for that genus.

The elongation of the pelvic-fin rays illustrated for *Tricuspidalestes* by Matthes (1964: Fig. A in pl. II, as *P. caeruleus*) is according to that author (p. 54) apparently a function of the pronounced elongation of the 'external' (presumably the unbranched lateralmost) pelvic-fin ray, a different condition than that present in *Bryconalestes* and *Nannopetersius*, in which the two lateralmost branched rays on the pelvic fin are elongate.

Anal fin. Various components of the Alestidae (e.g. *Arnoldichthys*, *Brycinus carolinae*, *B. lateralis*, *B. sadleri*, *Bryconaethiops boulengeri*, *Bryconalestes longipinnis*, *Clupeocharax*, *Lepidarchus*, *Micralestes elongatus*, *M. occidentalis*, *Rhabdalestes eburneensis*, *R. rhodesiensis*, *Virilia*) demonstrate sexual dimorphism in diverse aspects of the anal fin, most obviously in the anteroposterior thickening of the fin-rays of males relative to the proportional development of those rays in females.

This thickening results in the ray segments often appearing square when viewed laterally rather than being elongate along the axis of the ray, as is the case in females of these species and in both sexes of most characiforms. Analysis has shown, however, that any generalization based on the presence of sexual dimorphism in the anal fin encompasses a series of modifications in diverse components of the fin that are appropriately discussed in terms of the combination of morphological adaptations contributing to a particular condition. Preliminary analysis furthermore indicates that the thickening of the anal-fin rays being limited to males is possibly a derived character *per se* for some groups of alestids. Determination of whether that supposition is correct requires mature males for all species of the Alestidae and in the absence of such specimens, we defer the utilization of that character at this time.

179. Degree of development of fifth through eighth anal-fin rays and form of margin of fin in males: (0) not as in state 1; (1) individual segments of fin ray relatively to distinctly anteroposteriorly wide proportional to dimension of segment along axis of ray, with overall ray consequently rather anteroposteriorly wide and with distal portion forming variably distinct median anal-fin lobe (CI = 33; RI = 75)

In most, but not all, species of *Brycinus* (*B. bimaculatus*, *B. carolinae*, *B. imberi* [see Skelton, 1993: 201], *B. kingsleyae*, *B. lateralis* [see Paugy, 1986: fig. 28], *B. leuciscus*, *B. nurse* and *B. sadleri*) the pattern of sexual dimorphism in the form of the anal fin is as follows. The fourth through ninth branched rays, particularly the fifth through eighth, of the anal fin are longer to varying degrees than the proximate fin-rays and form a distinct lobe situated along the middle of the length of the fin (Fig. 37A).

The modifications of these anal-fin rays involve, however, not only elongation but also the restructur-

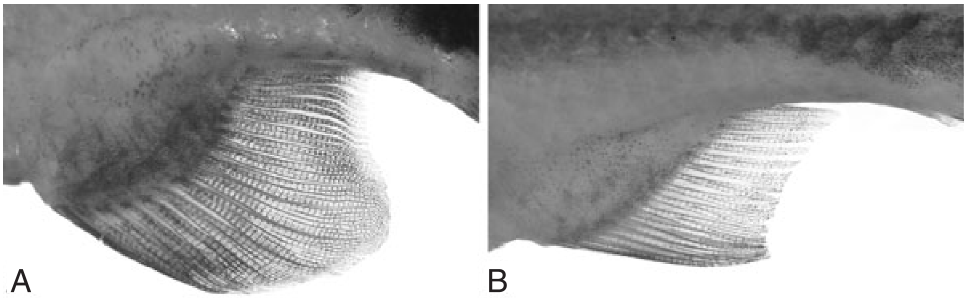

Figure 37. Anal fin of *Brycinus sadleri*, MCZ 145431, (A) male, 76.0 mm SL; (B) female, 82.7 mm SL; left side, lateral view.

ing of the individual ray segments. The anteroposterior width of individual ray segments in females of these species is distinctly narrower then their length along the axis of the fin ray (Fig. 37B), a condition also present in both sexes in other examined alestids. In the males of the listed species of *Brycinus*, nearly all ray segments in the branched portions of the rays are, in contrast, anteroposteriorly thickened, often being wider than long. This expansion is particularly obvious in the fin rays contributing to the anal-fin lobe in the central portions of the anal fin. As a consequence, the proximate borders of adjoining fin rays in that region of the fin maintain near contact even in the spread anal fin.

Such proximity contrasts with the distinct separation of the adjoining fin rays by intervening membranes in the spread fin of females of these species and in both sexes among other species of the Alestidae and examined outgroups. The coding of species as demonstrating state 1 is based on the examination of cleared and stained specimens of *B. imberi*, *B. lateralis*, *B. leuciscus*, *B. nurse* and *B. sadleri*. The coding of state 1 for *B. bimaculatus*, *B. carolinae* and *B. kingsleyae* is based on the examination of whole specimens.

Paugy (1986: 235) noted that a group consisting of *B. brevis*, *B. batesii*, *B. carmesinus* (Nichols & Griscom), *B. grandisquamis*, *B. macrolepidotus*, *B. poptae* (Pellegrin), *B. rhodopleura* (Boulenger) and *B. schoutedeni* (Boulenger) lacks sexual dimorphism of the shape of the anal fin. Although these species do not demonstrate state 1 of this character, there is an indication in the examined specimens of *B. macrolepidotus* that the anal fin, although falcate in both sexes, may have the first and second branched anal-fin rays longer in males than in females. This elongation accentuates the concavity of the anal-fin margins in males of *B. macrolepidotus*. However, this condition needs to be evaluated in a more extensive series of specimens than were available for this analysis. Nonetheless, this modification of the anal fin in *B. macrolepidotus* is confirmed as being different from state 1 above.

Looking at other groups in the Alestidae, we find that the species of *Bryconaethiops* also have an anteroposterior thickening of the individual fin segments in anal fin rays of sexually mature males. The condition of the anal fin in *Bryconaethiops* does not, however, form a lobe comparable to that described above for many species of *Brycinus*. Instead, *Bryconaethiops* retains a straight distal margin to the fin. Furthermore, the degree of development of the fifth through eighth branched anal-fin rays in the species of *Bryconaethiops* is not obviously greater than is the development of the remainder of the fin, a morphology that differs from the condition in the species of *Brycinus*.

Elsewhere in the Alestidae, we found that *Alestes baremoze* possesses a slightly developed anal-fin lobe positioned in the middle of the margin of the fin, a modification at first reminiscent of the lobe of the anal fin described above for *B. sadleri*. *A. baremoze*, however, lacks the anteroposterior thickening of the rays associated with this lobe, in contrast to the situation in *Brycinus*. More significantly, the somewhat longer anal-fin rays in *A. baremoze* are the seventh through tenth branched rays rather than the fifth through eighth, as in the species of *Brycinus*. Paugy (1986: 47, fig. 5) reported that a similar form of sexually dimorphic margin to the anal fin is present in all species of *Alestes*.

Various other alestids demonstrate modifications of the anal fin that differ from state 1 and are treated in other sections. Only one male of *Petersius* was available to us, and that individual could not be cleared and stained. We, nonetheless, find that the fifth through ninth rays of the anal fin in *Petersius* are expanded in a fashion comparable to that present in other species with state 1 and code that genus accordingly.

180. Sexual dimorphism in degree of development of fourth through eighth branched anal-fin rays:
(0) absent; (1) present, with distinct filamentous extensions in males (CI = 100; RI = 100)

As noted in character 179, various alestids have lobes developed along the margin of the anal fin. Among taxa examined in this study, however, definite filamentous extensions of the fourth through eighth branched anal-fin rays are limited to *Nannopetersius ansorgii* (Fig. 36). Similar extensions are also apparent in a photograph of the live holotype of *Phenacogrammus bleheri* Géry (Géry, 1995: fig. 35), a species not included in this analysis. Those filaments are not, however, apparent in the photograph of the preserved holotype of *P. bleheri* (Géry, 1995: fig. 34).

181. Sexual dimorphism in lengths of anterior vs. posterior anal-fin rays: (0) anterior rays moderately developed in females and in males, or longer in males, with posterior rays of about equal size in both sexes; (1) anterior rays distinctly longer in females than in males and posterior rays distinctly longer in males than in females (CI = 100; RI = 100)

Brachypetersius gabonensis and *B. notospilus* are unique among examined taxa in having the anterior rays of the anal fin distinctly longer in females than in males (Fig. 38). These elongate rays form a distinct anterior lobe to the fin (see Géry, 1995: fig. 47) that is absent in males of the species. In contrast, the posterior rays of the anal fin in the males of these two species are distinctly longer than those in females (compare Géry, 1995: figs 46, 47). This contrasting pattern of development in the anterior vs. posterior portions of the anal fin was unique to the species of *Brachypetersius* among the taxa that we examined in this study.

182. Distinct posterior curvature of third unbranched anal-fin ray and basal portions of immediately following rays: (0) absent; (1) present (CI = 100; RI = 100)

In the examined species of *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* the third, posteriormost, unbranched anal-fin ray is distinctly curved posteriorly (Fig. 39), rather than being relatively straight as in other members of the Alestidae. As a consequence, the anterior margin of the fin is usually obviously concave (but see below with respect to further modifications of this fin ray in *Virilia*). This modification is particularly pronounced in the species of *Rhabdalestes* in which it is readily apparent even in whole specimens (Fig. 35).

This curvature of the last unbranched anal-fin ray in *Rhabdalestes* and *Virilia* is paralleled, albeit to a lesser degree, in the basal portions of the subsequent one or two branched anal-fin rays. Comparable, although not as pronounced, modifications of the third unbranched and subsequent anal-fin rays are also present in *Hemmigrammopetersius*, with the curvature being more obvious in cleared and stained specimens.

Virilia also has a curvature of the posterior margin of the third unbranched ray comparable to that in *Hemmigrammopetersius* and *Rhabdalestes*. The massive anterior expansion of the central portions of that ray (see character 183) along with the relatively elongate first and second unbranched rays in that species serve, however, to mask the degree to which the overall posterior curvature of the third unbranched anal-fin ray is manifested along its anterior margins.

183. Distinct anteroposterior thickening of third unbranched anal-fin ray: (0) absent; (1) present and moderately to well-developed; (2) present and highly developed into anteriorly convex process (CI = 100; RI = 100)

One of the most distinctive of the modifications unique to *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* is the anteroposterior expansion of the third unbranched anal-fin ray (Fig. 39), the posteriormost unbranched ray in those genera. As a consequence of this expansion, this ray has a distinctly to remarkably greater overall anteroposterior width compared both to the dimension of the proximate branched anal-fin rays and with respect to the condition of the homologous unbranched anal-fin ray in examined outgroups.

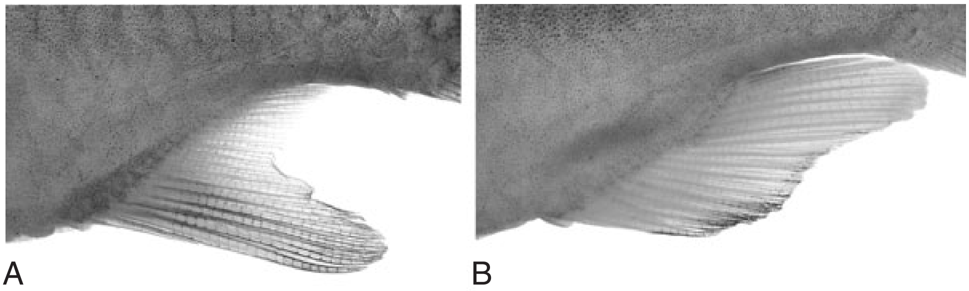

Figure 38. Anal fin of *Brachypetersius gabonensis*, AMNH 230285, (A) female, 58.5 mm SL; (B) male, 57.7 mm SL; left side, lateral view.

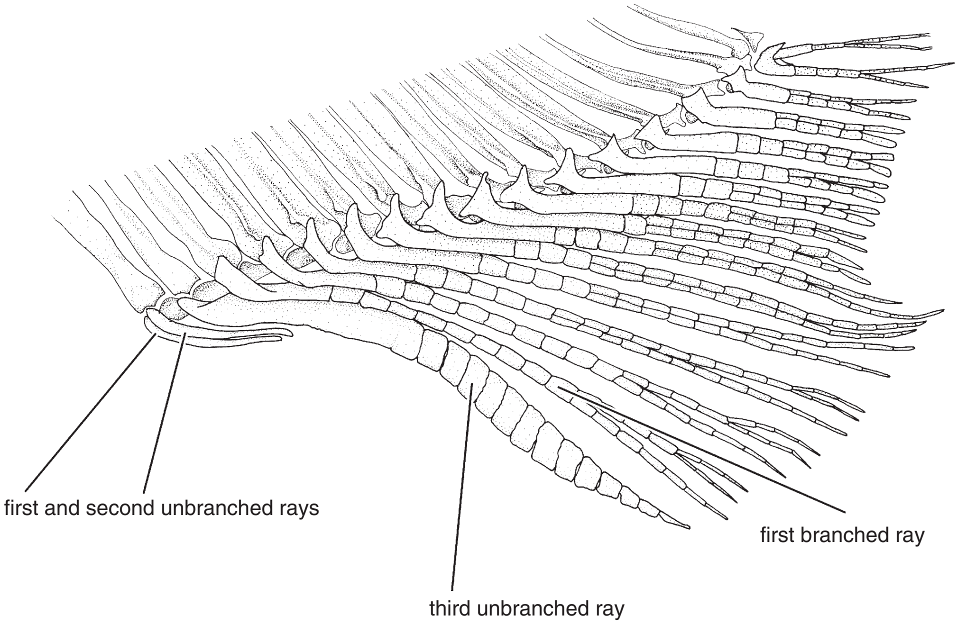

Figure 39. Anal fin of *Rhabdalestes eburneensis*, USNM 193974, 43.4 mm SL; left side, lateral view.

In *Hemmigrammopetersius* and *Rhabdalestes* the associated curvature of the third unbranched ray and the shortness of the first and second unbranched rays results in an anterior margin that has a distinctly concave margin. In *Virilia* the first and second unbranched rays are proportionally longer than those of *Hemmigrammopetersius* and *Rhabdalestes* and the third is proportionally thickened anteroposteriorly (according to Roberts, 1967b: 253, the thickness of that ray is about six times as great as that of other anal-fin rays; see also Roman, 1966; pl. 4, fig. 8). The expansions of the first through third unbranched fin rays in *Virilia* serve to mask the degree of posterior curvature of the third ray described in character 182. Roberts (1967b) also reported the presence in some specimens of *Virilia* of a peculiar fleshy structure situated along the anterior portion of the fin; however, the presence of such an elaboration was not apparent in the specimens of that genus examined in this study.

In the absence of a mature male of *R. septentrionalis* for examination, we base our coding of the state of this character for that species on the illustration of the species by Paugy (1990b: fig. 20.36). Radiographs of mature males of *H. intermedius* demonstrate that this species shares with its congeners and closely related taxa the just discussed anteroposterior thickening of the third unbranched anal-fin ray and we consequently code that species as state 1 for this character.

184. Form and degree of posterior expansion of basal portions of anterior branched anal-fin rays in males:
(0) without posterior expansion and not overlapped by anterolateral portions of subsequent ray; (1) basal portions of at least rays 1–5 with posterior medial expansion overlapped laterally by anterior section of following rays (CI = 100; RI = 100)

In characiforms, the basal portions of sequential branched anal-fin rays are usually distinctly separated along their entire lengths. As noted in the previous character, the basal portions of the anterior rays are distinctly curved posteriorly in males of *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia*, a modification bringing the adjoining margins of those portions of the rays into closer proximity than permitted by the morphology characteristic of other examined taxa.

Above and beyond the proximity resulting from such curvature of the anterior rays, the examined males of *Hemmigrammopetersius*, *R. eburneensis*, *R. loenbergi* (Svensson), *R. rhodesiensis* and *Virilia* have a posterior expansion of the median basal portions of the anterior five (*Virilia*) to eight (*H. barnardi*, *R. eburneensis*, *R. loenbergi*, *R. rhodesiensis*) branched rays fitting, other than in the case of the posteriormost ray of the series, into the slightly anteriorly expanded lateral portions of the basal portions of the subsequent branched rays (Fig. 39). The posteriormost of these modified rays, the fifth in *Virilia* and eighth in *H. barnardi*, *R. eburneensis*, *R. loenbergi* and *R. rhode-*

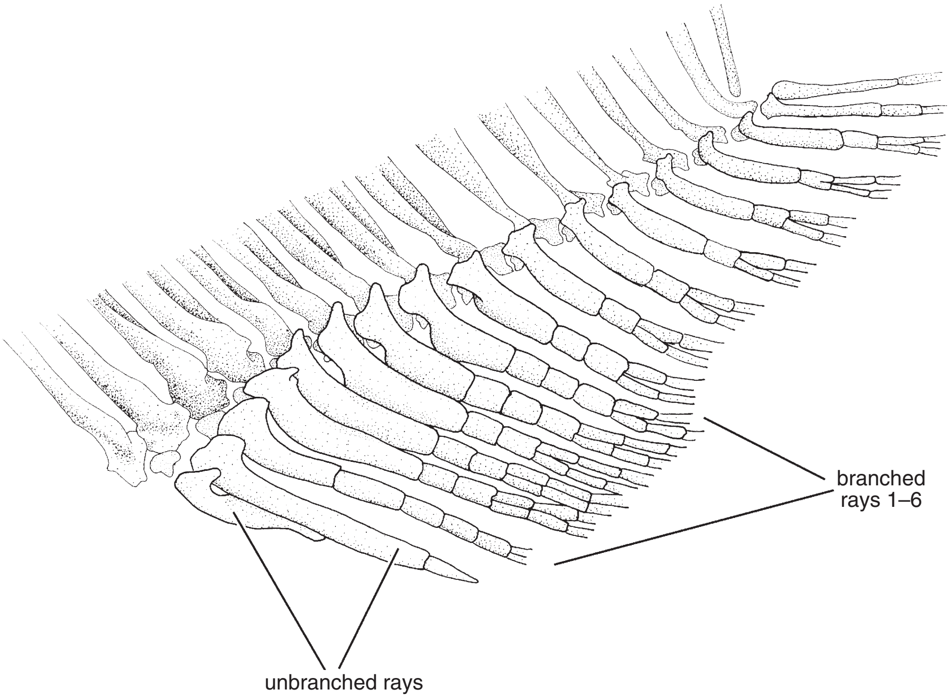

Figure 40. Anal fin of *Ladigesia roloffi*, USNM 365951, 29.9 mm SL; left side, lateral view.

siensis, bears a posterior expansion. However, the expanded region falls short of the anterior margin of the immediately following ray. This interdigitation of the basal portions of the anterior five or eight rays apparently serves to interlock the anterior portion of the anal fin in the males of these taxa into a single functional complex.

The lack of mature males of *R. septentrionalis* prevented us from determining whether this form of sexual dimorphism in the basal portion of the anterior five to eight branched anal-fin rays also occurs in that species. Although *R. septentrionalis* demonstrates the concavity of the anterior rays of the anal fin (see Paugy, 1990b: fig. 20.36) and likely also shares the expansion of the rays described above for congeners, we code this species as unknown for this feature.

185. Form and degree of anterior expansion of basal portions of anterior branched anal-fin rays in males:
(0) basal portions of third through sixth rays without medial anterior expansion fitting between lateral portions of preceding ray; (1) thickened basal portions of third through fifth rays, with anterior expansion of medial portion of these rays fitting between lateral portions of preceding ray (CI = 100; RI = 100)

In both sexes in most characiforms, and in females of *Ladigesia*, the basal portions of the anterior branched anal-fin rays are distinctly separated basally. Males of *Ladigesia* have instead basally anteroposteriorly thickened rays with a distinct anterior expansion of the medial portion of third through fifth rays fitting between the lateral portion of the preceding ones (Fig. 40).

A comparable, albeit not as pronounced, expansion of the medial portion is also present on the sixth branched anal-fin ray in the single cleared and stained male of the genus examined in this study. However, contrary to the situation in the third to fifth rays, the expansion of the sixth falls short of the posterior margin of the fifth. These elaborations of the basal portions in males of *Ladigesia* presumably serve to join those elements into a single functional complex and thereby parallel the modifications discussed under the previous character for *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia*.

The restructuring of these anal-fin rays in the males of *Ladigesia* involves an elaboration of the anterior portion of each involved ray, contrary to the modifications present in *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia*, in which the restructuring is situated on the posterior portions of those rays. We were unable to code the condition of this character for *R. septentrionalis* as a consequence of the lack of cleared and stained males of that species.

186. Area of attachment of ligaments of erector muscles on anterior branched anal-fin rays of males: (0) on lateral surface of dorsalmost portion of ray; (1) on anterolateral surface of somewhat more distal portion of ray (CI = 100; RI = 100)

In the majority of alestids available for this study and in all examined outgroup characiforms, the attachment point on each anal-fin ray for the ligament of the erector muscle on the anterior branched rays is located on the lateral surface of the dorsal portion of the ray. In males, but not females, of *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* the attachment point of these ligaments on the concave anterior branched rays is, alternatively, shifted more distally. In addition, in species of *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* the ligament attaches to an area situated more anterolaterally than in other alestids. This combination of attributes is unique to these three genera among examined species for which we have cleared and stained mature males.

The lack of mature males of *H. intermedius* and *R. septentrionalis* in our analysis prevented direct observation of potential sexual dimorphism in the attachment area of these ligaments in those two species. Radiographs of mature males of *H. intermedius* showed that this species shares the modifications of the anal-fin rays associated with the shift of the area of attachment of the ligament with its congeners and closely related taxa within the context of the final phylogeny. We consequently code *H. intermedius* as state 1 for this character.

Rhabdalestes septentrionalis demonstrates the pronounced concavity of the anterior rays of the anal fin (see Paugy, 1990b: fig. 20.36) and it is likely that it also demonstrates the associated shift in the position of the attachment of the ligaments on those rays. We were, however, unable to examine either cleared and stained specimens or radiographs of mature males of *R. septentrionalis* and we, thus, code this species as unknown for this feature.

187. Area of attachment of ligaments of erector muscles on branched anal-fin rays: (0) located on lateral surface of dorsalmost portion of ray or anterolateral surface of somewhat more distal portion of anteriormost ray; (1) located on lateral surface of somewhat more distal portion of rays on anterior half of fin (CI = 100; RI = 100)

As noted above, the ligament of the erector muscle typically attaches to the dorsal margin of each branched anal-fin ray among characiforms, including most examined members of the Alestidae. Even when located more distally on the ray, the area of attachment is positioned on the anterolateral surface. In the species of *Bryconaethiops* the area of attachment, although clearly shifted distally on the ray, nonetheless remains on the lateral surface, a combination of attributes absent in all other examined taxa.

Although the shift distally of the area of attachment is common to this condition and state 1 of character 186, the area of attachment in the *Bryconaethiops* (this character) vs. *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* (character 186) differs and these modifications are thus considered nonhomologous. Furthermore, in the case of *Bryconaethiops* the shift of the area of attachment occurs on the rays along the entire anterior half of the anal fin, whereas in the species of *Rhabdalestes* and *Virilia* it is limited to the few highly modified anteriormost branched rays.

188. Nearly dorsally directed, distally bifurcated digitiform process on anterior region of basal portion of anterior and middle branched anal-fin rays: (0) absent; (1) present (CI = 50; RI = 91)

The muscles associated with the erection, depression, and inclination of each branched anal-fin ray attach to the lateral surface of the basal portion of the corresponding ray. The sexually dimorphic modifications of the main body of the ray described for various alestids under previous characters are paralleled by restructurings of the basal portion. The erector muscle associated with many of the rays typically attaches to the basal portion in most examined taxa in the Alestidae in particular and the Characiformes in general.

A comparable attachment area for the erector muscles is present in females of *Alestopetersius, Bathyaethiops*, *Brachypetersius*, *Clupeocharax*, *Duboisialestes*, *Lepidarchus*, *Nannopetersius*, *Phenacogrammus* and *Tricuspidalestes*. Males of these nine genera have a dorsal expansion of the basal portion of the ray into a distally bifurcated, digitiform process. The rays demonstrating this modification vary within the group of species with such restructuring. *Tricuspidalestes*, for example, has such processes on the second to tenth rays (Fig. 41) whereas in *P. aurantiacus* the first through fourteenth rays are thus modified. The resultant digitiform process on the base of each ray has a nearly vertical orientation and barely, if at all, overlaps the posterior margin of the associated proximal radial (Fig. 41). Because of its absence in other examined characiforms, the possession of such a process by males of the listed nine genera is considered to be derived (see also comments in character 189).

The lack of cleared and stained mature males of *A. smykalai* Poll and *Brachypetersius notospilus* in our study made it impossible to determine whether those taxa demonstrate the sexual dimorphism of the basal portions of many of the branched anal-fin rays that are characteristic of their phylogenetically proximate relatives; these species are therefore coded as unknown for this feature.

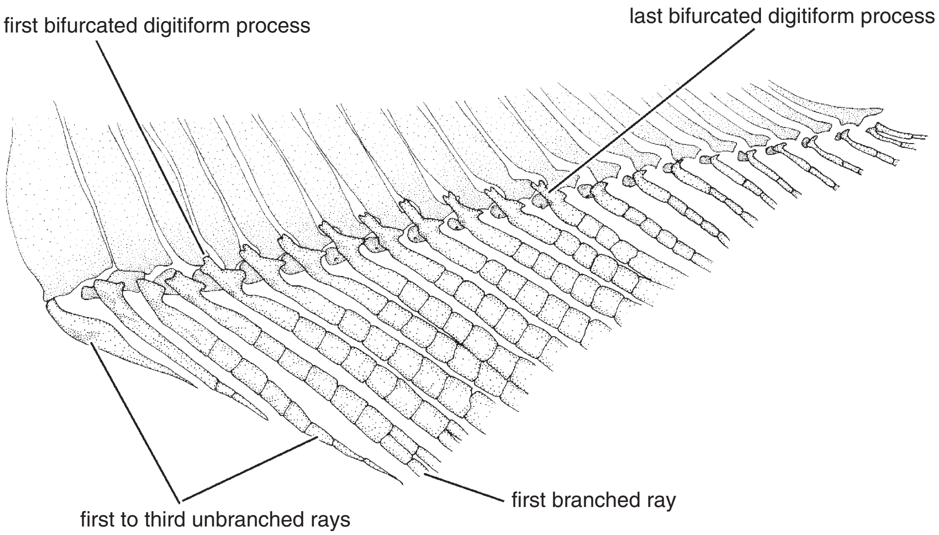

Figure 41. Basal portion of anal-fin rays of *Tricuspidalestes caeruleus*, USNM 365952, 29.9 mm SL, male; left side, lateral view.

189. Presence or absence of anterodorsally directed, triangular extension of anterior region of basal portion of anterior and middle branched anal-fin rays:
(0) absent; (1) present (CI = 50; RI = 66)
Two other subunits of the Alestidae have modifications of the basal portions of some of the anterior rays of the anal fin and of some, or nearly all, of the middle and posterior rays. In *Arnoldichthys* and *Bryconalestes* the anterodorsal portion of the basal sections of the third through approximately tenth rays are expanded into anterodorsally directed processes extending anteriorly to overlap the posterior portion of the associated proximal radials (Fig. 42). Although both *Arnoldichthys* and *Bryconalestes* have in common an expansion of the basal portions of some of the anterior and middle rays with the taxa discussed in character 188, the overall form and orientation of the processes described in characters 188 and 189 differ in various details. We consequently treat the two sets of distinct modifications as independent features.

Although the process of the basal portion of most of the rays in *Arnoldichthys* lacks the distinctly dorsally attenuating form of the process found in *Bryconalestes*, the processes in both genera demonstrate the same overall orientation and we consequently code them as equivalent in the phylogenetic analysis.

190. Posterodorsal extension of basal portions of anterior and middle branched anal-fin rays: (0) absent;
(1) present (CI = 100; RI = 100)
The posterodorsal portion of the basal section of each branched anal-fin ray serves as an area of attachment for the depressor muscles associated with it. The usual condition of this region among the examined species of the Characiformes is the lack of any pronounced process onto which that muscle attaches. That condition is also typical for nearly all examined members of the Alestidae, with females of *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* having at most a minor extension of that portion of the fin ray.

In males of these three genera, the posterior of the posterodorsal portion of the anterior and middle rays is, in contrast, developed into a large, posterodorsally attenuating, triangular process that distinctly overlaps the basal region of the subsequent proximal radials (Fig. 39). This condition is absent in the examined outgroups and is consequently considered to be derived. In the absence of available mature males of *R. septentrionalis* in our study, we code that species as unknown for this character.

191. Presence or absence of fusion of medial and proximal anal-fin radials: (0) absent; (1) present
(CI = 100; RI = 100)
In members of the Characidae, the morphology of the branched anal-fin rays is typically similar to the pattern described by Weitzman (1962: 40) for *Brycon meeki*, in which the first through fifth rays have only proximal and distal radials, whereas the remaining rays incorporate proximal, medial and distal radials. A comparable arrangement of the anal-fin radials is present in the majority of characiform outgroups examined in this study (see, however, comments below with respect to the conditions in the Neotropical families Serrasalminae, Erythrinidae and Ctenoluciidae).

Within the Alestidae, with the exception of *Chalceus*, we find some notable differences in the morphol-

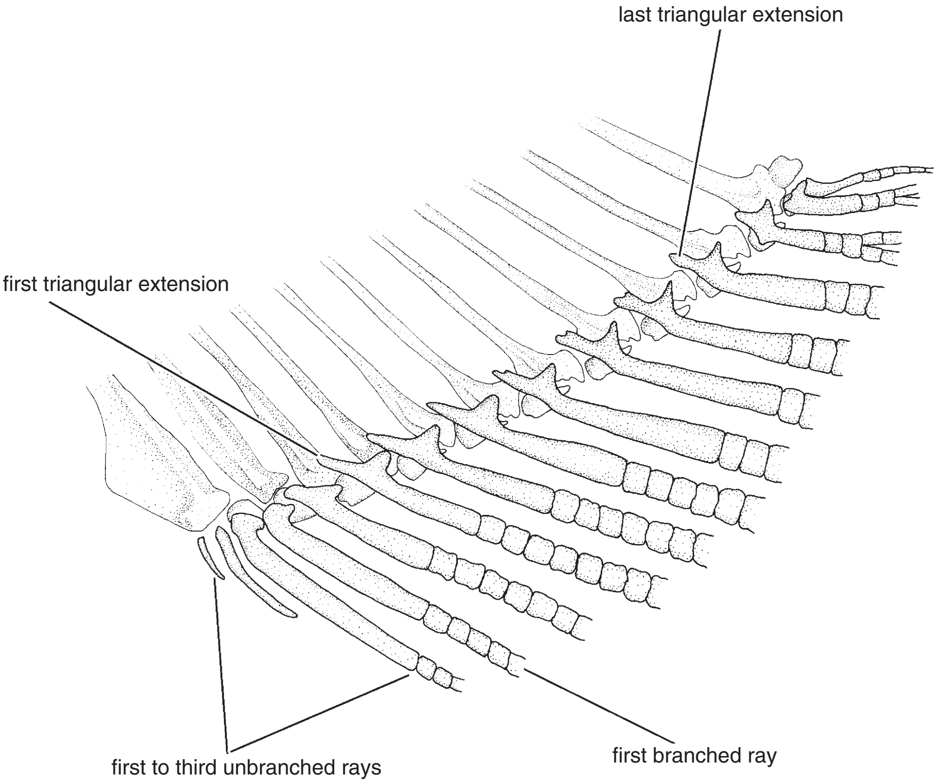

Figure 42. Basal portion of anal-fin rays of *Arnoldichthys spilopterus*, USNM 365945, 71.5 mm SL; left side, lateral view.

ogy of the medial and proximal radials, in particular the fusion of these elements into a single ossification articulating with the distal radial. Our analysis also indicates that there may be differences in the patterns of sexually dimorphic fusion of radials across the Alestidae. The available material is insufficient, however, to allow us to explore such differences in the detail necessary to resolve these questions. We consequently code a species as having fusion of the medial and proximal radials whenever such fusion is present, whether only in males or in both sexes. The examination of mature specimens of both sexes throughout the Alestidae will likely yield additional phylogenetic information in this character system.

In the case of the African genera of the Alestidae, we find that *Arnoldichthys* has a single basal element associated with the fifth and succeeding branched anal-fin rays, with this element having the overall morphology that would result from a fusion of the medial and proximal radials. The single element associated with these rays is thus hypothesized to represent the two conjoined radial elements.

The remaining members of the Alestidae demonstrate several conditions. Most other examined alestids, with the exception of *Alestes dentex*, *Bathyaethiops*, *Brycinus brevis* and *Bryconaethiops microstoma*, have at least some of the proximal and medial radials that are situated posterior to the radials associated with the fifth ray fused into a single ossification with a posteroventrally directed process contacting the distal radial (see also comments in following paragraph). The number of sequential units demonstrating such fusion of the proximal and medial radials varies both ontogenetically and intraspecifically in examined species of alestids. In light of the absence of such a fusion in outgroups, we consider the presence of such conjoined medial and proximal radials to be derived, regardless of the number of involved rays.

The examined cleared and stained specimens of *Alestopetersius smykalai*, species of *Hemmigrammopetersius* and *Micralestes* sp. have separate medial and proximal radials. In each instance the cleared and stained specimens are relatively small compared to the examined osteological preparations of other alestids. This limitation raises questions as to whether larger individuals of these species would demonstrate the fusion of these radials occurring later in ontogeny in some other alestids. In the absence of that ontogenetic information we code those species as '?' for this character.

Separate medial and proximal radials are present on all rays posterior to the fifth branched anal-fin ray in most examined outgroup taxa. In the Serrasalminae (*Catoprion*, *Piaractus*, *Serrasalmus* examined in this study) there is no indication of medial radials and the proximal radials lack a posteroventral extension contacting the distal radial that is apparently homologous with that element in some alestids. In light of the apparent absence of the medial radials in the Serrasalminae, the examined members of the subfamily are consequently coded as state 0.

Hoplias and other examined members of the Erythrinidae have a single element with a posteroventrally expanded process associated with each branched anal-fin ray other than in the anterior portion of the fin. This element is reminiscent in overall form to the conjoined medial and proximal radials present in many components of the Alestidae. Studies of specimens of erythrinid genera *Hoplerythrinus* and *Hoplias* over a range of sizes failed to reveal any ontogenetic fusion of separate medial and proximal radials. Rather, the posteroventral process on all but the anterior most proximal radials is cartilaginous in very small individuals of these genera and apparently ossifies as a single unit with the main body of the radial.

A comparable ontogenetic sequence occurs in the Ctenoluciidae, the group hypothesized by Vari (1995: 36) to be the sister group to the Erythrinidae. The Hepsetidae and Lebiasinidae, the other families hypothesized by Vari (1995) to be closely related to the clade formed by the Erythrinidae and Ctenoluciidae, in contrast, have distinctly separated medial and proximal radials. Because of these differences in the ontogeny of the fused medial and proximal radials in the Erythrinidae and Ctenoluciidae vs. the Alestidae we herein consider these elements in these taxa to be nonhomologous.

SEXUAL DIMORPHISM IN PIGMENTATION

192. Presence or absence of sexually dimorphic patterns of dark pigmentation of stripes vs. spot on anal fin: (0) absent; (1) present, with dark pigmentation in female limited to rotund dark spot on basal half of posterior portion of anal fin and dark pigmentation in male in form of three dark stripes extending from base to distal margin of anal fin and with dark pigmentation along distal margin of fin (CI = 100; RI = 100)

Although various members of the Alestidae demonstrate distinct sexually dimorphic modifications of various components of the anal fin, they typically lack correlated differences in the dark pigmentation of that fin. In *Arnoldichthys*, the scheme of pigmentation differs dramatically in males and females (Poll, 1967a: 67; Géry, 1977: 50, fig. 56; 1995, figs 18, 19), a pattern of sexual dimorphism absent in all other examined taxa. In females the pigmentation is limited to a variably developed, dark spot on the basal portion of the posterior half of the anal fin, usually positioned between the seventh and ninth branched anal-fin rays. In males there are three dark stripes extending across the anal fin. The first extends along the length of the unbranched anal-fin rays. The second arises at the base of second branched anal-fin ray and extends distally over the third through fifth branched anal-fin rays. The third extends approximately along the seventh branched anal-fin ray. The distal margin of the anal fin in males of *Arnoldichthys* is also dark. The regions that are pale in preserved individuals of the genus have a distinct golden coloration in life (see Géry, 1995: fig. 18).

193. Presence or absence of sexual dimorphism in form of stripe and spot on fin rays vs. basal stripe on anal fin: (0) absent; (1) present, females without dark pigmentation on anal-fin rays, but with basal stripe present along anterior portion of anal fin; males with dark stripe beginning at middle of anterior rays of anal fin and angled posteriorly to middle of distal margin of fin, with second spot of dark pigmentation on distal portions of posterior rays (CI = 100; RI = 100)

As noted for the previous character, sexual dimorphism in the distribution of dark chromatophores on the fins is rare in the Alestidae. The sexually dimorphic pigmentation described under state 1 was reported for *Lepidarchus* by Roberts (1966: 211) and is unique to that genus among examined taxa. This pigmentation differs from the sexually dimorphic anal-fin pigmentation character discussed under state 1 of the previous character in numerous details and is consequently considered to be nonhomologous with that condition.

194. Sexual dimorphism in dark pigmentation of pelvic fin: (0) absent; (1) present, female without dark pigmentation on pelvic fin; male with dark stripe beginning at middle of anterior rays of fin and angled posteriorly to middle of tip of fin, with second parallel dark stripe running slightly posterior to primary stripe in some males (CI = 100; RI = 100)

Dark pigmentation on the pelvic fin, when present, does not typically demonstrate sexual dimorphism among the characiforms examined in this study. The sexually dimorphic dark pigmentation described above under state 1 for this character is limited to *Lepidarchus* among the examined taxa.

195. Sexually dimorphic dark pigmentation on body: (0) male and female with comparable dark pigmentation on body; (1) female with little dark pigmentation on body, adipose fin and base of anal fin and without distinct spots; male with distinct dark rounded spots over much of body, on lateral surface of adipose fin and on base of anal fin (CI = 100; RI = 100)

The form of the sexually dimorphic dark pigmentation of males of *Lepidarchus* (Géry, 1995: fig. 11) described under state 1 for this character is unique to that genus among examined characiforms.

MISCELLANEOUS

196. Position of olfactory bulb: (0) in contact with telencephalon; (1) separated from telencephalon and connected to it by distinct olfactory tract (CI = 16; RI = 75)

In the hypothetical plesiomorphic condition for characiforms, the olfactory bulb lies immediately anterior to, and in contact with, the telencephalon and is laterally enclosed by the orbitosphenoid (Vari, 1979: 322). An anterior shift of the olfactory bulbs to contact, or nearly contact, the posterior surface of the lateral ethmoid and with the bulb and telencephalon connected by an olfactory tract was interpreted by Vari (1979) as an apomorphy for the clade formed by the Old World characiform families Citharinidae and Distichodontidae.

A comparable anterior location of the olfactory bulb was also reported by that author elsewhere in the Characiformes in the Neotropical genus *Salminus*, some members of the Alestidae (the African Characidae of that study) and the New World family Parodontidae. Within the Alestidae, Vari (1979: 323) noted the presence of a distinct anterior shift of the olfactory bulb in *Alestes baremoze*, *A. dentex*, *A. liebrechtsii*, *A. macrolepidotus*, *A. macrophthalmus*, *A. nurse*, *A. rhodopleura*, *Bryconaethiops* and *Hydrocynus* and cited a slight separation between the olfactory bulb and the telencephalon in *Alestes imberi* Peters and *A. lateralis* [NB: the concept of *Alestes* followed by Vari (1979) was subsequently narrowed (Paugy, 1986) and some of these species are assigned to *Brycinus* herein].

A distinct anterior position of the olfactory bulb with respect to the telencephalon was found to be present in the Alestidae in *Alestes*, the species of *Brycinus* (with the exception of *B. sadleri*), *Bryconaethiops* and *Hydrocynus*. In the outgroup it was found in the distichodontid genus *Xenocharax* and the Neotropical characiforms *Brycon falcatus*, *B. pesu* and *Salminus*.

Although the olfactory bulb is relatively anteriorly positioned in *Alestes*, the species of *Brycinus* (with the exception of *B. sadleri*), *Bryconaethiops* and *Hydrocynus*, it is, together with the tract, wholly or nearly wholly enclosed in the orbitosphenoid. Although the majority of examined species of *Brycinus* demonstrate an anterior position of the olfactory bulb, *B. sadleri*, one of the smaller species of the genus examined in this study, which matures at smaller body size, has the bulb located proximate to the telencephalon.

An ontogenetic correlation between body size and the position of the bulb with respect to the telencephalon was also noted in the examined population samples of some species of *Brycinus*, in which the separation between those structures is more pronounced in larger individuals, a developmental shift that may account for the condition observed in *B. sadleri*. In the case of *B. bimaculatus*, the separation between the bulb and telencephalon is less pronounced than the gap between those structures present in many congeners; however, that species is, nonetheless, coded as having state 1 in this analysis in light of the separation.

197. Adipose eyelid covering part of eye: (0) reduced or absent; (1) well-developed (CI = 25; RI = 66)

An adipose eyelid, a connective tissue structure overlying the lateral surface of the orbit to varying degrees, is present in diverse taxa across the Characiformes. When present, it ranges in its degree of development, with such differences utilized by Géry (1977: 19) to distinguish various genera of the Alestidae. The eyelid was cited by that author as being absent in *Brycinus* but present in *Alestes* and *Bryconaethiops*. Because of the effectively continuous range in the degree of development of the adipose eyelid across the Alestidae it is difficult, however, to parse the variation in the degree of development of this structure into multiple character states.

We herein define the well-developed adipose eyelid as one in which the borders of the anterior and posterior portions of the structure come relatively close to the middle of the eye and as a consequence delimit a relatively narrow, vertically elongate opening that is centred over the pupil (for illustrations comparing forms with and without an adipose eyelid, see Paugy, 1990b: fig. 20.2). It is limited within the Alestidae to *Alestes*, *Bryconaethiops* (Fig. 20) and *Hydrocynus* (Fig. 3). When present in the other examined genera of the Alestidae, the eyelid has a broad central opening, the margins of which parallel the shape of the orbit and consequently border a distinctly rounded aperture (Fig. 19). The vertically elongate, longitudinally narrow, form of the opening occurs in *Bryconops* and *Hemiodus* among the examined outgroups.

In their analysis of phylogenetic relationships within a subunit of the Alestidae, Murray & Stewart (2002: 1888) reported that *Alestes* (their '*Alestes* s. str.') and *Hydrocynus* have a well-developed adipose eyelid, but coded *Bryconaethiops* as lacking that feature. Those authors did not provide information on the size of the two specimens of *B. microstoma* that they examined in their study, but a well-developed adipose eyelid as defined herein is clearly present across the size range (54.9–129.2 mm SL) of the members of *Bryconaethiops* examined in this analysis.

198. Presence or absence of membranous keel extending between pelvic-fin insertion and vent: (0) absent; (1) present (CI = 100; RI = 100)
Lepidarchus is unique among examined taxa in possessing what Roberts (1966: 209) described as a 'thin, median, membranous keel' extending along the midventral surface of the body from the pelvic-fin insertion to the vent. Examined population samples of *Lepidarchus* demonstrate a degree of sexual dimorphism in the extent of development of the keel, with the structure somewhat larger in the males than in the largest females. Confirmation that sexual dimorphism in the degree of development of that membranous keel is universal across the species necessitates the examination of a more extensive series of population samples than were at our disposal.

199. Presence or absence of pseudotympanum: (0) absent; (1) present (CI = 50; RI = 50)
Lepidarchus is the only taxon among the examined alestids that possesses a pseudotympanum, a triangular opening in the body musculature that is largely situated anterior to the first full pleural rib. The presence of a large, nearly triangular hiatus within the muscles between the first and second pleural ribs in the region over the anterior chamber of the swimbladder (the pseudotympanum) was interpreted as a synapomorphy for the Neotropical characid subfamily Cheirodontinae by L.R. Malabarba (1998: 199). Various forms and degree of muscle reduction over the anterior portion of the swimbladder are present in diverse groups in the Characidae (*Aphyocharacidium* sp., *Charax stenopterus* (Cope), *Leptagoniates pi* Vari and *Phenacogaster*, Malabarba, 1998) in addition to the morphology of the aperture characteristic of the Cheirodontinae. None of these taxa shares the higher-level synapomorphies for the Alestidae (including *Lepidarchus*) and the common possession of a hiatus in *Lepidarchus* and the cited outgroup characiforms is most parsimoniously interpreted as being homoplastic.

200. Position of posterior limit of posterior chamber of swimbladder: (0) terminating at, or anterior to, proximal radial of first anal-fin ray; (1) extending posteriorly past anterior portion of base of anal fin to haemal spine of third preural centrum (CI = 100; RI = 100)
Posterior elongation of the posterior chamber of the swimbladder in a small subunit in the Alestidae was described by Poll (1969: 486, fig. 12) and Brewster (1986: 190: fig. 23). Brewster (1986), followed by Murray & Stewart (2002: 1893), interpreted this posterior elongation of the swimbladder and the associated reduction of the adjoining proximal radials (see character 145) as a synapomorphy for a group consisting of *Alestes ansorgii*, *A. baremoze*, *A. liebrechtsii*, *A. macrophthalmus* and *A. stuhlmanni*.

All remaining examined species in the Alestidae have the generalized characiform condition in which the posterior terminus of the swimbladder is located proximate to the anterior margin of the elongate proximal radial associated with the anterior anal-fin rays. Our studies confirm both the presence of the *Alestes* form of elongation of the posterior chamber of the swimbladder in all examined members of the genus and the unique nature of this modification among examined characiforms. We consequently agree with Brewster (1986) that the condition is derived.

The Neotropical genus *Hemiodus* is the only examined outgroup in which the swimbladder continues posteriorly beyond the first proximal radial of the anal fin. *Hemiodus* has a somewhat elongate swimbladder with a very narrow posterior portion terminating dorsal to the middle anal-fin rays. However, there is no reduction in the length of the proximal radials in that region, a very different condition from that present in the cited species of *Alestes*. An elongation of the swimbladder beyond the posterior terminus of the body cavity is also present in *Rhaphiodon vulpinus* Spix & Agassiz, a member of the Neotropical characiform subfamily Cynodontinae (see Nelson, 1949: 515; Lesiuk & Lindsey, 1978: fig. 3); however, the phylogenetic relationships of that genus lie with groups other than *Alestes* (Lucena & Menezes, 1998; Toledo-Piza, 2000).

UNUTILIZED CHARACTERS

Various authors have advanced characters that they hypothesized to be pertinent either to the question of the monophyly of the African components of the Alestidae (often cited as the African Characidae) or that were proposed as synapomorphic for components of that family. More thorough analysis has revealed difficulties with using these features as defined by these researchers. Our comments are arranged in the sequence of the discussion of various body systems under 'Character Description and Analysis'

1. *Shape of mesethmoid*. Murray & Stewart (2002: 1890) suggested that there were two forms of mesethmoid present in the Alestidae that they characterized as 'normal' vs. 'bulges laterally.' It is unclear from their description whether the lateral expansion involves the posterior portion of the bone or is in a more anteriorly positioned region (Murray & Stewart, 2002: fig. 4a, b). Based on the coding for the examined species in this study, the 'bulge' appears to be a lateral expansion of the mesethmoid in the region slightly posterior to the anterior processes. Our analysis has shown a broad variation in the form of this region of the mesethmoid across the Alestidae that renders impossible the unequivocal coding of this feature for various species.

2. *Lateral ethmoid very short*. Géry (1995: 39) proposed that a 'lateral ethmoid very short' was a distinguishing feature of the Alestidae vs. the Characidae. This brief characterization makes it impossible to determine what aspect of the morphology of the lateral ethmoid is purported to differ between the families. Comparison of the lateral ethmoids failed to reveal any obvious differences in the form of the ossification in the families that would correspond to such a distinguishing feature.
3. *Shape of vomer*. In their analysis, Murray & Stewart (2002: 1890) proposed that the form of the vomer in the Alestidae was distinctive among characiforms and noted that 'the anterior portion of the vomer is expanded laterally.' Although Murray & Stewart (2002: fig. 3) illustrate different forms of vomer in an alestid and an outgroup characid, the degree of lateral expansion in the two taxa appears to be effectively identical. Furthermore, an examination of a greater diversity of alestids than utilized by Murray & Stewart demonstrates a considerable range in the overall form of the vomer within that family, with the form of the vomer occurring in the alestid genera *Phenacogrammus*, *Tricuspidalestes*, *Arnoldichthys* and *Chalceus* comparable to that present in the outgroup characid illustrated by Murray & Stewart (2002).
4. *Groove on posterolateral surface of pterotic*. In her study of *Hydrocynus*, Brewster (1986: 189) proposed that the possession of a posterior (actually posterolateral) groove on the pterotic that serves to continue the dilatator fossa is a synapomorphy for the members of that genus. The groove on the pterotic was used with modifications by Murray & Stewart (2002: 1892) in their subsequent phylogenetic study. Our observations indicate that the groove is indeed prominent in *Hydrocynus*; however, examination of a broader sample of other taxa in the Alestidae reveals an effective continuum of variation in the degree of development of the groove. This variability renders it impossible to unequivocally delimit the condition in *Hydrocynus* to the exclusion of all other alestids.
5. *Relative size of dilatator fossa*. Brewster (1986: 191-2) noted that the dilatator fossa in the species of *Hydrocynus* and the lineage that she termed *Alestes sensu stricto* was long and deep and she utilized this feature as a synapomorphy for the clade consisting of those taxa. Although the fossa is distinctly elongate in *Hydrocynus* and also well-developed in *Alestes*, examination of various species of *Brycinus* and *Bryconalestes* (these two genera being equivalent to the *Alestes sensu lato* of Brewster, 1986: 192) and other alestids indicates that it is impossible to define the condition of the relative size of the dilatator fossa in *Hydrocynus* and *Alestes* to the exclusion of the condition of other alestids. We consequently were unable to utilize this character in our analysis.
6. *Cavum orbitonasale*. Géry (1995: 39) reported that the cavum orbitonasale in the Alestidae was 'different than in the Characidae' but did not elaborate on these differences. Again, comparison of members of the two families failed to demonstrate any differences that would serve to delimit the Alestidae.
7. *Spacing of dentition*. In her discussion of the spacing of the oral dentition, Brewster (1986: 189) noted that the dentition of the jaws in *Hydrocynus* is 'widely and evenly spaced', a condition that she contrasted with the contiguous teeth or teeth separated by irregular diastema in her outgroup taxa. As noted by Roberts (1969: 439) the elongation of the jaws among characiforms is apparently correlated with a 'wider spacing' of the jaw teeth. That generality, albeit applicable to *Hydrocynus,* does not hold across the breadth of the Characiformes (e.g. the members of the Ctenoluciidae that have elongate jaws, but very closely positioned teeth; see Lawson & Manly, 1973: fig. 1). Although the relative spacing of the oral dentition within *Hydrocynus* is likely derived relative to the condition of these teeth in many other characiforms, it is, nonetheless, not unique to that genus within the Alestidae. Distinct spacing between the dentition in the jaws also occurs in *Tricuspidalestes*, although in that genus such spacing may be a function of the relatively small teeth rather than an elongation of the jaws. Furthermore, it is difficult to unambiguously define the condition in *Hydrocynus* vs. that in some other groups in the Alestidae that also demonstrates increased spacing between the teeth. In light of the difficulty in delimiting the feature and given the numerous other unequivocal synapomorphies for the members of *Hydrocynus*, we did not utilize this character in our analysis.
8. *Presence of ventral flange on maxilla*. Murray & Stewart (2002: 1889) utilized the presence of a ventral flange on the maxilla as a distinguishing feature for alestids. No separate process of the maxilla is apparent in African alestids, but Murray & Stewart cited Roberts (1969), who brought attention to the 'rounded ventral contour' of that portion of the bone. Although a rounded ventral contour to the maxilla is present in many alestids, there is a notable degree of variation in the form of that ossification, with *Arnoldichthys, Hydrocynus, Micralestes and Rhabdalestes* among other alestids having a straighter margin to the maxilla. In

light of the range of conditions, this feature is not appropriately defined as a synapomorphy for the African members of the Alestidae.

9. *Absence of ectopterygoid teeth*. Brewster (1986: 175) noted that the ectopterygoid is edentulous in *Hydrocynus.* Later in that same publication (p 203) she proposed that the absence of dentition was derived at the level of *Hydrocynus* plus *Alestes* (Brewster's concept of the latter genus is equivalent to the *Alestes*, *Brycinus* and *Bryconalestes* of this study) or for all of the African Characidae (the Alestidae of this study with the exception of *Chalceus*). Our observations confirm Brewster's suggestion that the absence of teeth on the ectopterygoid is general for the Alestidae; however, they also demonstrate that edentulous ectopterygoids characterize numerous other groups within the Characiformes. In light of the broad distribution of edentulous ectopterygoids among characiforms, this feature is not utilized in this study to define the Alestidae.
10. *Preopercular ridge above lower limb laterosensory pores*. In their analysis of the Alestidae, Murray & Stewart (2002: 1892, fig. 3) hypothesized that the possession of laterosensory canal pores on the horizontal limb of the preopercle opening ventrally from under a ridge on the lateral surface of that bone was a synapomorphy for the Alestidae. Although there is indeed variation in the presence or absence of such a ridge on the lateral surface of the preopercle between members of the Alestidae, such variation does not demonstrate a pattern of presence vs. absence in the Alestidae in contrast to outgroups. Among the alestid taxa examined in this study we found a well-developed ridge to be present in *Alestes baremoze, A. macrophthalmus, Brycinus nurse and B. macrolepidotus* and some other taxa whereas no such ridge was apparent in *Arnoldichthys*, *Bryconalestes longipinnis*, *Micralestes elongatus*, *Phenacogrammus* and *Tricuspidalestes*, among others. An 'intermediate' level of development of the ridge occurs in *Hydrocynus* and some species of *Brycinus*. Among outgroup taxa, a ridge, albeit not as well developed as the process present in some, but not all, alestids was found in *Bryconops, Hemiodus, Piaractus, Salminus and Triportheus*. In light of the continuity of the degree of development of the ridge within the Alestidae, its absence in some members of that family and presence in some examined outgroups, we find that presence cannot serve as a synapomorphy for the African components of the Alestidae (the Alestidae of Murray & Stewart, 2002).
11. *Number of gill-rakers on the lower limb of the first gill arch*. In their phylogenetic analysis of the relationships of *Alestes* and *Brycinus* Murray & Stewart (2002: 1889) proposed a two-state character for the number of gill rakers on the lower limb of the first gill arch (21 or fewer vs. 23 or more). One of the species reported by Murray & Stewart as having 21 or fewer rakers was *Alestes dentex*. Paugy (1986: 66) reported that the type series of two junior synonyms of *A. dentex* had a range of 21–27, values overlapping the purported difference between the two character states advanced by Murray & Stewart (2002). Given this broader range of gill raker counts in *A. dentex* that straddle the gap in the coding for this feature proposed by Murray & Stewart (2002), that character cannot be utilized in the phylogenetic analysis.
12. *Neural spine of second preural centrum*. Brewster (1986: 183) cited a single sexually dimorphic feature in the species of *Hydrocynus* that was related to the relative degree of development of the neural spine on the second and third preural centra. In her examined material of that genus, females had neural spines on the second and third preural centra of approximately the same length; there were definite expanded anterior and posterior flanges on those spines (Brewster, 1986: fig. 20a). In the examined males of *Hydrocynus*, in contrast, the neural spine of the second preural centrum was shorter than that of the third. Furthermore, the neural spines associated with the third and fourth centra in the examined males of the genus were more elongate than those present in females and curved posteriorly to extend over the dorsal limit of the proportionally shortened neural spine on the second preural centrum (Brewster, 1986: fig. 20b). Brewster (1986: 192) went on to report that such dimorphism was present in all members of the African Characidae (the African component of the Alestidae of this study) that she examined (various species of *Alestes*, *Bryconaethiops*, *Hemmigrammopetersius*, *Phenacogrammus* and *Rhabdalestes*), but with such dimorphism absent, however, in *Lepidarchus*. In the legend to her phylogenetic tree, Brewster (1986: fig. 24) cited the sexual dimorphism of the neural spine of the second preural centrum as synapomorphic for the clade consisting of *Alestes* (= *Alestes*, *Brycinus* and probably *Bryconalestes* of this study) and *Hydrocynus*. Murray & Stewart (2002: 1893, fig. 3) similarly utilized sexual dimorphism of these neural spines in their phylogenetic analysis and proposed that this feature was a synapomorphy for their Alestidae.

Examination of a more extensive series of specimens of diverse species of the Alestidae than were available to Brewster demonstrated that at the level of the Alestidae the pattern of the variation in the relative lengths of the neural spines on the second vs. third and fourth preural centra does not correlate with the sex of the individual. The pattern of sexual dimorphism in the neural spines of the second through fourth preural centra described by Brewster (1986) and Murray & Stewart (2002) was observed in *Clupeocharax*, *Brycinus leuciscus* and *Phenacogrammus* cf. *interruptus*.

The opposite pattern, in which the neural spines of the second and third preural centra are approximately the same length in males but the spine of the second centrum is shorter in females, was observed in *Micralestes occidentalis* and *Rhabdalestes eburneensis*. Relatively short neural spines on the second neural preural centrum occur in both sexes in examined cleared and stained samples of *Bathyaethiops*, *Brachypetersius altus*, *Bryconalestes longipinnis*, *Phenacogrammus* sp. and *Virilia*. Alternatively, a proportionally long neural spine on the second preural centrum was observed in both sexes in *Alestes baremoze*, *Ladigesia* and *Micralestes elongatus*.

Our examined cleared and stained specimens of *Hydrocynus* are immature and of undetermined sex and all demonstrate the condition described by Brewster for males of the Alestidae. Radiographs of larger specimens of *H. brevis* and *H. forskahlii* demonstrate, however, that a spine on the second preural centrum that is shorter than the spines extending from the third and fourth preural centra occurs in some specimens of both sexes in both of these species. Finally, a series of 13 cleared and stained specimens of *Lepidarchus* included some individuals of each sex with the neural spine on the second preural centrum shortened relative to the spines of the third and fourth preural centra. Although variation exists in the relative length of the neural spines of the second through fourth preural centra across the Alestidae, there was no consistent correlation between such variation and the sex of the specimens in the material that we examined.

PHYLOGENETIC RECONSTRUCTION

Our analysis of phylogenetic relationships within the Alestidae was based on 200 osteological and soft anatomical characters. It encompassed 72 terminal taxa: 51 representing the ingroup and 21 representing the outgroup. Analyses utilizing both Henning86 and PAUP resulted in 256 equally parsimonious trees with 537 steps, with a consistency index (CI) of 0.40, and a retention index (RI) of 0.83. The strict consensus tree generated in the two programs was identical, with 541 steps; it is presented in Figure 43. The matrix of characters is presented in Appendix 2. Character numbers correspond to those in 'Character Description and Analysis', above. Numbers in Figure 43 indicate clades discussed in the following sections. Character listings correspond to the nodes in Figure 43, and are divided between unambiguous and ambiguous characters for each node (in instances when ambiguous characters apply to a particular node). The distribution of characters states was examined using ACCTRAN optimization.

The following listing of hypothesized synapomorphies commences at the level of the Alestidae and progressively continues to less inclusive groupings within that family. Phylogenetic relationships derived for the outgroup taxa in the course of the phylogenetic reconstruction are neither detailed nor discussed for several reasons. Paramount among these is the fact that the degree of taxonomic coverage for the rest of the Characiformes was of necessity proportionally less comprehensive than that within the Alestidae, given the hundreds of potential outgroup genera in the order. As such, the scheme of relationships among the outgroups utilized in the phylogenetic analysis would of necessity provide an incomplete, and more likely misleading, picture of the actual relationships among those taxa. Furthermore, the core purpose of this study was to investigate the question of the monophyly and relationships within the Alestidae, not to generate robust hypotheses of relationships among outgroups in the Characiformes.

Future studies incorporating many more taxa are required to provide a comprehensive hypothesis of relationships across the Characiformes and, thus, of the exact placement of the Alestidae within that order. We consequently refrain from making explicit comments on that issue at this time. Nonetheless, it is noteworthy that the scheme of relationships among outgroup taxa associated with this study indicates that families within the Characiformes other than the Characidae are the sister group to the Alestidae, a result in keeping with those of previous authors (Buckup, 1998; Zanata, 2000).

MONOPHYLY OF CLADE 1 (ALESTIDAE)

The hypothesis of the monophyly of the Alestidae is supported by the following series of synapomorphies:

1. Contralateral premaxillae with medial interdigitations present (char. 55, 0 > 1). Reversed in *Petersius conserialis* and in clade 20.
2. Two functional rows of teeth present on premaxilla (char. 57, 0 > 1). Further developed into three rows of teeth in *Chalceus* and *Bryconaethiops*.
3. Area of contact of ectopterygoid with palatine narrow, with anterior portion of ectopterygoid usually half as wide as proximate portion of palatine (char. 97, 0 > 1). Reversed in *Clupeocharax* and *Tricuspidalestes*.

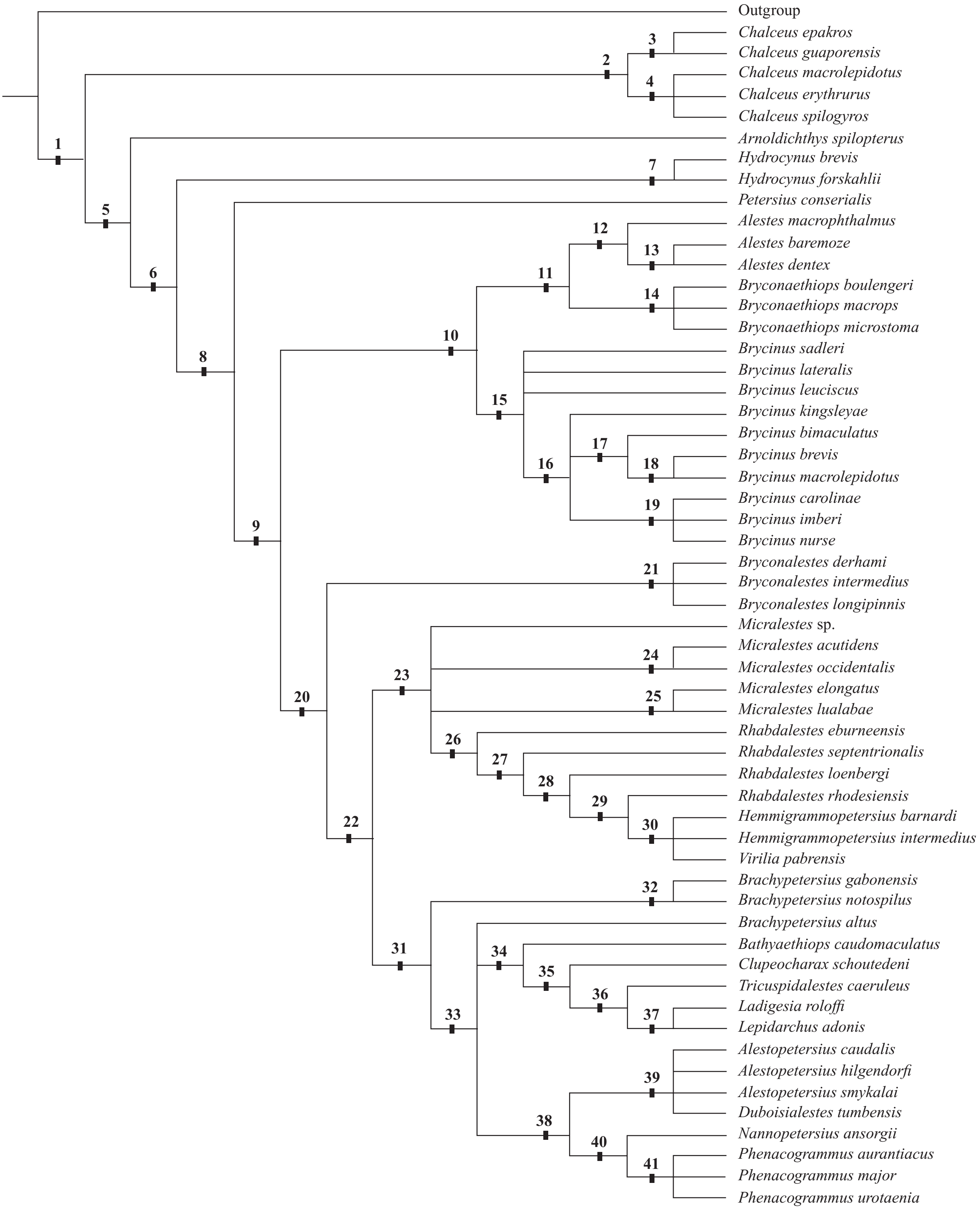

Figure 43. Most parsimonious hypothesis of relationships within the Alestidae based on 200 characters. Numbers represent nodes of clades discussed in the text.

4. Ligamentous attachment of ectopterygoid to neurocranium absent (char. 99, 0 > 1).
5. Four branchiostegal rays present (char. 112, 0 > 1). Further reduced to three branchiostegal rays in *Ladigesia*.
6. Small ossification associated with first dorsal-fin proximal radial absent (char. 124, 0 > 1).

The following characters are ambiguously optimized for this clade:

7. Lateral wings of mesethmoid reduced (char. 23, 1 > 0). Either derived at this level and lost at level of clade 6, or independently acquired in *Arnoldichthys* and *Chalceus*.
8. Orbital lamella of frontal relatively anteroposteriorly short with major portion, or nearly all, of articulation of orbitosphenoid with frontal being with main body of frontal (char. 34, 0 > 1). Either derived at this level and lost at level of clade 6, or independently acquired in *Arnoldichthys* and *Chalceus*.
9. Anterior dentary teeth tri- to pentacuspid and relatively elongate, with borders of teeth, including margins of cusps, running in parallel and with margins of adjoining teeth distinctly separated from each other (char. 87, 0 > 1). Either derived at this level and lost at level of clade 6, or independently acquired in *Arnoldichthys* and *Chalceus*.
10. Posteriormost proximal radial of dorsal fin supports two fin rays (char. 126, 1 > 0). Either derived at this level and reversed in *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, or the opposite condition (state 1) is a synapomorphy for clade 36.
11. Two pairs of uroneural bones present (char. 149, 0 > 1). Either derived at this level and reversed in *Arnoldichthys* and *Lepidarchus*, or acquired independently in *Chalceus* and clade 6 and reversed in *Lepidarchus*.
12. Relative position of the laterosensory canal of lateral line on body ventrally decurved and located approximately at level of base of second to sixth of principal caudal-fin rays of lower caudal-fin lobe at point where lateral line crosses vertical through hypural joint (char. 164, 0 > 1). Either derived at this level and reversed in *Arnoldichthys* and *Bryconaethiops*, or independently acquired in *Chalceus* and clade 6 and reversed in *Bryconaethiops*.
13. Scales dorsal to lateral line much larger than scales ventral to lateral line (char. 169, 0 > 1). Either derived at this level and reversed at level of clade 6, or independently acquired in *Arnoldichthys* and *Chalceus*.
14. Relative size of scales along lateral line other than on caudal peduncle alternatively large and small (char. 170, 0 > 1). Either derived at this level and reversed at level of clade 6, or independently acquired in *Arnoldichthys* and *Chalceus*.

One striking aspect of the ambiguously optimized characters for this clade is the predominance of such characters (five of seven) that are either derived at the level of the Alestidae and lost at the level of clade 6, or independently acquired in *Chalceus* and *Arnoldichthys* (chars. 7, 8, 9, 13, 14; see also chars. 52, 54, 58, 59, 60 under clade 6). The occurrence of numerous ambiguously optimized characters at the level of the Alestidae under the ACCTRAN option would seemingly raise the question of whether an alternative topology of the phylogeny would result under DELTRAN. Analysis of the data under the latter option does not result in any changes to the topology of the final most parsimonious hypothesis of relationships based on the strict consensus tree. These ambiguously optimized characters parallel the situation described by de Pinna (1992) and elaborated by Stiassny & de Pinna (1994), under which basal taxa will often display character states that are modified within the phylogeny to a degree to render them effectively unrecognizable.

Comments on Alestidae. Members of the Alestidae, with the exception of *Chalceus*, constitute the African characids or the African Characidae of most previous authors (e.g. Greenwood *et al*., 1966). Under that concept, the Alestidae was subsumed into a broadly encompassing Characidae that was composed primarily of New World genera and species. Some recent treatments (e.g. Nelson, 1994) regarded the African characids as constituting a subfamily of the Characidae. The Alestidae was, in turn, proposed as a family separate from the Characidae by Géry (1977) followed by Eschmeyer (1990) and Buckup (1998). Géry (1977, 1995) delimited the Alestidae on the basis of a series of characters that, however, were either not exclusive to the Alestidae, not universal across the family, or were defined in such a fashion that we were unable to evaluate their utility for the purposes of a phylogenetic analysis.

Buckup (1998: 139) emphasized that under his proposed phylogenetic scheme, the continued inclusion of ‘African characids’ in the Characidae rendered the latter family polyphyletic. Our hypothesis is that the Alestidae is a monophyletic group delimited on the basis of a series of derived characters. The results of our study furthermore indicate that the Alestidae, although including the genus *Chalceus* previously assigned to the Characidae is, however, not the closest relative of the other taxa that are currently included in the Characidae. This conclusion necessitates a recognition of an Alestidae distinct from the Neotropical Characidae; a hypothesis in agreement with that proposed by Buckup (1998).

The conclusions of Malabarba & Weitzman (2003) are also pertinent to this question. Ossified hooks on the rays of various fins, most often the anal and pelvic fins, have been reported for numerous Neotropical members of the Characiformes (see listing by Malabarba & Weitzman, 2003: 74). Such hooks are apparently secondary sexual characters of males and seasonably variable in their degree of development. In their analysis, Malabarba & Weitzman (2003) proposed that the possession of hooks on the fin rays was a synapomorphy for a clade encompassing a major part of the Characidae along with the Gasteropelecidae and a subunit of the Cynodontinae. Such hooks are unknown in the Alestidae, with the absence of those structures in *Chalceus*, the single New World genus in the Alestidae, specifically cited by Malabarba & Weitzman (2003: fig. 2). Although the plesiomorphic absence of these hooks in the Alestidae is admittedly uninformative as to the relationships of that family within the Characiformes, the phylogenetic hypothesis of Malabarba & Weitzman indicates that the closest relatives of the Characidae are Neotropical taxa rather the African Alestidae.

MONOPHYLY OF CLADE 2 (*CHALCEUS*)

The five species included in the Neotropical genus *Chalceus* as recently revised by Zanata & Toledo-Piza (2004) form a monophyletic group defined by the following synapomorphies:

15. Dorsomedial process of second infraorbital present (char. 10, 0 > 1). Reversed in *Chalceus erythrurus* and independently acquired in *Phenacogrammus major*.
16. Ventral diverging lamellae of mesethmoid well-developed (char. 22, 0 > 1).
17. Three functional rows of teeth on premaxilla (char. 57, 1 > 2). Also independently acquired in *Bryconaethiops*.
18. Supramaxilla present (char. 81, 0 > 1).
19. Relatively large inner row tooth proximate to dentary symphysis present (char. 88, 0 > 1). Tooth gained and lost in various species and groups of taxa in the Alestidae.
20. Medially directed process on base of second rib present (char. 117, 0 > 1). Independently acquired in *Lepidarchus*.
21. First intermuscular bones located more anteriorly than in most other alestids and proximate to rear of neurocranium (char. 123, 0 > 1). Also independently acquired in *Alestes*, *Brycinus macrolepidotus*, *Hydrocynus* and clade formed by *Micralestes elongatus* and *M. lualabae*.
22. Sensory canal segment of lateral-line scales in portion of scale located distinctly posterior to limit of overlap of sequential scales highly divided, with branches dorsal and ventral to primary horizontal canal arising distinctly posterior to limit of posterior margin of preceding scale and with each branch terminating in pore (char. 166, 0 > 1).

Comments on relationships of Chalceus. Diverse interpretations have been advanced as to the phylogenetic relationships of *Chalceus* and some authors (e.g. Eigenmann & Allen, 1942: 277; Géry, 1977: 342) considered the genus difficult to assign taxonomically. Eigenmann (1910: 439) placed *Chalceus* together with *Plethodectes* (since synonymized into *Chalceus*) in his Piabucininae, a subfamily that is now a component of the Lebiasinidae (*sensu* Greenwood *et al*., 1966). Regan (1911) soon thereafter questioned the validity of the character 'presence or absence of cranial fontanels' as useful for delimiting the group composed of these taxa and noted that '*Chalceus* has mouth and dentition of *Brycon* and is certainly related to that genus . . . on the other hand, the large scales, the short anal fin, the flattish head suggest relationship to *Pyrrhulina*, that is confirmed by the large size of the mesethmoid bone and by the somewhat intermediate dentition of *Plethodectes*.' Such contradictory statements, which propose that the relationships of *Chalceus* lay with both *Brycon* and *Pyrrhulina*, genera that are assigned to the Characidae and Lebiasinidae, respectively, failed to resolve the problem of the relationships of *Chalceus*.

Based on perceived similarities in dentition, Eigenmann (1912: 372) incorporated *Chalceus* together with *Brycon* in the subfamily Bryconinae of the Characidae. Subsequently, and without reference to Eigenmann's (1912) comments, Eigenmann & Allen (1942: 277) proposed that *Chalceus* was rather related to *Piabucina* and included those two genera in the subfamily Lebiasininae. These authors, nonetheless, confirmed that based on the morphology of its oral dentition, *Chalceus* should be placed together with *Brycon*. They also alluded to unspecified 'skeletal characters' reported by Gregory & Conrad (1938), which alternatively indicated a 'close affinity' of *Chalceus* with the 'Erythrinine' group. Weitzman (1960: 243) and subsequent authors included *Chalceus* together with *Brycon* and *Triportheus* in the tribe Bryconini, a component of the family Characidae (*sensu* Greenwood *et al*., 1966), based on similarities of cranial morphology, dentition, jaws, facial bones and vertebrae.

Several more recent studies focusing on other phylogenetic questions in characiform systematics have arrived at dissimilar conclusions concerning the phylogenetic placement of *Chalceus*. Based on a series of morphological characters Lucena (1993: 121) proposed *Chalceus* as the sister group of *Brycon*, a hypothesis that echoed the phylogenetic suggestions of some earlier researchers. In their analysis of higher level relationships within the Characiformes utilizing molecular techniques, Ortí & Meyer (1997: 92) hypothesized that *Chalceus* was the sister group of the clade formed by *Acestrorhynchus*, *Alestes*, *Boulengerella*, *Brycinus*, *Ctenolucius*, *Gnathocharax*, *Hydrocynus* and *Salminus*, an assemblage that included the three taxa of the African component of the Alestidae (*Alestes*, *Brycinus*, *Hydrocynus*) that were incorporated into that study. Ortí (1997: 238) further noted that *Chalceus* failed to form a monophyletic group with the other members of the Characidae that he included in his molecular analysis, but instead was the sister group of the clade formed by *Alestes*, *Boulengerella*, *Hoplias* and *Phenacogrammus*.

The morphologically based study of Zanata (2000) centred on the relationships of *Brycon* also failed to yield evidence in support of the hypothesis of a close phylogenetic relationship of *Chalceus* with *Brycon*, a break from many previous phylogenetic hypotheses. That study also highlighted the fact that some of the putative similarities previously thought to be common to *Chalceus* and *Brycon* were invalidated by a detailed analysis of the characters in question. Instead, *Chalceus* was proposed by Zanata (2000) to be a component of the clade formed by the members of the Alestidae incorporated into her analysis along with two Neotropical taxa, *Crenuchus* and *Hemiodus*.

The phylogenetic hypothesis proposed herein indicates that *Chalceus* is positioned within the Alestidae rather than being most closely related to members of the family Characidae. The alternative (although not rigorously proposed) earlier hypothesis of a relationship between *Chalceus* and the Lebiasinidae or some component of the latter, is incongruent with the available phylogenetic evidence. Examination of the synapomorphies proposed for the Lebiasinidae and clades within the Characiformes that include that family by Vari (1995), Buckup (1998) and Oyakawa (1998) demonstrated that the overwhelming preponderance of the evidence fails to support a relationship between *Chalceus* and those clades. Furthermore, the characters possibly common to *Chalceus* on the one hand and components of the Lebiasinidae on the other, failed to demonstrate a consistent pattern of occurrence within the Lebiasinidae. More significantly, such features are proportionally few in number, both relative to the overall number of synapomorphies for the pertinent clades within the Characiformes that include the Lebiasinidae and in comparison to the characters that justify the inclusion of *Chalceus* in the Alestidae.

Finally, although not justifying the *a priori* exclusion of these characters from a phylogenetic analysis, it is also noteworthy that many of the similarities between *Chalceus* and the lebiasinids involve character systems demonstrating high levels of homoplasy across the Characiformes.

INTRAGENERIC RELATIONSHIPS IN *CHALCEUS* (CLADES 3 AND 4)

Derived features define two clades within *Chalceus*. The first clade consists of two species, *C. epakros* and *C. guaporensis* (clade 3), sharing a single synapomorphy:

23. Deep-lying midlateral stripe extending along body onto caudal peduncle present (char. 173, 0 > 1). Stripe also present independently in *Brycinus lateralis*, *B. leuciscus*, *B. sadleri*, *Bryconaethiops microstoma* and in the clade formed by *Hemmigrammopetersius*, *Micralestes*, *Rhabdalestes* and *Virilia*.

Chalceus guaporensis is defined by two autapomorphies:

A_1. Parasphenoid relatively straight anteroposteriorly and with posterior portion of bone aligned approximately along longitudinal axis of anterior portion of vertebral column (char. 41, 1 > 0).

A_2. Eight unbranched plus branched pelvic-fin rays present (char. 138, 1 > 2).

The second clade within *Chalceus* (clade 4) consists of three species, *C. erythrurus*, *C. macrolepidotus* and *C. spilogyros* and is characterized by the following four synapomorphies:

24. Anterior border of first infraorbital either aligned with anterior border of antorbital or situated slightly posterior to that point (char. 6, 0 > 1).
25. Frontal fontanel restricted to posterior portion of frontal with anterior limit of opening located only slightly anterior to epiphyseal bar (char. 36, 2 > 1). Independently acquired as a synapomorphy for the members of clade 9.
26. Parietal fontanel present in adult specimens (char. 37, 1 > 0). Independently acquired as a synapomorphy for the members of clade 8.
27. First tooth on maxilla distinctly larger than remaining teeth in that series (char. 79, 0 > 1).

Chalceus erythrurus is defined by a single autapomorphy:

B_1. Dorsomedial process of second infraorbital absent (char. 10, 1 > 0).

No autapomorphies were identified in the study for either *Chalceus macrolepidotus* or *C. spilogyros*.

MONOPHYLY OF CLADE 5

Arnoldichthys has been usually defined as a member of the Petersiini (e.g. Poll, 1967a; Paugy, 1990a), a tribe that also included taxa (e.g. clade 22) that are deeply internested within the phylogeny of the Alestidae and thus not hypothesized to be closely related to *Arnoldichthys* under the final most parsimonious hypothesis of relationships. The hypothesis of relationships arrived at in this study indicates that contrary to the implicit hypotheses of a naturalness of the Petersiini, *Arnoldichthys* has a very separate position in the phylogeny from other taxa traditionally assigned to that tribe, being the most basal member of the Alestidae to the exclusion of *Chalceus* and thus the sister group of all African members of that family. The monophyly of the clade formed by *Arnoldichthys* and all other taxa in the Alestidae with the exception of *Chalceus* is supported by the following synapomorphies:

28. Orbital ring complete, with dorsal margin of orbital rim bordered by the sixth infraorbital and supraorbital or in some instances solely by the latter ossification (char. 5, 0 > 1). Reversed in clade 22 and reacquired within that lineage in *Brachypetersius notospilus*.
29. First infraorbital nearly or totally overlapping ascending process of maxilla and with the anterior border of the infraorbital reaching at least posterolateral portion of premaxilla (char. 7, 0 > 1). Secondarily lost in clade consisting of *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, but secondarily reacquired in that clade in *Ladigesia*.
30. Three teeth in outer tooth row of premaxilla (char. 59, 0 > 3). Further modified in various groups of alestids, with four teeth present in clade 15, two in clades 28 and 31 and *Petersius conserialis* and five teeth present in *Brycinus macrolepidotus*.
31. Teeth on maxilla absent (char. 78, 1 > 0).
32. Lateral surface of dorsal portion of hyomandibular with ridge or distinct lateral process (char. 103, 0 > 1). Reversed in *Bathyaethiops* and in the clade formed by *Ladigesia* and *Lepidarchus*.
33. Laterosensory canal segment in vertical arm of preopercle located proximate to, or along, anterior margin of vertical arm of preopercle and near to, or sometimes overlapping posterior margin of hyomandibular and overlapped by posterior margins of third and fourth infraorbitals other than when these latter ossifications are proportionally reduced (char. 108, 0 > 1).
34. Fusion of medial and proximal radials of anal fin present (char. 191, 0 > 1).

The following characters are ambiguously optimized for this clade:

35. Metapterygoid-quadrate fenestra longitudinally elongate, with longest axis aligned along horizontal axis of body and with extensive gap between posteroventral process of posterior portion of metapterygoid and posterodorsal process of quadrate; dorsal border of symplectic consequently forms major portion of posteroventral border of fenestra (char. 102, 0 > 1). Either derived at this level and reversed in *Hydrocynus*, or independently acquired in *Arnoldichthys* and in clade 9.
36. Caudal-fin bony stays present (char. 150, 0 > 1). Either derived at this level and reversed in clade 31, or acquired in clade 6 and reversed in clade 31. Ambiguity at this level is a consequence of coding *Arnoldichthys* as '?' in matrix for this feature (see comments under char. 150).

Arnoldichthys is considered to consist of only one species, *A. spilopterus* (Paugy, 1990a: 80; Géry, 1995: 40) and is characterized by the following autapomorphies:

C_1. Ventral surface of supraorbital with distinct ventrally directed process, anterior portion of which contacts blade-like ventrolateral process of lateral ethmoid (char. 3, 0 > 1).
C_2. Wavy ridges on lateral surface of maxilla present (char. 77, 0 > 1).
C_3. Supraneural anterior to neural spine associated with fourth vertebrae absent (char. 122, 0 > 1).
C_4. Eight unbranched plus branched pelvic-fin rays present (char. 138, 1 > 2).
C_5. Four or five unbranched anal-fin rays present (char. 142, 1 > 2).
C_6. Anterodorsally directed, triangular extension of anterior region of basal portion of anterior and middle branched anal-fin rays present (char. 189, 0 > 1).
C_7. Sexually dimorphic patterns of dark pigmentation of stripes vs. spot on anal fin present, with dark pigmentation in female limited to rotund dark spot on basal half of posterior portion of anal fin; dark pigmentation in males takes form of three dark stripes extending from base to distal margin of anal fin, with dark pigmentation along distal margin of fin (char. 192, 0 > 1).

The following characters are ambiguously optimized as autapomorphies for this species:

C_8. One pair of uroneural bones (char. 149, 1 > 0).
C_9. Laterosensory canal of lateral line on body located approximately along horizontal mid-line of body or only slightly ventral to that location and approximately at middle of caudal fin at hypural joint (char. 164, 1 > 0).

MONOPHYLY OF CLADE 6

Hydrocynus is hypothesized to be a relatively basal clade within the Alestidae, forming the sister group of the lineage including the majority of the other taxa within the Alestidae with the exception of *Arnoldichthys* and *Chalceus*. The monophyletic clade formed by *Hydrocynus* and the remaining clades of the Alestidae is defined by the following synapomorphies:

37. Anterior margin of nasal falling short of lateral process of mesethmoid (char. 18, 1 > 0). Reversed independently in *Bryconaethiops* and in the clade consisting of *Brachypetersius gabonensis* and *B. notospilus*.
38. Orbital lamella of frontal aligned approximately in parallel to supraorbital laterosensory canal segment in frontal (char. 35, 1 > 0).
39. Presence of post-temporal fossae located entirely within the epioccipital (char. 43, 0 > 1). Reversed in the clade consisting of *Ladigesia* and *Lepidarchus*.
40. Paired, vertically elongate processes along posterior margin of supraoccipital enveloping anterodorsal portion of neural complex present (char. 46, 0 > 1). Reversed in *Lepidarchus*.
41. Posterolateral portion of premaxilla represented by an elongate, pedicle-like process, always without concave posterior surface (char. 52, 0 > 1). Reversed in *Lepidarchus*.
42. Area of insertion of premaxillary-maxillary ligament located on lateral surface of maxilla (char. 66, 0 > 1). Secondarily lost independently in the clade consisting of *Hemmigrammopetersius* and *Virilia*, and in the clade formed by *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* and reacquired in that clade in *Ladigesia*.
43. Anterodorsal portion of ascending process of maxilla terminating in a concave surface (char. 67, 0 > 1). Reversed in clades 27 and 31.
44. Ascending process of maxilla relatively straight when viewed dorsally and approximately aligned parallel to axis of posterior portion of the maxilla (char. 68, 0 > 1).
45. Ascending process of maxilla about as long as, or longer than, lamellar portion of maxilla (char. 69, 0 > 1). Secondarily lost in clade formed by *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*, and reacquired within that clade in *Ladigesia*.
46. Area of attachment on neurocranium of ligament extending from anterodorsal portion of suspensorium to anteroventral portion of neurocranium situated on lateral margin of vomer in area of articulation of vomer and mesethmoid (char. 100, 0 > 1).
47. Medially directed, elongate process arising distinct distance from base of first rib absent (char. 115, 1 > 0). Reversed in *Lepidarchus*.
48. Posteriorly directed projection near base of first rib present (char. 116, 0 > 1). Reversed in *Lepidarchus*.
49. Nine dorsal-fin proximal radials present (char. 125, 1 > 3). Further modified to ten radials in *Lepidarchus*.
50. Scales along posterodorsal margin of head arranged along margin of supraoccipital spine (char. 168, 1 > 0). Reversed in clade 16.
51. Circuli on exposed portion of scales without overall posterior orientation and without individual circuli relatively straight or slightly inclined towards horizontal midline of scale (char. 171, 1 > 0). Reversed independently in clade 15, the clade consisting of *Micralestes acutidens* and *M. occidentalis* and in *Brachypetersius gabonensis*.

Ambiguous features for this clade are:

52. Lateral wings of mesethmoid well-developed (char. 23, 0 > 1). Either derived at this level as a reversal of a synapomorphy acquired at level of clade 1 (synapomorphy 7), or the opposite condition (state 0) is independently acquired in *Arnoldichthys* and *Chalceus*.
53. Anterolateral portion of orbitosphenoid with anteriorly directed expansion that at least partially overlaps lateral surface of olfactory bulb (char. 33, 0 > 1). Either derived at this level and reversed in clade 20, or a synapomorphy independently acquired in *Hydrocynus* and the members of clade 10.
54. Orbital lamella of frontal relatively anteroposteriorly elongate and forming all, or nearly all, of articulation between orbitosphenoid and frontal (char. 34, 1 > 0). Either derived at this level as a reversal of a synapomorphy acquired at level of clade 1 (synapomorphy 8), or the opposite condition (state 1) is independently acquired in *Arnoldichthys* and *Chalceus*.
55. Ventral margin of lagenar portion of basioccipital situated distinctly dorsal to joint between parasphenoid and basioccipital (char. 47, 0 > 1). Either derived at this level, reversed in clade 9 and secondarily acquired in clade formed by *Alestes* and *Bryconaethiops*, or independently acquired in *Hydrocynus*, *Petersius* and the clade consisting of *Alestes* and *Bryconaethiops*.
56. Inner tooth row of premaxilla with four or fewer teeth (char. 61, 0 > 1). Either derived at this level or at level of clade 8. Ambiguity at this level is a consequence of coding of *Hydrocynus* as '-' in matrix (see comments in character 61).
57. Primordial ligament broad, robust and attaching to the posterior half of the maxilla (char. 80, 0 > 1). Either derived at this level and further

modified in *Hydrocynus*, reversed in clade formed by *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* and reacquired in that clade in *Ladigesia*, or acquired at level of clade 8, reversed in clade 35 and reacquired in *Ladigesia*.

58. Anterior dentary teeth not having combination of tri- to pentacuspid form and relatively elongate, with borders of teeth including margins of cusps, running in parallel and with margins of adjoining teeth distinctly separate from each other (char. 87, 1 > 0). Either derived at this level or the opposite condition (state 1) is independently acquired in *Arnoldichthys* and *Chalceus*.
59. Scales dorsal and ventral to lateral line approximately of the same size overall and gradually decreasing in relative size ventrally (char. 169, 1 > 0). Either acquired at this level as a reversal of a synapomorphy acquired at level of clade 1 (synapomorphy 13) or the opposite condition (state 1) is independently acquired in *Arnoldichthys* and *Chalceus*.
60. Scales along lateral line gradually diminish in size towards caudal peduncle (char. 170, 1 > 0). Either acquired at this level as a reversal of a synapomorphy acquired at level of clade 1 (synapomorphy 14), or the opposite condition (state 1) is independently acquired in *Arnoldichthys* and *Chalceus*.
61. Olfactory bulb separated from telencephalon and connected to it by distinct olfactory tract (char. 196, 0 > 1). Either derived at this level, reversed in *Brycinus sadleri* and in clade 20, or acquired independently in *Hydrocynus* and clade 10 with a secondary loss in *Brycinus sadleri*.

MONOPHYLY OF CLADE 7 (*HYDROCYNUS*)

The monophyly of *Hydrocynus* was previously proposed by Brewster (1986: 189) on the basis of 18 synapomorphies. The following listing includes both 13 of the synapomorphies for *Hydrocynus* spp. proposed by Brewster and 13 additional synapomorphies discovered in the course of this study. Characters 3 and 15 of Brewster (1986) were not incorporated into our analysis for the reasons discussed under ‘Unutilized Characters’ above. The other three synapomorphies (4, 5 and 6) proposed by Brewster (1986) are discussed under chars. 39, 55 and 56, respectively, of this paper.

62. First and second infraorbitals greatly enlarged and covering at least part of lateral surfaces of premaxilla and maxilla (char. 8, 0 > 1).
63. Anterior portion of mesethmoid without distinct medial process (char. 20, 0 > 1).
64. Lateral portion of mesethmoid wings terminating laterally in distinct concavity (char. 24, 0 > 1).
65. Sphenotic spine located distinctly anterior to anterior limit of articular fossa for hyomandibular that, in turn, is situated distinctly posterior to posterior margin of orbital opening (char. 39, 0 > 1).
66. Ventral portion of sphenotic spine with process posteriorly and with spine distinctly thickened short distance dorsal to ventral margin (char. 40, 0 > 1). Independently acquired in *Alestes*.
67. Parasphenoid relatively straight anteroposteriorly and with posterior portion of bone aligned approximately along longitudinal axis of anterior portion of vertebral column (char. 41, 1 > 0). Independently acquired in *Chalceus guaporensis*.
68. Teeth in both jaws all tricuspid at some point in ontogeny, but with anterior teeth in adults strongly conical, with posterior teeth tricuspid and anterior teeth in upper and lower jaws distinctly overlapping (char. 50, 0 > 1).
69. Posterior portion of premaxilla distinctly vertically expanded and transversely flattened (char. 53, 0 > 1).
70. Ascending process of premaxilla absent (char. 54, 1 > 0).
71. Articulation between premaxillae and mesethmoid with deep articular fossa on dorsomedial portion of posterior surface of premaxilla and with second, more laterally situated fossa articulating with lateral process of anterior portion of mesethmoid (char. 56, 0 > 1).
72. One functional row of teeth present on premaxilla (char. 57, 1 > 0). Independently acquired in *Clupeocharax* and *Lepidarchus*.
73. Premaxilla and maxilla ankylosed (char. 65, 0 > 1).
74. Expanded portion of ascending arm of maxilla terminating at posterior limit of premaxilla (char. 71, 0 > 1).
75. Process along posterodorsal margin of maxilla present (char. 73, 0 > 1). Independently acquired in *Micralestes lualabae*.
76. Replacement tooth cavity in dentary with replacement teeth aligned at distinct angle relative to functional dentary teeth and with replacement teeth enclosed within individual cavities within dentary (char. 91, 0 > 1).
77. Ectopterygoid relatively short but transversely wide with overall ovoid form, and falling short of anterodorsal margin of palatine (char. 98, 0 > 1).
78. Attachment on suspensorium of ligament extending from anterodorsal portion of suspensorium to anteroventral portion of neurocranium primarily onto medial region of anterodorsal portion of palatine, with small area of attachment on anterodorsal portion of mesopterygoid (char. 101, 0 > 1).

79. Hyomandibular spine present (char. 104, 0 > 1).
80. Fossa on anterior ceratohyal receiving head of third branchiostegal ray present (char. 110, 0 > 1).
81. Parapophyses of fifth and subsequent vertebrae elongate and with anterior limit extending distinctly anterior to anterior limit of centrum (char. 120, 0 > 1). Independently acquired in clade formed by *Alestes baremoze* and *A. dentex*.
82. More than ten intermediate-type vertebrae (char. 121, 0 > 1).
83. First intermuscular bones located anteriorly and proximate to rear of neurocranium (char. 123, 0 > 1). Independently acquired in *Alestes*, *Brycinus macrolepidotus*, *Chalceus* and the clade formed by *Micralestes elongatus* and *M. lualabae*.
84. Postcleithrum 3, when present, without lamella (char. 135, 0 > 1). Also present independently in *Alestes*, *Brycinus macrolepidotus* and clade 22.
85. Epiphyseal branch of supraorbital canal short, with two or three short branches arising from main body of supraorbital canal (char. 155, 0 > 1). Independently acquired in *Alestes*.
86. Adipose eyelid covering part of eye well-developed (char. 197, 0 > 1). Independently present in clade formed by *Alestes* and *Bryconaethiops*.

The following features are ambiguously optimized for this genus:

87. Primordial ligament relatively narrow and attached to posterolateral surface of ascending process of maxilla (char. 80, 1 > 2). Either state 1 is a synapomorphy at a more inclusive level (node 6) and the morphology in the examined species of *Hydrocynus* is derived from this condition or it is a synapomorphy at lower level (node 8) and the *Hydrocynus* condition is derived from state 0.
88. Metapterygoid-quadrate fenestra rounded and bordered mainly by those bones (char. 102, 1 > 0). Either derived at this level as a reversal of synapomorphy 35 or the opposite condition (state 1) is a synapomorphy for clade 9, independently acquired in *Arnoldichthys*.

Hydrocynus forskahlii is defined by a single autapomorphy:

D_1. Connection between sensory canal in sixth infraorbital and laterosensory canals on neurocranium through anteriorly located pore located in frontal (char. 154, 0 > 1).

No autapomorphies were identified in this study for the other examined species of *Hydrocynus*.

Comments on phylogenetic relationships of Hydrocynus. Although Roberts (1969: 442) suggested that *Hydrocynus* was derived from an *Alestes*-like ancestor, he erected a separate subfamily, the Hydrocyninae, for the genus. Vari (1979: 342) reported on various derived features (presence of orbitosphenoid tube, anterior shift of olfactory bulb, interdigitations of contralateral premaxillae) that suggested a close phylogenetic relationship between *Hydrocynus*, *Bryconaethiops* and a subunit of *Alestes*. Under such a scheme of relationships, the recognition of the Hydrocyninae as proposed by Roberts (1969) rendered the Alestinae nonmonophyletic. In order to resolve that issue, Vari (1979) synonymized the Hydrocyninae into the Alestinae.

Brewster (1986: 192) delved further into the question of the phylogenetic position of *Hydrocynus* and proposed that a subunit within *Alestes* (the *Alestes sensu stricto* of her study) was the sister-group of *Hydrocynus* based on three synapomorphies (a long, deep dilatator fossa, a well-developed, ventrally thickened sphenotic process, and the presence of 8–11 pairs of fine, elongate pleural ribs articulating with the posteroventral surface of the haemal spines). Her scheme of relationships indicated that the recognition of a separate Hydrocyninae as proposed by Roberts (1969) was unjustified, a conclusion that corroborated the hypothesis previously proposed by Vari (1979). More recently, Murray & Stewart (2002) incorporated Brewster's (1986) data into an analysis of the phylogenetic relationships of a subset of the Alestidae and supplemented her synapomorphies with one additional feature involving the well-developed adipose eyelid present in *Hydrocynus*.

Contrary to the hypotheses of Vari (1979), Brewster (1986) and Murray & Stewart (2002), a close relationship between *Hydrocynus* and *Alestes* or between *Hydrocynus* and a subset of *Alestes* is not supported in this phylogenetically more encompassing analysis. Rather, the hypothesis proposed here places *Hydrocynus* in a relatively basal position in the topology of the Alestidae, as the sister group of the clade composed by the remaining members of that family with the exception of *Chalceus* and *Arnoldichthys*. The various characters proposed by previous authors as supporting a sister-group relationship between *Hydrocynus* and *Alestes* are either applicable at other levels of the phylogeny, homoplastic under the final most parsimonious hypothesis of relationships arrived at in this study, or could not be unambiguously coded and therefore were not utilized in this study.

MONOPHYLY OF CLADE 8

The monophyly of clade 8 is supported by the following synapomorphies:

89. Parietal fontanel present in adult specimens (char. 37, 1 > 0). Reversed in clade 16 and independently acquired in the clade formed by

Chalceus erythrurus, *C. macrolepidotus* and *C. spilogyros*.

90. Posterior margin of the maxilla falling short of, or aligned with, vertical through lateral blade of lateral ethmoid (char. 72, 1 > 0).
91. Four dentary teeth present (char. 84, 0 > 1). Independently reversed in clades 30, 32, 35 and secondarily reacquired in *Hemmigrammopetersius barnardi*.
92. Articulation between angulo-articular and quadrate situated anterior to, or along, vertical through ventral tip of lateral process of lateral ethmoid (char. 93, 0 > 1). Reversed in *Lepidarchus*.

The following features are ambiguously optimized for this clade:

93. Contralateral premaxillae without medial interdigitations (char. 55, 1 > 0). Either derived at this level and reversed in clade 10, or a synapomorphy for clade 20 occurring independently in *Petersius*.
94. Interdigitating processes in symphyseal dentary processes complex with undulating subprocesses and scalloped margins (char. 83, 0 > 1). Either derived at this level with secondary loss in clade 22 and reacquired in *Brachypetersius altus* and *Phenacogrammus urotaenia*, or a synapomorphy for clade 10 and independently acquired in *B. altus*, *Bryconalestes* and *P. urotaenia*.
95. Posterolateral portion of second dentary tooth distinctly overlapping anteromedial portion of third tooth present and with portion of second tooth inserting into a distinct depression on anteromedial surface of third tooth present (char. 86, 0 > 1). Either derived at this level with secondary loss in clade 22, or independently acquired in clade 10 and *Bryconalestes*.
96. Palatine articulating with anterolateral margin of vomer and posterolateral margin of mesethmoid (char. 96, 0 > 1). Either derived at this level or at level of clade 9. The ambiguity at this level is a consequence of *Petersius* being coded as '?' (see comments in character 96).
97. Anal fin stay represented by elongated bone similar in overall form to the adjoining proximal radials (char. 147, 0 > 1). Either derived at this level, secondarily lost in clades 11 and 22 and reacquired in *Brachypetersius gabonensis*, or gained independently at level of clade 15, *Bryconalestes*, *Brachypetersius gabonensis* and *Petersius*.

Petersius conserialis is defined by two autapomorphies:

E_1. Outer tooth row of premaxilla with two teeth present (char. 59, 3 > 4).

E_2. Fifth through eighth anal-fin rays with individual segments of fin rays relatively to distinctly anteroposteriorly wide proportional to dimension of segment along axis of ray, with overall ray consequently rather anteroposteriorly wide and with distal portions of rays forming variably distinct median anal-fin lobe (char. 179, 0 > 1).

Comments on the phylogenetic position of Petersius. Prior to Myers (1929), the concept of *Petersius* encompassed both the type species of the genus, *P. conserialis,* and also a number of alestids, mostly of small body size that had in common the possession of cuspidate teeth, a completely pored lateral line and the absence of an inner symphyseal tooth on the dentary. Myers (1929: 5) restricted *Petersius* to its type-species, *P. conserialis*, a form of moderately large body size, on the basis of the absence in that species of the extensive median frontoparietal fontanel that was clearly present in the other species assigned to *Petersius* under the prior more encompassing concept of that genus.

Notwithstanding that difference, *Petersius* was subsequently consistently included in the Petersiini (e.g. Poll, 1967a; Géry, 1977, 1995; Paugy, 1990a), a tribe defined on the base of small body size of its component taxa and the absence of 'mammilliform' (= wide multicuspid) teeth. These attributes both fail to delimit the assemblage phenetically and have, furthermore, proved to be inadequate to define a monophyletic lineage within the Alestidae.

In their recent analysis of some members of the Alestidae, Murray & Stewart (2002: 1895) found that the components of the Petersiini that they incorporated into their analysis (*Petersius*, *Nannopetersius* and *Rhabdalestes*) were not united by any synapomorphies and then went on to propose that the tribe 'is probably nonmonophyletic'. That statement went beyond the evidence advanced by Murray & Stewart (2002) in so far as the phylogeny proposed in that publication was in actuality uninformative as to the monophyly, or lack thereof, of the Petersiini.

Our comparative anatomical analysis of the phylogenetic placement of *Petersius* in the Alestidae was constrained in the absence of cleared and stained specimens of *P. conserialis*. Consequently, only features amenable to external examination or to evaluation via radiographs could be coded for the species. A further corroborated hypothesis of the relationships of *Petersius* depends on future studies utilizing information from cleared and stained specimens evaluated within a context of a broad sample of taxa. Nonetheless, the available information clearly indicates that the phylogenetic position of *Petersius* differs significantly from the vaguely defined concepts of the relationships of that genus implicit in previous classifications.

According to our results, *Petersius* is relatively basally positioned in the cladogram of the Alestidae (Fig. 43) and is phylogenetically distinctly separated from clade 22, a lineage composed of the alestid species of small body size that traditionally constituted the bulk of species in the Petersiini. *Petersius* furthermore lacks all of the unambiguous synapomorphies amenable to examination on whole specimens or radiographs of such material (155, 157, 158, 160) characterizing clade 22. The preponderance of the evidence thus indicates that the association of *Petersius* and the name Petersiini under previous classifications with the species forming clade 22 in this study is inappropriate.

Although the lack of cleared and stained specimens constrains the exact placement of *Petersius*, we find that the genus similarly lacks the synapomorphies (99, 100, 144, 148) that can be evaluated by external examination or via radiography and which characterize various clades in the Alestidae. *Petersius* furthermore lacks both of the externally visible synapomorphies (102, 103) diagnosing the clade formed by *Alestes*, *Brycinus* and *Bryconaethiops*.

MONOPHYLY OF CLADE 9

The following synapomorphies for the taxa of clade 9 have been identified in this study:

98. Frontal fontanel restricted to posterior portion of frontal with anterior limit of opening located only slightly anterior to epiphyseal bar (char. 36, 2 > 1). Further modified in a group of *Brycinus* species (clade 16), secondarily expanded in *Bathyaethiops* and *Lepidarchus* and independently acquired in three species within *Chalceus* (clade 4).
99. Relatively large inner row tooth proximate to dentary symphysis present (char. 88, 0 > 1). Independently acquired in *Chalceus* and independently reversed in clades 26, 35, 39 and *Micralestes occidentalis*; reacquired in *Virilia* and *Tricuspidalestes*.

The following features are ambiguously optimized for this clade:

100. Ventral margin of lagenar portion of basioccipital situated ventral to, or aligned with, joint between parasphenoid and basioccipital (char. 47, 1 > 0). Either derived at this level and reversed in the clade formed by *Alestes* and *Bryconaethiops*, or the opposite condition independently acquired in *Hydrocynus*, *Petersius* and the clade formed by *Alestes* and *Bryconaethiops*.
101. Cusps on distal margin of first through third teeth of inner premaxillary tooth row arranged in distinctly pronounced arch (char. 63, 0 > 1). Either derived at this level and secondarily lost in clade 22, or independently acquired in *Bryconalestes* and clade 10.

MONOPHYLY OF CLADE 10 (*ALESTES*, *BRYCINUS* AND *BRYCONAETHIOPS*)

The monophyly of this clade is diagnosed by the following synapomorphies:

102. Posterior portion of third tooth of inner premaxillary tooth row expanded posteromedially (char. 62, 0 > 1).
103. Included cusps on first through third teeth on inner tooth row on premaxilla present (char. 64, 0 > 1).
104. Profile of posterodorsal portion of maxilla in lateral view distinctly convex (char. 74, 0 > 1).
105. Attachment on dentary of main portion of ligament from adductor mandibulae muscle located on posterior wall of replacement tooth trench and distinctly dorsal to ventral margin of dentary (char. 92, 0 > 1).

The following feature is ambiguously optimized for this clade:

106. Contralateral premaxillae with medial interdigitations present (char. 55, 0 > 1). Either derived at this level as a reacquisition of a feature lost in a more inclusive group (node 8), or the opposite condition (state 0) is a synapomorphy for clade 20 and independently acquired in *Petersius*.

Comments on the interrelationships of Alestes, Brycinus and Bryconaethiops. These genera were recognized as the tribe Alestini within the subfamily Alestinae by Géry (1977: 19, 1995: 39). The limits of the subunits of the subfamily Alestinae were interpreted by Géry (1977: 19) as artificial, being based solely on body size and the presence for absence of ‘excavated molariform teeth’ in the upper jaw.

Variably encompassing definitions of *Alestes* occur in the literature. Some authors followed a definition of *Alestes sensu lato* (e.g. Boulenger, 1909; Monod, 1950) that incorporated species assigned in this study not only to *Alestes*, but also *Brycinus* and *Bryconalestes*. Although phenetically similar, these three genera fail to constitute a monophyletic group under the overall most parsimonious hypothesis of relationships arrived in our analysis.

Other concepts of *Alestes* are much more restrictive (*Alestes sensu stricto* of Myers, 1929; Géry, 1977; Paugy, 1986), under which the genus incorporated only a limited number of forms closely related to the type species of *Alestes*, *A. dentex*. Under that more restrictive definition, the remaining species traditionally assigned to *Alestes* under the broader definition were removed to *Brycinus*. Although no critical analysis of relationships were developed in those earlier studies, an idea of a natural (i.e. monophyletic) *Alestes* was presumably an underlying operational concept for all of these authors.

The monophyletic nature of the genus *Alestes sensu lato* was questioned by Vari (1979: 352). Based on the distribution of apomorphic characters, Vari indicated that some members of *Alestes* were more closely related to the species of *Bryconaethiops* and *Hydrocynus* than they were to the remaining species of *Alestes*. Brewster (1986: 190) delved further into this question and suggested that *Alestes* (*sensu* Boulenger) incorporates at least three taxa, each of which has closer relatives among species of other genera than with nominal congeners. Brewster (1986: 192) proposed a close relationship between her *Alestes sensu stricto* and *Hydrocynus* based on three synapomorphies.

The comparative analysis carried out in the present study revealed that just one of the synapomorphies proposed by Brewster (the well-developed, ventrally thickened sphenotic process; discussed in character 40) was definable as a character shared by *Alestes* and *Hydrocynus* under a more enveloping analysis. This feature was, however, optimized in our analysis as being independently acquired in *Alestes* and *Hydrocynus* (see 'Unutilized Characters' for a discussion concerning the subset of the characters used by Brewster at different levels in her phylogenetic scheme, but not incorporated into this analysis). Contrary to the hypothesis advanced by Brewster (1986), our results show *Alestes* (*sensu stricto*) to be closely related to *Bryconaethiops*, with the clade formed by those two genera being the sister-group to *Brycinus*.

In their analysis of a component of the Alestidae, Murray & Stewart (2002: fig. 3 and synapomorphies therein) proposed that *Alestes, Hydrocynus* and the species of *Brycinus*, with the exception of *B. lateralis* and *B. leuciscus*, formed a monophyletic group based on a single feature, the presence or absence of interdigitations between the contralateral premaxilla. In contrast, our analysis has found that interdigitations joining the premaxillae are present in *B. lateralis* and *B. leuciscus*. Recoding of *B. lateralis* and *B. leuciscus* as exhibiting such premaxillary interdigitations would unite those two species into a clade with the other species of *Brycinus* under the Murray & Stewart matrix.

In the final most parsimonious hypothesis of relationships arrived at in this study, the possession of such interdigitations joining the premaxillae is not derived at the level of *Alestes*, *Brycinus* and *Hydrocynus*, but is rather a synapomorphy for the Alestidae, albeit with reversals to the absence of premaxillary interdigitations in *Petersius* and clade 20.

MONOPHYLY OF CLADE 11 (*ALESTES* AND *BRYCONAETHIOPS*)

A close relationship between *Alestes* and *Bryconaethiops* was previously proposed by Géry (1968: 183) in a phenetic study based primarily on morphometric and meristic characters. A phylogenetic hypothesis based on the derived features shared by these two genera is presented herein for the first time and the clade formed by those two genera is defined by the following synapomorphies:

107. Junction of fifth and sixth infraorbitals along margin of orbit with very well-developed indentation (char. 16, 0 > 1).
108. Adipose eyelid covering part of eye well-developed (char. 197, 0 > 1). Independently acquired in *Hydrocynus*.

The following characters are ambiguously optimized for this clade:

109. Ventral surface of supraorbital with distinct, ventrally directed process, anterior portion of which contacts blade-like ventrolateral process of lateral ethmoid (char. 3, 0 > 1). Either derived at this level, secondarily lost in *Alestes macrophthalmus* and independently acquired in *Arnoldichthys* and *Bryconalestes*, or independently acquired in clades 13, 14 and in *Arnoldichthys* and *Bryconalestes*.
110. Ventral margin of lagenar portion of basioccipital situated distinctly dorsal to joint between parasphenoid and basioccipital (char. 47, 0 > 1). Either derived at this level as a reacquisition of a feature lost in a more inclusive group (node 9), or independently acquired in *Hydrocynus*, *Petersius* and the clade formed by *Alestes* and *Bryconaethiops*.
111. Anal-fin stay totally cartilaginous or represented by a small plate-like bone (char. 147, 1 > 0). Either derived at this level as a secondary loss of a feature acquired in a more inclusive group (node 8), or the opposite condition (state 1) is a synapomorphy for clade 15, independently acquired in *Brachypetersius gabonensis*, *Bryconalestes* and *Petersius*.

MONOPHYLY OF CLADE 12 (*ALESTES*)

The following eight synapomorphies include one of the synapomorphies for *Alestes sensu stricto* proposed by Brewster (1986: 190) and seven additional synapomorphies (113–119) discovered in the course of this study:

112. Ventral portion of sphenotic spine with process posteriorly and with spine distinctly thickened short distance dorsal to ventral margin (char. 40, 0 > 1). Independently acquired in *Hydrocynus*.

113. First intermuscular bones located anteriorly and proximate to rear of neurocranium (char. 123, 0 > 1). Independently acquired in *Chalceus*, *Brycinus macrolepidotus*, *Hydrocynus* and in clade formed by *Micralestes elongatus* and *M. lualabae*.
114. Postcleithrum 3, when present, without lamella (char. 135, 0 > 1). Independently acquired in *Brycinus macrolepidotus*, *Hydrocynus* and clade 22.
115. Basal portion of first proximal radial with dorsally directed process on anterior surface (char. 143, 0 > 1).
116. Orientation of posterior proximal anal-fin radials distinctly more anteriorly inclined than orientation of anterior proximal radials (char. 146, 0 > 1).
117. Epiphyseal branch of supraorbital canal short, with two or three short branches arising from main body of supraorbital canal (char. 155, 0 > 1). Independently acquired in *Hydrocynus*.
118. Posterior limit of posterior chamber of swimbladder extending posteriorly past anterior portion of base of anal fin to haemal spine of third preural centrum (char. 200, 0 > 1).

The following character is ambiguously optimized at this level:

119. Connection between sensory canal in sixth infraorbital and laterosensory canals on neurocranium through more anteriorly located pore located in frontal (char. 154, 0 > 1). Either derived at this level or at level of the clade formed by *Alestes baremoze* and *A. dentex*. The ambiguity is a consequence of *A. macrophthalmus* being coded as '?' (See comments under char. 154).

INTRAGENERIC RELATIONSHIPS IN *ALESTES* (INCLUDING CLADE 13)

Within the species of *Alestes* examined in this study (*A. baremoze*, *A. dentex*, *A. macrophthalmus*), *A. macrophthalmus* is hypothesized to be the sister group to the clade formed by *A. baremoze* and *A. dentex* (clade 13). *Alestes macrophthalmus* is characterized by the following autapomorphies:

F_1. Posterior bony tube on lateral ethmoid present (char. 29, 0 > 1).

F_2. Sensory canal on lateral-line scales in portion of scale proximate to region of overlap of sequential scales highly divided, with branches extending dorsal and ventral to primary horizontal canal and with each branch terminating in pore (char. 165, 0 > 1)

The following character is ambiguously optimized as an autapomorphy for this species:

F_3. Ventral surface of supraorbital with relatively smooth surface and without distinct ventral process (char. 3, 1 > 0).

Clade 13, consisting of *Alestes baremoze* and *A. dentex,* is diagnosed by the following four synapomorphies:

120. Parapophyses of fifth and subsequent vertebrae elongate and with anterior limit extending distinctly anterior to anterior limit of centrum (char. 120, 0 > 1). Also present independently in *Hydrocynus*.
121. Rod-shaped portion of lateral surface of pelvic bone extending distinctly anterior to lamellar portion of pelvic bone (char. 140, 0 > 1).
122. Contralateral ischiatic processes positioned close to each other, with distinct area of direct contact via wide smooth flat surface on each ischiatic process (char. 141, 0 > 1).
123. Posterior proximal radials abruptly decreasing in length approximately at centre of base of anal fin (char. 145, 0 > 1).

No autapomorphies were identified in this study for *A. baremoze* or *A. dentex*.

MONOPHYLY OF CLADE 14 (*BRYCONAETHIOPS*)

The three species of *Bryconaethiops* examined in this study (*B. boulengeri*, *B. macrops*, *B. microstoma*) share the following seven synapomorphies:

124. Anterior margin of nasal extending anteriorly to overlie or extend beyond lateral process of mesethmoid (char. 18, 0 > 1). Present independently in the clade formed by *Brachypetersius gabonensis* and *B. notospilus*, and also in the more basal taxa in the Alestidae (*Arnoldichthys* and *Chalceus*).
125. Three functional rows of teeth on premaxilla present (char. 57, 1 > 2). Also present independently in *Chalceus*.
126. Distinct dorsolateral expansion on ascending process of maxilla present (char. 70, 0 > 1).
127. Pelvic bone distinctly bifurcated anteriorly (char. 139, 1 > 0).
128. Laterosensory canal of lateral line on body located approximately along horizontal mid-line of body or only slightly ventral to that location and approximately at middle of caudal fin at hypural joint (char. 164, 1 > 0). Also present independently in *Arnoldichthys*.
129. Sexual dimorphism in degree of development of anterior branched dorsal-fin rays present (char. 177, 0 > 1). Also acquired independently in *Bryconalestes* and in the clade formed by *Alestopetersius*, *Duboisialestes*, *Nannopetersius* and *Phenacogrammus*.

130. Area of attachment of ligaments of erector muscles on branched anal-fin rays located on lateral surface of somewhat more distal portion of ray (char. 187, 0 > 1).

Bryconaethiops boulengeri is defined by a single autapomorphy:

G_1. Position of anterior tip of transverse process of third vertebra extending distinctly over scaphium or if transverse process more anterodorsally orientated, then tip of transverse process positioned along vertical running through main body of scaphium (char. 114, 0 > 1).

Bryconaethiops microstoma is defined by a single autapomorphy:

H_1. Deep-lying midlateral stripe extending along body onto caudal peduncle present (char. 173, 0 > 1).

No autapomorphies for *B. macrops* were discovered in the course of this study.

MONOPHYLY OF CLADE 15 (*BRYCINUS*)

Brycinus as delimited herein is more restrictive than the concept of that genus utilized by recent authors (e.g. Géry, 1977: 22; Paugy, 1986: 93) that proved to encompass a nonmonophyletic assemblage under the overall most parsimonious hypothesis of relationships arrived at herein. Species of what was previously termed the '*Brycinus longipinnis*-group', represented herein by *B. derhami*, *B. intermedius* and *B. longipinnis,* were found to be more closely related to the members of clade 22 than they are to the other species traditionally assigned to *Brycinus*.

In order to resolve the consequent nonmonophyly of *Brycinus*, the species of the '*Brycinus longipinnis*-group' examined in this study are recognized as the genus *Bryconalestes*. Several species assigned to *Brycinus* in recent studies were unavailable for examination in the present analysis and a determination of their phylogenetic position necessitates future analysis. *Brycinus* is characterized herein by the presence of the following synapomorphies:

131. Four teeth in outer tooth row of premaxilla present (char. 59, 3 > 2). Reversed in *Brycinus leuciscus* and further modified in *B. macrolepidotus*.
132. Circuli on exposed portions of scales with overall posterior orientation and with individual circuli relatively straight or slightly inclined towards horizontal midline of scale (char. 171, 0 > 1). Reversal of synapomorphy 51, also independently present in *Brachypetersius gabonensis* and in the clade formed by *Micralestes acutidens* and *M. occidentalis*.
133. Deep-lying midlateral stripe extending along body onto caudal peduncle present (char. 173, 0 > 1). Reversed in clade 16 and also present independently in *Bryconaethiops microstoma*, in the clade formed by *Chalceus epakros* and *C. guaporensis* and in clade 23.
134. Individual segments of fifth through eighth anal-fin rays in males relatively to distinctly anteroposteriorly wide proportional to dimension of segment along axis of ray, with overall ray consequently rather anteroposteriorly wide and with distal portions of rays forming variably distinct median anal-fin lobe (char. 179, 0 > 1). Reversed in the clade formed by *Brycinus brevis* and *B. macrolepidotus* and independently acquired in *Petersius*.

INTRAGENERIC RELATIONSHIPS WITHIN *BRYCINUS* (CLADES 16–19)

In his revision of *Alestes* and *Brycinus*, Paugy (1986: 16, 22) proposed three subgroups within *Brycinus* that he identified as the '*longipinnis*-group', the '*macrolepidotus*-group' and the '*nurse*-group.' These groups were delimited by Paugy primarily on the basis of three features: the relative position of the dorsal fin, the relative body size of the species and the number of teeth in the outer premaxillary tooth row. As noted above, the results of the present study indicate that the '*longipinnis*-group' assigned to *Brycinus* by previous authors is not most closely related to the other species assigned to that genus under recent concepts. As a consequence, the species of the '*longipinnis*-group' of *Brycinus* are herein recognized as the genus *Bryconalestes* (see also under 'Monophyly of clade 21 (*Bryconalestes*)).

The phylogenetic relationships among the remaining *Brycinus* species have been only partially resolved in this study. *Brycinus lateralis*, *B. leuciscus* and *B. sadleri* form a polytomy with the clade consisting of seven species: *B. bimaculatus*, *B. brevis*, *B. carolinae*, *B. imberi*, *B. kingsleyae*, *B. macrolepidotus* and *B. nurse*.

Brycinus lateralis is defined by a single autapomorphy:

I_1. Process on ridge on lateral surface of hyomandibular present (char. 105, 0 > 1).

Brycinus leuciscus is defined by a single autapomorphy:

J_1. Outer tooth row of premaxilla with three teeth (char. 59, 2 > 3).

Brycinus sadleri is characterized by two autapomorphies:

K_1. Process on ridge on lateral surface of hyomandibular present (char. 105, 0 > 1).

K_2. Olfactory bulb in contact with telencephalon (char. 196, 1 > 0).

A clade of seven species within *Brycinus* (clade 16) is defined by the following synapomorphies:

135. Frontal fontanel absent (char. 36, 1 > 2). Secondary reacquisition of a feature lost in at more inclusive level (node 9).
136. Parietal fontanel absent in adult specimens (char. 37, 0 > 1). Secondary reacquisition of a feature lost at a more inclusive level (node 8).
137. Scales along posterodorsal margin of head cover supraoccipital spine and insert into groove along posterior margin of parietal bones (char. 168, 0 > 1). Secondary reacquisition of a feature lost at a more inclusive level (node 6).
138. Deep-lying midlateral stripe extending along body onto caudal peduncle absent (char. 173, 1 > 0).

Within clade 16 two subclades, each with three species, form a trichotomy together with *B. kingsleyae*. No autapomorphies for *B. kingsleyae* were identified in this study. The first of the multispecific clades within clade 16 consists of *Brycinus bimaculatus*, *B. brevis* and *B. macrolepidotus* and is defined by a single synapomorphy:

139. Supraorbital distinctly sigmoid with anterior portion distinctly anterodorsally angled (char. 4, 0 > 1).

Within clade 17, *Brycinus bimaculatus* is the sister group to a clade (clade 18) consisting of *B. brevis* and *B. macrolepidotus*. No autapomorphies for *Brycinus bimaculatus* were identified in this study. The clade consisting of *B. brevis* and *B. macrolepidotus* (clade 18) is defined by the following synapomorphies:

140. Supraneural anterior to neural spine associated with fourth vertebrae absent (char. 122, 0 > 1). Also occurs independently in *Arnoldichthys* and clade 22.
141. Lack of sexual dimorphism in the shape of the anal fin (char. 179, 1 > 0). Secondary loss of a feature acquired at a higher level (node 15).

Brycinus brevis is defined by two autapomorphies:

L_1. Distinct ridge on anterodorsal portion of orbitosphenoid present (char. 32, 0 > 1).
L_2. Process on ridge on lateral surface of hyomandibular present (char. 105, 0 > 1).

Brycinus macrolepidotus is characterized by three autapomorphies:

M_1. Outer tooth row of premaxilla with five teeth (char. 59, 2 > 1).
M_2. First intermuscular bones located more anteriorly and proximate to rear of neurocranium (char. 123, 0 > 1).
M_3. Third postcleithrum without lamella (char. 135, 0 > 1).

The second subclade within clade 16 includes *Brycinus carolinae*, *B. imberi* and *B. nurse* (clade 19) and is defined by the following synapomorphies:

142. Distinct ridge on anterodorsal portion of orbitosphenoid present (char. 32, 0 > 1). Independently acquired in *B. brevis*.
143. Process on ridge on lateral surface of hyomandibular present (char. 105, 0 > 1). Also acquired independently in *B. brevis*, *B. lateralis*, *B. sadleri* and in the clade formed by *Nannopetersius* and *Phenacogrammus*.

No characters were identified to resolve the relationships among these species nor were autapomorphies for *B. carolinae*, *B. imberi*, or *B. nurse* identified in this study.

MONOPHYLY OF CLADE 20

The hypothesis of a close relationship between the species included herein in *Bryconalestes* (*B. derhami*, *B. intermedius*, *B. longipinnis*), all of which were previously assigned to *Brycinus* (see 'Monophyly of clade 15 (*Brycinus*)' above) and the remaining components of clade 20 that we informally term 'small alestids' is proposed for the first time in this analysis. Monophyly of this clade is supported by the following seven synapomorphies:

144. Posterior margin of fourth infraorbital distinctly angled anterodorsally at least on posterodorsal portion of bone, with width of dorsal portion of bone distinctly narrower than the ventral margin (char. 13, 0 > 1).
145. Area of insertion of Baudelot's ligament on the neurocranium located on portion of basioccipital anteroventral to lagenar capsule (char. 48, 0 > 1).
146. Anterior tip of transverse process of third vertebra extending distinctly over scaphium; or, if transverse process more anterodorsally orientated, then tip of transverse process positioned along vertical running through main body of scaphium (char. 114, 0 > 1). Also independently acquired in *Bryconaethiops boulengeri*.
147. Spine-like, medially directed process on medial surface of supracleithrum present (char. 131, 0 > 1). Reversed in *Hemmigrammopetersius intermedius*, *Micralestes lualabae*, *M. occidentalis*, *Rhabdalestes septentrionalis* and the clade formed by *Ladigesia* and *Lepidarchus*.

148. Eight unbranched plus branched pelvic-fin rays present (char. 138, 1 > 2). Also independently acquired in *Arnoldichthys* and *Chalceus guaporensis*.

The following characters are ambiguously optimized at this level:

149. Anterolateral portion of orbitosphenoid without expansion lateral to olfactory bulb (char. 33, 1 > 0). Either derived at this level or the opposite condition (state 1) is a synapomorphy for clade 10 and is independently acquired in *Hydrocynus*.
150. Olfactory bulb in contact with telencephalon (char. 196, 1 > 0). Either derived at this level and independently acquired in *B. sadleri*, or the opposite condition (state 1) is a synapomorphy for clade 10 that is reversed in *B. sadleri* and is independently acquired in *Hydrocynus*.

MONOPHYLY OF CLADE 21 (*BRYCONALESTES*)

Bryconalestes was proposed by Hoedeman (1951) to include *B. longipinnis longipinnis* and *B. longipinnis chaperi* (the latter synonymized with *B. longipinnis* by Paugy, 1986). The name *Bryconalestes* was not accompanied by a thorough definition, but was rather only utilized by Hoedeman in an identification key to the species of that genus. Perhaps as a consequence of this abbreviated original proposal of the genus, subsequent authors dealing with the classification of *Brycinus*-like alestids did not recognize *Bryconalestes,* but rather retained *Brycinus longipinnis*, together with its supposedly closely related species, as a subgroup of *Brycinus* (e.g. Géry, 1977: 25; Paugy, 1986: 16).

The phylogenetic hypothesis presented herein revealed that the continued retention within *Brycinus* of the ‘*longipinnis*-group’, represented in this study by *B. derhami*, *B. intermedius*, *B. longipinnis*, would, however, render the latter genus polyphyletic (see Fig. 43) and we consequently utilize the genus *Bryconalestes* for this group of species.

The hypothesis of the monophyly of *Bryconalestes* is supported by the following four synapomorphies:

151. Ventral surface of supraorbital with distinct, ventrally directed process, anterior portion of which contacts blade-like ventrolateral process of lateral ethmoid (char. 3, 0 > 1). Also independently acquired in *Arnoldichthys* and clade 11 with a secondary loss in *Alestes macrophthalmus*.
152. Sexual dimorphism in degree of development of anterior branched dorsal-fin rays present (char. 177, 0 > 1). Also independently acquired in *Bryconaethiops* and clade formed by *Alestopetersius*, *Duboisialestes*, *Nannopetersius* and *Phenacogrammus*.
153. Sexually dimorphic elongation of pelvic-fin rays in males present (char. 178, 0 > 1). Also independently acquired in *Nannopetersius*.
154. Anterodorsally directed, triangular extension of anterior region of basal portion of anterior and middle branched anal-fin rays present (char. 189, 0 > 1). Independently acquired in *Arnoldichthys*.

No synapomorphies were identified to resolve the phylogenetic relationships among the examined species of *Bryconalestes*. *Brycinus intermedius* is characterized by two autapomorphies:

N_1. Tooth of inner dentary tooth row, when present, small and falling distinctly short of dorsal limit of symphyseal tooth of outer tooth series and of approximately same size as lateral cusp of symphyseal tooth of outer series (char. 89, 0 > 1).
N_2. Laterosensory canal system in sixth infraorbital with anterodorsal branch absent and single remaining canal segment extending from fifth infraorbital to neurocranium (char. 153, 0 > 1).

No autapomorphies were identified in this study for either *Bryconalestes derhami* or *B. longipinnis*.

MONOPHYLY OF CLADE 22

Clade 22 consists of members of the Alestidae characterized by relatively small body size as adults and includes nearly all of what was previously known in the literature as the tribe Petersiini, albeit not *Petersius*. According to the phylogenetic hypothesis presented here, *Petersius*, the type-genus of the Petersiini, occupies a much more basal position in the topology of the Alestidae than does clade 22. The placement of *Petersius* within our phylogenetic scheme is potentially influenced to an undetermined degree by the lack of any specimens of the genus that we could clear and stain. Notwithstanding that limitation, it is noteworthy that *Petersius* lacks all of the externally obvious unambiguous synapomorphies characterizing clade 22 (synapomorphies 155, 157 and 160).

Although it was impossible to observe the condition in *Petersius* of the other derived attributes pertinent at this level in the phylogeny in the absence of cleared and stained material of the genus, it is noteworthy that it also lacks synapomorphy 158, the single internal synapomorphy for clade 22 that is amenable to coding via radiographs. Furthermore, *Petersius* lacks all of the externally obvious synapomorphies (99, 144, 148) characterizing the higher-level clades within the Alestidae that include clade 22. *Petersius* also lacks the single synapomorphy (100) for these higher level clade that could be coded via information that could be accessed via radiographs. As a consequence, the association of *Petersius* with members of clade 22 as implied by the traditional concept of the Petersiini is unwarranted. In the absence of a formal name for the assemblage of genera that constitute clade 22, we informally referred to this group of taxa as 'small alestids', given that all of them share small to miniature body size.

The clade of 'small alestids', consisting of *Alestopetersius*, *Bathyaethiops*, *Brachypetersius*, *Clupeocharax*, *Duboisialestes*, *Hemmigrammopetersius*, *Ladigesia*, *Lepidarchus*, *Micralestes*, *Nannopetersius*, *Phenacogrammus*, *Rhabdalestes* and *Virilia* is characterized by the following synapomorphies:

155. Orbital ring incomplete, with lateral margin of frontal forming portion of dorsal margin of orbital rim (char. 5, 1 > 0). Reversal of synapomorphy 28, secondarily lost in *Brachypetersius notospilus*.
156. Lateral margin of anterior portion of the mesethmoid with distinct lateral, shelf-like process (char. 21, 0 > 1).
157. Tooth of inner dentary row, when present, small and falling distinctly short of dorsal limit of symphyseal tooth of outer tooth series and of approximately same size as lateral cusp of symphyseal tooth of outer tooth series (char. 89, 0 > 1). Reversed in *Micralestes* sp. and independently acquired in *Bryconalestes intermedius*.
158. Supraneural anterior to the neural spine associated with fourth vertebrae absent (char. 122, 0 > 1). Reversed in *Micralestes occidentalis* and occurs independently in *Arnoldichthys* and in clade formed by *Brycinus brevis* and *B. macrolepidotus*.
159. Postcleithrum 3, when present, without lamella (char. 135, 0 > 1). Character also occurs independently in *Alestes*, *B. macrolepidotus* and *Hydrocynus*.
160. Laterosensory canal system in sixth infraorbital with anterodorsal branch absent and single remaining canal segment present extending from fifth infraorbital to neurocranium (char. 153, 0 > 1). Character also occurs independently in *Bryconalestes intermedius*.

Ambiguous features optimized for this clade are as follows:

161. Cusps on distal margin of first through third teeth of inner premaxillary tooth row aligned in a nearly straight line or a gentle arch (char. 63, 1 > 0). Either derived at this level as a reversal of synapomorphy 101 or the opposite condition (state 1) is a synapomorphy for clade 10 and independently acquired in *Bryconalestes*.
162. Interdigitating processes in symphyseal dentary processes relatively simple with smooth margins (char. 83, 1 > 0). Either derived at this level and reversed in *Brachypetersius altus* and *Phenacogrammus urotaenia*, or the opposite condition (state 1) is a synapomorphy for clade 10 and independently acquired in *B. altus*, *P. urotaenia* and *Bryconalestes*.
163. Second and third dentary teeth not overlapping or if second and third teeth overlapping, then second tooth lacks posterolateral margin inserting into distinct depression on anteromedial surface of third tooth (char. 86, 1 > 0). Either derived at this level or the opposite condition (state 1) is a synapomorphy for clade 10 and independently acquired in *Bryconalestes*.
164. Anal fin stay totally cartilaginous or represented by a small plate-like bone (char. 147, 1 > 0). Either derived at this level, reversed in *Brachypetersius gabonensis* and independently acquired in clade 11, or the opposite condition (state 1) is a synapomorphy for clade 15 and independently acquired in *Brachypetersius gabonensis*, *Bryconalestes* and *Petersius*.

MONOPHYLY OF CLADE 23 (*HEMMIGRAMMOPETERSIUS*, *MICRALESTES*, *RHABDALESTES* AND *VIRILIA*)

Two major clades are defined within clade 22 on the basis of a series of derived features. The first clade consists of *Hemmigrammopetersius*, *Micralestes*, *Rhabdalestes* and *Virilia* (clade 23) and the second consists of 10 genera (see clade 31). *Hemmigrammopetersius*, *Micralestes*, *Rhabdalestes* and *Virilia* form a monophyletic group, clade 23, defined by the following synapomorphies:

165. Supraorbital absent (char. 2, 0 > 1). Reversed in *Rhabdalestes septentrionalis* and character occurs independently in the clade formed by *Ladigesia* and *Lepidarchus*.
166. Deep-lying midlateral stripe extending along body onto caudal peduncle present (char. 173, 0 > 1). Also independently acquired in *Bryconaethiops microstoma*, the clade formed by *Chalceus epakros* and *C. guaporensis* and clade 15 with a reversal in clade 16.
167. Band of dark chromatophores above anal fin present (char. 174, 0 > 1). Also independently acquired in *Ladigesia*.

The following character is ambiguously optimized for this clade:

168. Connection between sensory canal in sixth infraorbital and laterosensory canals on neurocranium through anteriorly located pore located in frontal (char. 154, 0 > 1). Either derived at this

level, with secondary loss independently in *Micralestes elongatus* and clade 26 and with independent acquisition in *Alestes* and *Hydrocynus forskahlii*, or independently acquired in clade 24, *M. lualabae*, *Micralestes* sp., *Alestes* and *H. forskahlii*.

Within clade 23 we have a multitomy formed of *Micralestes* sp., clades 24, 25 and 26, with the lack of resolution among these clades involving the examined species of *Micralestes*. *Micralestes* sp., a sample that could not be unequivocally assigned to presently recognized species of the genus, is defined by a single autapomorphy:

O_1. Tooth of inner dentary tooth row, when present, large and extending to approximately same height as, or higher than, dorsal limit of symphyseal tooth of outer dentary tooth row (char. 89, 1 > 0).

MONOPHYLY OF CLADE 24 (*MICRALESTES ACUTIDENS* AND *M. OCCIDENTALIS*)

The first clade within clade 23 consists of *M. acutidens* and *M. occidentalis* (clade 24) and is defined by the following two synapomorphies:

169. Circuli on exposed portion of scales with overall posterior orientation and with individual circuli relatively straight or slightly inclined towards horizontal midline of scale (char. 171, 0 > 1). Also independently acquired in *Arnoldichthys*, *Brachypetersius gabonensis*, *Brycinus* and *Chalceus*.
170. Dark pigmentation on dorsal fin in two patches, the first along margins of basal half of fin rays, the second distinctly separated field covering distal portion of last unbranched and first through third or fourth branched rays and intervening membranes (char. 175, 0 > 1).

Micralestes acutidens is defined by a single autapomorphy:

P_1. Posterolateral margin of palatine with posteroventral process extending along anterodorsal portion of ectopterygoid (char. 95, 0 > 1).

Micralestes occidentalis is defined by three autapomorphies:

Q_1. Relatively large inner row tooth proximate to dentary symphysis absent (char. 88, 1 > 0).
Q_2. Supraneural anterior to neural spine associated with fourth vertebrae present (char. 122, 1 > 0).
Q_3. Spine-like, medially directed process on medial surface of supracleithrum absent (char. 131, 1 > 0).

MONOPHYLY OF CLADE 25 (*MICRALESTES ELONGATUS* AND *M. LUALABAE*)

The second two species clade within *Micralestes* consists of *M. elongatus* and *M. lualabae* (clade 25) and is defined by two synapomorphies.

171. Posterolateral margin of palatine with posteroventral process extending along anterodorsal portion of ectopterygoid (char. 95, 0 > 1). Also present in *M. acutidens*.
172. First intermuscular bones located anteriorly and proximate to rear of neurocranium (char. 123, 0 > 1). Also independently acquired in *Alestes*, *Brycinus macrolepidotus*, *Chalceus* and *Hydrocynus*.

Micralestes elongatus is defined by the following autapomorphy:

R_1. Posteriorly directed, pointed process on posterior surface of lateral wing of lateral ethmoid present (char. 28, 0 > 1).

The following character is ambiguously optimized as an autapomorphy for this species:

R_2. Connection between sensory canal in sixth infraorbital and laterosensory canals on neurocranium through pore located on pterotic or between junction of pterotic and frontal (char. 154, 1 > 0).

Micralestes lualabae is defined by three autapomorphies:

S_1. Process along posterodorsal margin of maxilla present (char. 73, 0 > 1).
S_2. Posteriorly directed process on posterodorsal margin of upper portions of first through eight ribs present (char. 119, 0 > 1).
S_3. Spine-like, medially directed process on medial surface of supracleithrum absent (char. 131, 1 > 0).

MONOPHYLY OF CLADE 26 (*HEMMIGRAMMOPETERSIUS*, *RHABDALESTES* AND *VIRILIA*)

The remaining components of clade 23 include species currently assigned to the genera *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia*. Difficulties in defining and distinguishing these genera led some authors to propose the synonymy of these taxa in various combinations (Paugy, 1990a: 80; Géry, 1995: 46). Our phylogenetic results highlight some of the problems with the continued recognition of these taxa as now defined.

According to our analysis, the recognition of *Hemmigrammopetersius* and *Virilia* renders *Rhabdalestes* as an unnatural group. Despite the tree topology of these groups that indicates that the species of *Rhab-*

dalestes and *Virilia* included in this analysis should be synonymized in *Hemmigrammopetersius,* the first described of the three genera, such an action is clearly premature.

Possible changes in generic-level nomenclature within the clade would only be appropriately undertaken following a comprehensive phylogenetic study of *Hemmigrammopetersius*, *Micralestes, Rhabdalestes* and *Virilia*, including the type-species of *Hemmigrammopetersius* and *Rhabdalestes*, neither of which were available for inclusion in this analysis. *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* are consequently conserved as presently defined for the purpose of the following discussion. The clade composed of the examined species of *Hemmigrammopetersius*, *Rhabdalestes* and *Virilia* (Fig. 43, clade 26) is supported by the following seven synapomorphies:

173. Relatively large inner row tooth proximate to dentary symphysis absent (char. 88, 1 > 0). Reversed in *Virilia* and occurs independently in *Micralestes occidentalis*, clade 39, clade 35 and in the basal genera *Arnoldichthys*, *Hydrocynus* and *Petersius*.
174. Distinct posterior curvature of third unbranched anal-fin ray and basal portions of immediately following rays present (char. 182, 0 > 1).
175. Distinct anteroposterior thickening of third unbranched anal-fin ray present and moderately to well-developed (char. 183, 0 > 1). Further modified in *Virilia* (see autapomorphy X_4 under that genus).
176. Basal portions of anterior branched anal-fin rays in males with posterior medial expansion overlapped laterally by anterior section of following rays (char. 184, 0 > 1).
177. Attachment of ligaments of erector muscles on anterior branched anal-fin rays of males on anterolateral surface of somewhat more distal portion of ray (char. 186, 0 > 1).
178. Posterodorsal extension of basal portions of anterior and middle branched anal-fin rays present (char. 190, 0 > 1).

One ambiguous synapomorphy has been identified for this clade:

179. Connection between sensory canal in sixth infraorbital and laterosensory canals on neurocranium through pore located on pterotic or between junction of pterotic and frontal (char. 154, 1 > 0). Either derived at this level or the opposite condition (state 1) was independently acquired in the clade consisting of *Micralestes acutidens* and *M. occidentalis*, in *M. lualabae*, *Micralestes* sp., *Alestes* and *Hydrocynus forskahlii*.

MONOPHYLY OF CLADE 27

Within clade 26, *Rhabdalestes eburneensis*, for which no autapomorphies have been identified, is hypothesized to be the sister species to the clade consisting of *Hemmigrammopetersius*, *R. septentrionalis*, *R. loenbergi*, *R. rhodesiensis* and *Virilia*. This group, identified herein as clade 27, is supported by the following two synapomorphies:

180. Separation of inner and outer tooth rows on premaxilla less distinct than in most other alestids, with gaps present between first and second and second and third teeth of inner row and with two teeth of outer row partially repositioned into resultant gaps in inner tooth row (char. 58, 0 > 1). Also independently acquired in clade 35.
181. Anterodorsal portion of ascending process of maxilla terminating in relatively pointed process (char. 67, 1 > 0). Reversal of synapomorphy 43 at level of clade 6; also present independently in clade 31.

Rhabdalestes septentrionalis, the sister group to the clade consisting of *Hemmigrammopetersius*, *R. loenbergi*, *R. rhodesiensis* and *Virilia*, is characterized by the following three autapomorphies:

T_1. Supraorbital present (char. 2, 1 > 0).
T_2. Posteriorly directed, pointed process on posterior surface of lateral wing of lateral ethmoid present (char. 28, 0 > 1).
T_3. Spine-like, medially directed process on medial surface of supracleithrum absent (char. 131, 1 > 0).

MONOPHYLY OF CLADE 28

The clade formed by *Hemmigrammopetersius*, *Rhabdalestes loenbergi*, *R. rhodesiensis* and *Virilia* (clade 28) is defined by one synapomorphy:

182. Two teeth present in outer tooth row of premaxilla (char. 59, 3 > 4). Also independently present in *Petersius* and clade 31.

No autapomorphies were identified for *R. loenbergi*.

MONOPHYLY OF CLADE 29

The clade consisting of *Hemmigrammopetersius*, *Rhabdalestes rhodesiensis* and *Virilia* (clade 29) is defined by one synapomorphy:

183. Medially directed, spine-like process on post-temporal absent (char. 130, 0 > 1). Reversed in *H. intermedius* and independently acquired in *Brachypetersius gabonensis*, *Phenacogrammus aurantiacus* and clade 34.

Rhabdalestes rhodesiensis, the sister taxon to the clade consisting of *Hemmigrammopetersius* plus *Virilia*, is defined by two autapomorphies:

U_1. Second postcleithrum absent (char. 133, 0 > 1).
U_2. Third postcleithrum absent (char. 134, 0 > 1).

MONOPHYLY OF CLADE 30 (*HEMMIGRAMMOPETERSIUS* AND *VIRILIA*)

Diverse opinions about the relationships of *Hemmigrammopetersius* and *Virilia* have been advanced in the literature; but the hypothesis of their sister-group relationships arrived at in this study has not been proposed previously. In the case of *Virilia*, the unique species of the genus (*V. pabrensis*) was originally described within *Phenacogrammus* by Roman (1966). Subsequently, Roberts (1967b: 256) erected *Virilia* that included only *P. pabrensis* of Roman (1966). Roberts also suggested a close relationship of *Virilia* with *Lepidarchus* and *Micralestes* (presumably based on body size, sexual dimorphism and dentition).

Recently, Paugy (1990a: 80) proposed the synonymy of *Virilia* with *Micralestes*, together with the genera *Hemmigrammopetersius*, *Rhabdalestes* and *Alestopetersius*. Under Paugy's scheme these five genera were brought together on the basis of the presence of a second row of inner dentary teeth. That character was, however, found to demonstrate a low level of consistency in this study (see also comments in character 88 concerning interspecific variation in this feature). Alternatively, Géry (1995: 46) discussed the sexual dimorphic anal-fin of *Virilia* and *Rhabdalestes* and proposed that those two genera should be synonymized based on the similarities that he observed in that body system.

Géry (1995: 46) also considered it appropriate to shift *H. pulcher*, the type species of *Hemmigrammopetersius*, into *Phenacogrammus*. Although *H. pulcher* was not examined in this study, the other two species of *Hemmigrammopetersius* incorporated in our analysis (*H. barnardi* and *H. intermedius*) are not closely related to *Phenacogrammus* within the final most parsimonious hypothesis of relationships. The results of our study, albeit based on hypothesized synapomorphies rather than overall similarity, parallel those of Géry (1995) in having *Virilia* and *Rhabdalestes* as closely related taxa. A more encompassing study involving all nominal species in *Virilia* and *Rhabdalestes* plus those of *Hemmigrammopetersius* must precede any change in the generic-level taxonomy of these taxa, as proposed by Géry (1995). Clade 30, formed by *H. barnardi*, *H. intermedius and Virilia* is defined by the following synapomorphies:

184. Inferior lamella of lateral ethmoid reduced and falling short of contact with vomer anteriorly (char. 27, 0 > 1). Further modified in *Virilia*.
185. Lateral line distinctly reduced and with number of scales lacking laterosensory canal and pore greater than number of scales with those structures (char. 162, 0 > 1). Also independently acquired in *Phenacogrammus* and clade 35.

The following features are ambiguously optimized for this clade:

186. Area of insertion of premaxillary-maxillary ligament on maxilla on anterior surface of maxilla (char. 66, 1 > 0). Either derived at this level, reversed in *Virilia* and independently acquired in clade 35 with a reversal in *Ladigesia*, or independently acquired in *Hemmigrammopetersius barnardi* and *H. intermedius* and a synapomorphy for clade 35 that is reversed in *Ladigesia*.
187. More than four dentary teeth present (char. 84, 1 > 0). Either derived at this level, reversed in *H. barnardi* and independently acquired in clades 32 and 35, or independently acquired in *H. intermedius*, *Virilia* and clades 32 and 35.

The relationships among *H. barnardi*, *H. intermedius* and *Virilia* remain unresolved in this analysis. *H. barnardi* is characterized by the following autapomorphies:

V_1. Third postcleithrum absent (char. 134, 0 > 1).
V_2. Laterosensory canal in parietal absent (char. 157, 0 > 1).

The following character is ambiguously optimized as an autapomorphy for this species:

V_3. Four dentary teeth present (char. 84, 0 > 1)

H. intermedius is defined by two autapomorphies:

W_1. Medially directed, spine-like process on posttemporal present (char. 130, 1 > 0).
W_2. Spine-like, medially directed process on medial surface of supracleithrum absent (char. 131, 1 > 0).

Virilia is characterized by the following autapomorphies:

X_1. Inferior lamella of lateral ethmoid absent (char. 27, 1 > 2).
X_2. Ridge on lateral surface of maxilla present (char. 76, 0 > 1).
X_3. Relatively large inner row tooth proximate to dentary symphysis present (char. 88, 0 > 1).
X_4. Distinct anteroposterior thickening of third unbranched anal-fin ray present and highly developed into anteriorly convex process (char. 183, 1 > 2).

The following character is ambiguously optimized as an autapomorphy for this genus:

X_5. Area of insertion of premaxillary-maxillary ligament on maxilla on lateral surface of maxilla (char. 66, 0 > 1).

MONOPHYLY OF CLADE 31

Clade 31 represents the second major clade of 'small alestids' within clade 22 and is defined by the following seven synapomorphies:

188. Outer tooth row of premaxilla with two teeth present (char. 59, 3 > 4). Also independently acquired in *Petersius* and clade 28.
189. Anterodorsal portion of ascending process of maxilla terminates in a relatively pointed process (char. 67, 1 > 0). Also independently acquired in clade 27.
190. Ridge on lateral surface of maxilla present (char. 76, 0 > 1). Reversed in clade 35 and independently acquired in *Virilia*.
191. Narrow ring-like process of scapula forming anterior border of scapular foramen absent (char. 136, 0 > 1). Reversed in clade consisting of *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*.
192. Degree of development of dorsal process on base of first branched pectoral-fin ray similar to that of remaining branched rays (char. 137, 1 > 0).
193. Caudal-fin bony stays absent (char. 150, 1 > 0).
194. Nearly dorsally directed, digitiform process on anterior region of basal portion of anterior and middle branched anal-fin rays present (char. 188, 0 > 1). Reversed in *Ladigesia*.

A clade formed by two species assigned to *Brachypetersius* (*B. gabonensis* and *B. notospilus*) is hypothesized to be the sister group of the remaining taxa included in clade 31. A third species, *B. altus*, type of the genus, does not form a monophyletic unit with *B. gabonensis* and *B. notospilus*, a conclusion indicating the apparent nonmonophyly of the genus. A future phylogenetic study incorporating all species currently assigned to *Brachypetersius* may demonstrate the need to propose a new genus to include *B. gabonensis* and *B. notospilus*.

MONOPHYLY OF CLADE 32 (*BRACHYPETERSIUS GABONENSIS* AND *B. NOTOSPILUS*)

The clade formed by *B. gabonensis* and *B. notospilus* is characterized by the following three synapomorphies:

195. Anterior margin of nasal extending anteriorly to overlie or extend beyond lateral process of mesethmoid (char. 18, 0 > 1). Also independently acquired in *Bryconaethiops* and in the basal alestid genera *Arnoldichthys* and *Chalceus*.
196. More than four dentary teeth present (char. 84, 1 > 0). Also independently acquired in clade 30 and clade 35 with a reversal in *Hemmigrammopetersius barnardi*.
197. Anterior anal-fin rays distinctly longer in females than in males and posterior anal-fin rays distinctly longer in males than in females (char. 181, 0 > 1).

Brachypetersius gabonensis is characterized by three autapomorphies:

Y_1. Medially directed, spine-like process on posttemporal absent (char. 130, 0 > 1).
Y_2. Anal-fin stay represented by elongate bone similar in overall form to adjoining proximal radial (char. 147, 0 > 1).
Y_3. Circuli on exposed portion of scales with overall posterior orientation and with individual circuli relatively straight or slightly inclined towards horizontal midline of scale (char. 171, 0 > 1).

Brachypetersius notospilus is defined by a single autapomorphy:

Z_1. Orbital ring complete, with dorsal margin of orbital rim bordered by sixth infraorbital and supraorbital or in some instances solely by latter ossification (char. 5, 0 > 1).

MONOPHYLY OF CLADE 33

The hypothesis of the monophyly of clade 33 consisting of *Alestopetersius*, *Bathyaethiops*, *Brachypetersius altus*, *Clupeocharax*, *Duboisialestes*, *Ladigesia*, *Lepidarchus*, *Nannopetersius*, *Phenacogrammus* and *Tricuspidalestes* is supported by the following three synapomorphies:

198. Anal-fin proximal radials with anteroposterior expansion but no lateral expansion (char. 144, 0 > 1). Reversed in *Ladigesia*.
199. Parietal branch of supraorbital laterosensory canal either absent or distinctly shortened and falling short of parietal (char. 156, 0 > 1).
200. Laterosensory canal in parietal absent (char. 157, 0 > 1). Canal also independently absent in *Hemmigrammopetersius barnardi*.

Within clade 33, *Brachypetersius altus* forms a trichotomy together with two major clades. As noted above, *B. altus* was not found in this study to be most closely related to the remaining species of *Brachypetersius* that were examined in this study.

Brachypetersius altus is defined by a single autapomorphy:

AA_1. Interdigitating processes in symphyseal dentary processes complex with undulating subprocesses and scalloped margins (char. 83, 0 > 1).

MONOPHYLY OF CLADE 34

The first of the two other clades within clade 33 is formed by *Bathyaethiops*, *Clupeocharax*, *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* (clade 34). The sister-group relationship of *Bathyaethiops* with the remaining members of this clade (clades 35–37) is supported by one synapomorphy:

201. Medially directed, spine-like process on post-temporal absent (char. 130, 0 > 1). Also occurs independently in *Brachypetersius gabonensis*, *Phenacogrammus aurantiacus* and clade 29 with reversal in *Hemmigrammopetersius intermedius*.

Bathyaethiops caudomaculatus (Pellegrin) is defined by two autapomorphies:

AB_1. Frontal fontanel reaching mesethmoid anteriorly (char. 36, 1 > 0).
AB_2. Lateral surface of dorsal portion of hyomandibular unelaborated (char. 103, 1 > 0).

MONOPHYLY OF CLADE 35 (*CLUPEOCHARAX*, *LADIGESIA*, *LEPIDARCHUS* AND *TRICUSPIDALESTES*)

The monophyly of clade 35, with its four genera, is strongly supported by 18 synapomorphies:

202. First infraorbital not overlapping ascending process of maxilla and falling distinctly short of lateral portion of premaxilla (char. 7, 1 > 0). Reversed in *Ladigesia*.
203. Sixth infraorbital absent (char. 15, 0 > 1).
204. Mesethmoid without distinct anteromedial process but with dorsal expansion extending over anterodorsal portion of premaxilla (char. 19, 0 > 1). Reversed in *Ladigesia*.
205. Inferior lamella of lateral ethmoid orientated directly anteriorly (char. 26, 0 > 1). Reversed in *Ladigesia*.
206. Insertion of premaxillary-maxillary ligament on maxilla on anterior surface of maxilla (char. 66, 1 > 0). Reversed in *Ladigesia* and also independently acquired in clade 30 with reversal in *Virilia*.
207. Ascending process of maxilla shorter than lamellar portion of maxilla (char. 69, 1 > 0). Reversed in *Ladigesia*.
208. Canal running through maxilla absent or relatively short and limited to ascending process (char. 75, 1 > 0). Reversed in *Ladigesia*.
209. Ridge on lateral surface of maxilla absent (char. 76, 1 > 0).
210. Primordial ligament relatively narrow and attaching to posteromedial portion of ascending process of maxilla (char. 80, 1 > 0). Reversed in *Ladigesia*.
211. More than four dentary teeth present (char. 84, 1 > 0). Also independently acquired in clades 30 and 32 with reversal in *Hemmigrammopetersius barnardi*.
212. Portion of laterosensory canal dorsal to main body of preopercle absent (char. 106, 0 > 1).
213. Lateral lamellae of urohyal reduced or absent (char. 113, 1 > 0). Reversed in *Ladigesia* and independently acquired in *Phenacogrammus major*.
214. Laterosensory canal segment in pterotic absent (char. 159, 0 > 1).
215. Lateral line distinctly reduced and with number of scales lacking laterosensory canal and pore greater than number of scales with those structures (char. 162, 0 > 1). Also independently acquired in *Phenacogrammus* and clade 30.

The following characters are ambiguously optimized at this level:

216. Inner and outer tooth rows on premaxilla less distinct than in most other alestids, with gaps between first and second, and second and third, teeth of inner row with two teeth of outer row partially repositioned into resultant gaps in inner tooth row (char. 58, 0 > 1). Either derived at this level and independently acquired in clade 27, or a synapomorphy for *Ladigesia*, *Lepidarchus* and *Tricuspidalestes* and independently acquired in clade 27. The ambiguity is a consequence of *Clupeocharax* being coded as '-' (see comments in character 58).
217. Relatively large inner row tooth proximate to dentary symphysis absent (char. 88, 1 > 0). Either derived at this level, reversed in *Tricuspidalestes* and independently acquired in *Micralestes occidentalis* and clades 26 and 39, or derived at level of clade 37 and independently acquired in *Clupeocharax*, *M. occidentalis* and clades 26 and 39.
218. Area of contact of ectopterygoid and palatine broad, with anterior portion of ectopterygoid as wide as proximate portion of palatine (char. 97, 1 > 0). Either derived at this level and reversed in *Ladigesia* and *Lepidarchus*, or independently acquired in *Clupeocharax* and *Tricuspidalestes*.
219. Laterosensory canal segment in post-temporal absent (char. 160, 0 > 1). Either derived at this level or at the level of clade 36. The ambiguity is

a consequence of *Clupeocharax* being coded as '?' (see comments in character 160).

Within clade 35, *Clupeocharax* is the sister taxon to the clade consisting of *Ladigesia*, *Lepidarchus* and *Tricuspidalestes*.

Clupeocharax schoutedeni is characterized by four autapomorphies:

AC_1. Teeth with one cusp present throughout ontogeny (char. 49, 2 > 0).
AC_2. One row of teeth present on premaxilla (char. 57, 1 > 0).
AC_3. Replacement tooth trench or crypt in dentary absent (char. 90, 0 > 1).
AC_4. Third postcleithrum absent (char. 134, 0 > 1).

MONOPHYLY OF CLADE 36 (*LADIGESIA*, *LEPIDARCHUS* AND *TRICUSPIDALESTES*)

The three genera of clade 36 share the five following synapomorphies:

220. One fin ray supported by posteriormost proximal radial of dorsal fin (char. 126, 0 > 1).
221. Extrascapular absent (char. 127, 0 > 1).
222. Narrow ring-like process of scapula forming anterior border of scapular foramen present (char. 136, 1 > 0).
223. Supratemporal laterosensory canal absent (char. 158, 0 > 1).

The following characters are ambiguously optimized for this clade:

224. Fourth infraorbital without laterosensory canal segment (char. 151, 0 > 1). Either derived at this level and optimized as absent in *Ladigesia* and *Lepidarchus* in which the fourth infraorbital is absent and the character was coded as '-', or an autapomorphy for *Tricuspidalestes*.
225. Fifth infraorbital without laterosensory canal segment (char. 152, 0 > 1). Either derived at this level and optimized as absent in *Ladigesia* and *Lepidarchus* in which the fifth infraorbital is absent and the character was coded as '-', or an autapomorphy for *Tricuspidalestes*.

Tricuspidalestes is the sister group to the clade consisting of *Ladigesia* and *Lepidarchus*. *Tricuspidalestes caeruleus* (Matthes) is defined by the following autapomorphy:

AD_1. Medial process on central portion of body of first rib present (char. 118, 0 > 1).

The following character is ambiguously optimized as autapomorphy for this species:

AD_2. Relatively large inner row tooth proximate to dentary symphysis present (char. 88, 0 > 1).

MONOPHYLY OF CLADE 37 (*LADIGESIA* PLUS *LEPIDARCHUS*)

In his discussion of the relationships of *Lepidarchus,* Roberts (1966: 214) compared that genus with various other taxa in the Alestidae (his African Characidae) but did not explicitly identify the hypothesized close relatives of *Lepidarchus*. In his subsequent discussion of the relationships of *Virilia*, Roberts (1967b: 256) suggested a close relationship of *Virilia* and *Lepidarchus*. The phylogenetic relationships of *Ladigesia* have not been previously analysed and the hypothesis by Géry (1968: 82) that '*Ladigesia* may be considered as a very specialized offshoot of some elongate *Micralestes*-like species . . .' was not corroborated by the evidence of this analysis.

Contrary to those previous hypotheses, *Ladigesia* is hypothesized to be the sister group of *Lepidarchus* (clade 37) on the basis of the following 11 synapomorphies:

226. Supraorbital absent (char. 2, 0 > 1). Also independently acquired in clade 23 with a reversal in *Rhabdalestes septentrionalis*.
227. Fourth infraorbital absent (char. 12, 0 > 1).
228. Fifth infraorbital absent (char. 14, 0 > 1).
229. Intercalar absent (char. 42, 0 > 1).
230. Third post-temporal fossa located entirely in epioccipital absent (char. 43, 1 > 0).
231. Lateral surface of dorsal portion of hyomandibular unelaborated (char. 103, 1 > 0). Also independently acquired in *Bathyaethiops*.
232. Spine-like, medially directed process on medial surface of supracleithrum absent (char. 131, 1 > 0). Also occurs independently in *Hemmigrammopetersius intermedius*, *Micralestes lualabae*, *M. occidentalis* and *R. septentrionalis*.
233. Two unbranched anal-fin rays present (char. 142, 1 > 0).
234. Dorsal region of body without scales over broad region from rear of head to posterior to dorsal-fin base (char. 167, 0 > 1). Further modified in *Lepidarchus* (see autapomorphy AF_{25} under that genus).

The following characters are ambiguously optimized for this clade:

235. Area of contact of ectopterygoid with palatine narrow, with anterior portion of ectopterygoid usually half as wide as proximate portion of palatine (char. 97, 0 > 1). Either derived at this level as a reacquisition of a feature lost in a more inclusive level (node 35) or the opposite condition (state 0) is an autapomorphy independently acquired in *Clupeocharax* and *Tricuspidalestes*.
236. Post-temporal very slender throughout and relatively short without ventral expansion or in-

cluded laterosensory canal segment (char. 129, 0 > 1). Either derived at this level or an autapomorphy for *Ladigesia*. The ambiguity is a consequence of *Lepidarchus* being coded as '?' for this character in the phylogenetic analysis (see comments in character 129).

Ladigesia, the first component of clade 37, is characterized by the following 13 autapomorphies:

AE$_1$. First infraorbital nearly or totally overlapping ascending process of maxilla, with anterior border of infraorbital reaching at least posterolateral portion of premaxilla (char. 7, 0 > 1)

AE$_2$. Mesethmoid with distinct triangular anteromedial process, without broad dorsal expansion over anterodorsal portion of premaxilla (char. 19, 1 > 0).

AE$_3$. Inferior lamella of lateral ethmoid orientated anteromedially (char. 26, 1 > 0).

AE$_4$. Insertion of premaxillary-maxillary ligament located on lateral surface of maxilla (char. 66, 0 > 1).

AE$_5$. Ascending process of maxilla about as long as, or longer than, lamellar portion of that bone (char. 69, 0 > 1).

AE$_6$. Canal running through maxilla highly developed, with at least portion of canal system extending onto lamellar portion of maxilla and often to posterior margin of ossification (char. 75, 0 > 1).

AE$_7$. Primordial ligament broad, robust and attaching to posterior half of maxilla (char. 80, 0 > 1).

AE$_8$. Three branchiostegal rays present (char. 112, 1 > 2).

AE$_9$. Lateral lamellae of urohyal present and well-developed (char. 113, 0 > 1).

AE$_{10}$. Main body of proximal anal-fin radials cylindrical or with varyingly developed lateral expansion in addition to anteroposterior expansion (char. 144, 1 > 0).

AE$_{11}$. Band of dark chromatophores above anal fin present (char. 174, 0 > 1).

AE$_{12}$. Thickened basal portions of third through sixth branched rays of anal fin in males with medial anterior expansion; with anterior expansion of medial portion of third through fifth rays fitting between lateral portions of preceding ray (char. 185, 0 > 1).

AE$_{13}$. Nearly dorsally directed digitiform process on anterior region of basal portion of anterior and middle branched anal-fin rays absent (char. 188, 1 > 0).

Lepidarchus, the second component of clade 37, is characterized by the following 30 autapomorphies:

AF$_1$. Antorbital absent (char. 1, 0 > 1).

AF$_2$. Sensory canal of first and second infraorbitals lacking distinct bony lamella dorsal and ventral to laterosensory canal segment and with these infraorbitals consisting primarily of ossified laterosensory canal segment (char. 9, 0 > 1).

AF$_3$. Third infraorbital absent (char. 11, 0 > 1).

AF$_4$. Nasal bone absent (char. 17, 0 > 1).

AF$_5$. Medial frontal fontanel reaching mesethmoid anteriorly (char. 36, 1 > 0).

AF$_6$. Pterotic excluded from contact with frontal by sphenotic (char. 38, 0 > 1).

AF$_7$. Dorsal post-temporal fossa significantly smaller than ventral post-temporal fossa (char. 44, 0 > 1).

AF$_8$. Lateral occipital foramen absent (char. 45, 1 > 0).

AF$_9$. Paired, vertically elongate processes along posterior margin of supraoccipital enveloping anterodorsal portion of neural complex absent (char. 46, 1 > 0).

AF$_{10}$. Teeth with one cusp present throughout ontogeny (char. 49, 2 > 0).

AF$_{11}$. Posterolateral portion of premaxilla represented by short process, usually with concave posterior surface accommodating proximate portion of maxilla (char. 52, 1 > 0).

AF$_{12}$. One row of teeth present on premaxilla (char. 57, 1 > 0).

AF$_{13}$. Dentary symphysis without bony interdigitating articulations anteriorly (char. 82, 1 > 0).

AF$_{14}$. Replacement tooth trench or crypt in dentary absent (char. 90, 0 > 1).

AF$_{15}$. Articulation between angulo-articular and quadrate situated posterior to vertical through ventral tip of lateral process of lateral ethmoid (char. 93, 1 > 0).

AF$_{16}$. Ossified palatine absent (char. 94, 0 > 1).

AF$_{17}$. Medially directed, elongate process arising distinct distance from base of first rib present (char. 115, 0 > 1).

AF$_{18}$. Posteriorly directed projection near base of first rib absent (char. 116, 1 > 0).

AF$_{19}$. Medially directed process on base of second rib present (char. 117, 0 > 1).

AF$_{20}$. Ten dorsal-fin proximal radials present (char. 125, 3 > 2).

AF$_{21}$. Post-temporal and supracleithrum fused (char. 128, 0 > 1).

AF$_{22}$. First postcleithrum absent (char. 132, 0 > 1).

AF$_{23}$. One pair of uroneural bones present (char. 149, 1 > 0).

AF$_{24}$. Laterosensory canal segment in supracleithrum absent (char. 161, 0 > 1).

AF$_{25}$. Body completely without scales except for one small canal-bearing scale located at anterior limit of lateral line system on body and one scale situated at anterior to base of anal fin (char. 167, 1 > 2).

AF_{26}. Sexual dimorphism in anal fin pigmentation present, with females lacking dark pigmentation on anal-fin rays, but with basal stripe present along anterior portion of anal fin, and with males having dark stripe beginning at middle of anterior rays of anal fin and angling posteriorly to middle of distal margin of fin and with second spot of dark pigmentation on distal portions of posterior rays (char. 193, 0 > 1).

AF_{27}. Sexual dimorphism of pelvic fin present, with females lacking dark pigmentation on pelvic fin and males having dark stripe beginning at middle of anterior rays of fin and angling posteriorly to middle of tip of fin and with second parallel dark stripe running slightly posterior to primary stripe in some males (char. 194, 0 > 1).

AF_{28}. Sexually dimorphic dark pigmentation on body present, females with limited dark pigmentation on body, adipose fin and base of anal fin, and without distinct spots, and males with distinct dark rounded spots over much of body, on lateral surface of adipose fin and on base of anal fin (char. 195, 0 > 1).

AF_{29}. Membranous keel extending between pelvic-fin insertion and vent present (char. 198, 0 > 1).

AF_{30}. Pseudotympanum present (char. 199, 0 > 1).

MONOPHYLY OF CLADE 38 (*ALESTOPETERSIUS, DUBOISIALESTES*, *NANNOPETERSIUS* AND *PHENACOGRAMMUS*)

This clade is characterized by one synapomorphy:

237. Sexual dimorphism in degree of development of anterior branched dorsal-fin rays present (char. 177, 0 > 1). Also independently acquired in *Bryconaethiops* and *Bryconalestes*.

Clade 38 includes two clades: clade 39 consists of *Alestopetersius* plus *Duboisialestes*, clade 40 consists of *Nannopetersius* plus *Phenacogrammus*.

MONOPHYLY OF CLADE 39 (*ALESTOPETERSIUS* AND *DUBOISIALESTES*)

This clade, consisting of the species of *Alestopetersius* and *Duboisialestes*, is defined by one synapomorphy:

238. Relatively large inner row tooth proximate to dentary symphysis absent (char. 88, 1 > 0). Occurs independently in clades 26 and 35, *Micralestes occidentalis* and in the basal alestid genera *Arnoldichthys*, *Hydrocynus* and *Petersius*.

No synapomorphies were discovered in the course of this study to resolve the relationships among the examined species of *Alestopetersius* and *Duboisialestes*. Similarly, no autapomorphies for the examined species of *Alestopetersius* were identified in this study.

Duboisialestes tumbensis (Hoedeman) is defined by a single autapomorphy:

AG_1. Teeth in both upper and lower jaws compressed, distally expanded and overlap proximate teeth in each jaw (char. 51, 0 > 1).

MONOPHYLY OF CLADE 40 (*NANNOPETERSIUS* AND *PHENACOGRAMMUS*)

Nannopetersius is hypothesized to be the sister group of *Phenacogrammus* based on one synapomorphy:

239. Process on ridge on lateral surface of hyomandibular present (char. 105, 0 > 1). Also independently acquired in various species of *Brycinus*.

Nannopetersius ansorgii is characterized by the following three autapomorphies:

AH_1. Sexual dimorphism in degree of development of first through third pectoral-fin rays present, with first through third rays filamentous distally (char. 176, 0 > 1).

AH_2. Sexually dimorphic elongation of pelvic-fin rays in males present (char. 178, 0 > 1).

AH_3. Sexual dimorphism in degree of development of fourth to eighth branched anal-fin rays present, with distinct filaments present on fourth to eighth branched anal-fin rays in males (char. 180, 0 > 1).

MONOPHYLY OF CLADE 41 (*PHENACOGRAMMUS*)

The three species of *Phenacogrammus* examined in this study (*P. aurantiacus*, *P. major* and *P. urotaenia*) share only one synapomorphy:

240. Lateral line distinctly reduced and with number of scales lacking laterosensory canal and pore greater than number of scales with those structures (char. 162, 0 > 1). Also independently acquired in clade 35 and clade 30.

No synapomorphies were identified in the study to resolve the relationships among the examined species of *Phenacogrammus*.

Phenacogrammus aurantiacus is defined by a single autapomorphy:

AI_1. Medially directed, spine-like process on posttemporal absent (char. 130, 0 > 1).

Phenacogrammus major is characterized by two autapomorphies:

AJ$_1$. Dorsomedial process of second infraorbital present (char. 10, 0 > 1).
AJ$_2$. Lateral lamellae of urohyal reduced or absent (char. 113, 1 > 0).

Phenacogrammus urotaenia is defined by a single autapomorphy:

AK$_1$. Interdigitating processes in symphyseal dentary processes complex with undulating subprocesses and scalloped margins (char. 83, 0 > 1).

COMPARISONS WITH PREVIOUS CLASSIFICATIONS

Previous authors advanced alternative proposals as to both the limits of the Alestidae and the composition of various subunits of that family. Some of the more significant differences are summarized in the following sections, along with additional pertinent comments.

Alestidae

Most of the authors who published on what is now considered to be the Alestidae did not recognize that taxon as separate from the Characidae (e.g. Greenwood *et al.*, 1966), a family otherwise composed of New World genera and species. The Alestidae was first proposed as a family separate from the Characidae by Géry (1977: 18) who limited the Characidae to Neotropical groups, one of which, *Chalceus*, is assigned to the Alestidae in this analysis. Géry (1977) defined the Alestidae on the basis of the combination of features that did not delimit an identifiable assemblage of species (see remarks under 'Comments on Alestidae', above).

Our analysis leads us to hypothesize that the Alestidae is (1) a monophyletic group delimited on the basis of a series of derived characters; and (2) is not the closest relative of the taxa, excepting *Chalceus*, that are currently included in Characidae. This conclusion, that is in agreement with the hypothesis proposed by Buckup (1998), necessitates a recognition of an Alestidae distinct from the Neotropical Characidae, with the concept of the Alestidae expanded herein to include the genus *Chalceus* (see next section).

Murray & Stewart (2002) advanced 11 hypothesized synapomorphies for the Alestidae, that in their sense of that term, was limited to the African members of the family as defined herein. One of these, their character 9, was found to be a synapomorphy for the African members of that family (char. 31 of this study), whereas the ten other synapomorphies they proposed for the clade were either found in the present study to be derived at less inclusive levels than the Alestidae or were problematic in diverse ways.

Synapomorphies proposed by Murray & Stewart (2002) based on characters 3 and 6 of their analysis apparently both reflect a modification that is treated as a single character (char. 52, see discussion in that section). Regardless of whether they are treated as one or two characters, these modifications are absent in the basal African alestid *Arnoldichthys* and are thus synapomorphic not for the Alestidae or all of the African components of that family, but rather for the clade within the Alestidae composed of all genera of the family with the exception of *Arnoldichthys* and *Chalceus*. The synapomorphies derived from two of the other characters proposed by Murray & Stewart (their characters 17 and 24) are also absent in *Arnoldichthys* and, thus, synapomorphic for a clade within the Alestidae (clade 6 of this study) rather than for all of the African members of that family.

Character 13 of Murray & Stewart (2002), the form of the parasphenoid, is coded as different for *Hydrocynus* in this study than by those authors and the definitions of the character in question differ between the two studies. Changing the coding for that feature and the inclusion of additional alestids in the analysis would eliminate their character 13 as a synapomorphy at the level of the African alestids.

Character 31 of Murray & Stewart (2002), the presence of three epurals, was found by those authors to be unique to alestids among examined taxa. Our more encompassing analysis has revealed that three epurals are present in additional outgroup characiform taxa and the character would be derived at a more encompassing phylogenetic level than the Alestidae within the Characiformes.

Finally the features discussed in characters 8, 14, 25 and 32 of Murray & Stewart were not used in this analysis for the reasons discussed under 'Unutilized Characters' above.

Chalceus

Eigenmann & Allen (1942): 277) and Géry (1977: 342) suggested that *Chalceus* is difficult to place taxonomically. Alternative hypotheses aligned *Chalceus* with a component of the Lebiasinidae (Eigenmann, 1910: 439) or close to *Brycon* and *Triportheus* (Weitzman, 1960: 243), all of which are Neotropical groups. Subsequently, Lucena (1993: 121) proposed *Chalceus* as the sister group of *Brycon*, whereas the molecular-based analysis of Ortí & Meyer (1997: 92) indicated that *Chalceus* was the sister group of the clade consisting of the African members of the Alestidae of this study along with several Neotropical characiforms. Most recently, Zanata (2000) hypothesized *Chalceus* to be a component of the clade formed by the Alestidae, *Crenuchus* and *Hemiodus*. The hypothesis proposed herein indicates that *Chalceus* is the sister group of the African members of the Alestidae under the expanded limits of that family proposed in this analysis

Arnoldichthys

Arnoldichthys has been usually defined as a member of the subfamily Alestinae, tribe Petersiini (e.g. Poll, 1967a; Paugy, 1990a). The results of this study demonstrate that *Arnoldichthys* is instead the most basal member of the Alestidae with the exception of *Chalceus* and is distinctly separated phylogenetically from all other taxa that were traditionally included in the Petersiini.

Hydrocynus

Roberts (1969: 442) erected a separate subfamily, the Hydrocyninae, for *Hydrocynus*, notwithstanding his suggestion that *Hydrocynus* was derived from an *Alestes*-like ancestor that presumably was retained in the Alestinae. Alternatively, Vari (1979): 342) reported various derived features (see 'Comments on phylogenetic relationships of *Hydrocynus*', above) that suggested a close relationship between *Hydrocynus*, *Bryconaethiops*, and a subunit of the species of *Alestes* and consequently synonymized the Hydrocyninae into the Alestinae. Brewster's (1986: 192) scheme of relationships similarly indicated an association of *Hydrocynus* with *Alestes*, as did the analysis by Murray & Stewart (2002) that drew extensively from Brewster's evidence. The more encompassing phylogenetic analysis in this study places *Hydrocynus* in a distinctly more basal position in the topology of the Alestidae than is the case with *Alestes*, with *Hydrocynus* the sister group of the clade comprised of all other alestids with the exception of *Chalceus* and *Arnoldichthys*.

Petersius

Prior to Myers (1929), *Petersius* included *P. conserialis* and a number of alestids of small body size that had in common cuspidate teeth, the absence of the inner symphyseal dentary tooth, and a complete lateral line. Myers (1929: 5) restricted *Petersius* to its type species, *P. conserialis*, a species of moderately large body size and the other species previously assigned to that genus were shifted to other genera. Those taxa along with *Petersius*, nonetheless, formed the tribe Petersiini of later authors (e.g. Poll, 1967a; Géry, 1977; Paugy, 1990a). The information obtained in this study indicates that *Petersius* is more basally positioned in the phylogeny than are the other alestid species traditionally included in the Petersiini, and that this tribe as traditionally defined constitutes a nonmonophyletic assemblage.

Brycinus and Bryconalestes

The genus *Bryconalestes* was proposed by Hoedeman (1951) to include the species *B. longipinnis longipinnis* (Günther) and *B. longipinnis chaperi* (Sauvage), nominal forms usually assigned to *Brycinus*. The majority of subsequent authors did not, however, recognize *Bryconalestes*. The overall most parsimonious phylogenetic hypothesis reveals that the '*longipinnis*-group' within *Brycinus* is not most closely related to the other members of that genus, but rather to the members of clade 22. We consequently recognize a separate *Bryconalestes* for the species previously assigned to the '*longipinnis*-group' within *Brycinus*.

MINIATURIZATION AND GIGANTISM IN THE ALESTIDAE

Miniaturization and gigantism in freshwater fishes have been discussed by Weitzman & Vari (1988), Kottelat & Vidthayanon (1993), de Pinna (1996) and other authors. The Alestidae is striking in demonstrating both of these evolutionary trends. In their analysis of South American miniature freshwater fishes, Weitzman & Vari (1988) adopted an arbitrary maximum of 26 mm standard length (SL) for a species to be considered a miniature, a value subsequently applied by Kottelat & Vidthayanon (1993) in their analysis of the phenomenon in South and South-east Asian freshwater fishes. Weitzman & Vari (1988: 450) emphasized that this length criterion served, however, only as a first approximation for miniatures and was inappropriate as an absolute standard in instances of unusually elongate species, such as taxa with proportionally distinctly longer postabdominal regions. They noted that numerous other, typically reductive traits often characterize such 'elongate' miniaturized species that, nonetheless, exceed the 26 mm SL standard.

Within the Alestidae, various species, most notably those *Virilia* populations that mature at 18.8 mm SL would definitely be considered miniatures both on the basis of both their body length and the possession of multiple reductive features of various body systems. At the other end of the size spectrum within the Characiformes we have *Hydrocynus goliath*; with a standard length reaching at least 1320 mm (Eccles, 1992: 122) it is the largest member of the Characiformes, not only in Africa, but across the order (Weitzman & Vari, 1998: 101).

This range in standard lengths of species within the Alestidae is striking in absolute terms, but more so when considered in a phylogenetic context. Although some Neotropical characiform species mature at a smaller body size than does *Virilia* (see Weitzman & Vari, 1988: table 1), all such miniatures are either (1) components of groups all of whose members tend to be small or are at most mid-sized (e.g. Characidiinae, Cheirodontinae, Glandulocaudinae, Lebiasinidae) and all of which are distinctly smaller than *Hydrocynus goliath*, or (2) are members of groups of somewhat uncertain limits and monophyly (e.g. Tetragonopterinae) but that, nonetheless, lack any known giant forms.

Turning to other 'giant' characiforms, we find that the largest characiforms in the Neotropics are the serrasalmine *Colossoma* (970 mm SL; Goulding, 1981: 97), the ctenoluciid *Boulengerella cuvieri* (675 mm SL; Vari, 1995: 78) and the characid *Salminus* (approximately 1000 mm SL for *S. brasiliensis*; Britski, de Silimon & Lopes, 1999: 50; Lima *et al*., 2003: 156). In the case of the Serrasalminae and Ctenoluciidae, the remaining members of that subfamily and family, respectively, are species of moderate to large body size and miniatures are thus absent in those groups. The relationships of *Salminus* have been considered problematic (Roberts, 1969: 435), but an association of that genus with *Brycon* has been proposed based on molecular evidence by Ortí (1997: fig. 10) and Ortí & Meyer (1997: fig. 10), implicitly (Géry, 1977: fig. 10), and based on sperm ultrastructure (Pompiani, 2003) and karyotypes (Margarido & Galetti, 1999). Subsequently Castro *et al*. (2004) proposed that *Salminus* was most closely related to *Brycon* plus *Henochilus* based on molecular data. No member of *Brycon* can be considered to be a miniature.

Thus, the presence of both miniatures (*sensu* Weitzman & Vari, 1988) and 'giants' within the not particularly speciose family Alestidae (approximately 105 species; Paugy, 1984, 1986; Teugels & Thys van den Audenaerde, 1990; Géry, 1995, 1996) is noteworthy, as is the sheer range in lengths between the smallest and largest species in the Alestidae (a 70× range).

Although their focus was on Neotropical freshwater fishes, Weitzman & Vari (1988: 458) also provided preliminary estimates of the number of miniature freshwater fishes on other continents. In the case of African freshwater fishes, based on the incomplete information available in Daget, Gosse & Thys van den Audenaerde (1984, 1986) and applying the 26 mm SL standard, they estimated that there were approximately a dozen miniature fish. Within the Characiformes these include species in the Distichodontidae (*Neolebias bidentatus*, Daget & Gosse, 1984: 193) and the Alestidae (*Lepidarchus adonis*, Paugy, 1990b: 235; *Virilia*, this study) and outside of that order among African fishes in various taxa including the Cyprinidae (e.g. *Barbus nigrifilis*, Lévêque & Daget, 1984: 274) and Cyprinodontiformes (e.g. *Aplocheilichthys stuhlmanni*, Wildekamp, Romand & Scheel, 1986: 186). Thus, the Alestidae features prominently among African freshwater fish miniatures. These estimates of the number of miniatures by Weitzman & Vari (1988), although interesting in their own right, did not deal with the question of the relative number of evolutionary events represented by such miniature species.

As noted by Weitzman & Vari (1988) and de Pinna (1996), an estimate of the minimum number of occurrences of gigantism or miniaturization within a group of fishes, or indeed any group of organisms, requires a hypothesis of the phylogenetic relationships of the involved taxa. In his elaboration on that concept, de Pinna (1996: 71) noted that both gigantism and miniaturization are often the terminal states in a progressive increase or decrease, respectively, in size among closely related taxa relative to the body size present in the more encompassing phylogenetic group. The phylogenetic scheme for the Alestidae presented herein allows for the first evaluation of the evolutionary context under which gigantism and miniaturization originated within a group of African freshwater fishes.

A single case of gigantism occurs within the Alestidae, in the species of *Hydrocynus*. This gigantism reaches its maximum in *H. goliath* (1320 mm SL), with other members of the genus also distinctly larger than most characiforms (550–800 mm SL in *H. brevis, H. forskahlii* and *H. vittatus*; Paugy & Guégan, 1989: 68; Paugy, 1990b). Evaluating the body size of *Hydrocynus* within a phylogenetic context, we find that *Arnoldichthys*, a moderately small species (98 mm SL; Poll, 1967a: 67), is the sister group to *Hydrocynus* and all other members of the Alestidae. *Hydrocynus* is, in turn, the sister group to the remaining alestids, the largest species of which are some species of *Alestes* and *Brycinus* (*A. baremoze*, 425 mm SL; *A. dentex*, 410 mm SL; *A. macrophthalmus*, 600 mm SL, *Brycinus macrolepidotus*, 530 mm SL; Paugy, 1990b) that approximate the body size of some of the smaller species of *Hydrocynus*.

Most members of the clade including *Alestes* and *Brycinus* have maximum known standard lengths that are, however, shorter to distinctly shorter than is the case in the larger species in *Alestes* and *Brycinus*. It consequently appears that the plesiomorphic condition in the lineage (clade 8) that encompasses all alestids other than *Arnoldichthys*, *Chalceus* and *Hydrocynus* is a body size that is distinctly smaller than that present in the species of *Hydrocynus*. Thus, within the context of the phylogeny, the gigantism of the species of *Hydrocynus* represents an abrupt increase in size, apparently at the level of the ancestor of the Recent members of that genus rather than being the terminus of a gradual phylogenetic increase in body size such as occurs in some groups of fishes (see comments by de Pinna, 1996: 76). The very large relative body size of *H. goliath* does, however, apparently represent the terminus of a progressive intrageneric increase in body size given the relatively large body size achieved by its congeners.

Under the phylogenetic scheme proposed herein, the larger body size of some species within *Alestes* and *Brycinus* (see above) is an independent increase in size within the Alestidae. The degree of increase in body size in *Alestes* and *Brycinus* is less pronounced relative to body size of phylogenetically proximate alestids than is the case in *Hydrocynus* and cannot be considered to represent gigantism in the admittedly non-quantitative sense under which that the term is most often applied.

Turning to the question of miniaturization, we find two taxa within the Alestidae that are miniatures under the criteria proposed by Weitzman & Vari (1988) – *Lepidarchus* and *Virilia* (see also comments concerning the latter genus under 'Osteological Preparations', above). Examined specimens of *Lepidarchus* with a maximum SL of 19.1 mm are apparently sexually mature (male holotype of *L. adonis* 21.0 mm), a length distinctly below the 26.0 mm SL standard often utilized for miniatures. Furthermore, *Lepidarchus* demonstrates numerous reductive features of the type proposed by Weitzman & Vari (1988) as typical of miniatures (see listing of synapomorphies for the genus under 'Phylogenetic Reconstruction', above).

Although the closest relatives to *Lepidarchus*, the genera *Clupeocharax*, *Ladigesia* and *Tricuspidalestes*, have maximum SL of 29.0, 29.9 and 29.9 mm, respectively, all larger than the 26 mm SL limit for miniatures, they all demonstrate various paedomorphic features of several osteological systems. These modifications include the absence of certain ossifications of the head and pectoral girdle, diverse reductions in the degree of development of the laterosensory canal system on the head and body, and decreased numbers of fin rays and body scales relative to the condition of these systems in phylogenetically proximate taxa (see characters listed under 'Monophyly of clade 35', above).

Less dramatic reductions in the laterosensory canal system characterize the six genera (*Alestopetersius*, *Bathyaethiops*, *Brachypetersius*, *Duboisialestes*, *Nannopetersius* and *Phenacogrammus*) that form progressive sister taxa to the clade consisting of *Clupeocharax*, *Lepidarchus*, *Ladigesia* and *Tricuspidalestes*. These 10 genera thereby jointly demonstrate a pattern of progressive reduction of body size and a successive increase in paedomorphic features terminating in a definite miniature species, *Lepidarchus adonis*, falling under the 26 mm SL size limit for such taxa proposed by Weitzman & Vari (1988). The phenomena of progressive phylogenetic reductions in body size terminating in miniatures was highlighted by de Pinna (1996: 71) as common to many lineages of fishes.

All specimens of *Virilia* examined in this study apparently are mature, with the largest examined specimen 19.7 mm SL, a size making the genus a miniature under the standard proposed by Weitzman & Vari (1988). Under our phylogenetic hypothesis *Virilia* is closely related to species of *Hemmigrammopetersius* and *Rhabdalestes*, all of which are also of relatively small body size (largest examined specimens of each genus 32.1 and 47.5 mm SL, respectively). Thus, we again encounter a pattern of apparent progressive reduction within a clade terminating in a distinct miniature. Nonetheless, *Virilia* does not demonstrate the same pronounced degree of reductive paedomorphic traits typical of miniatures that are characteristic of *Lepidarchus*. Furthermore, *Virilia* and its closest relatives *Hemmigrammopetersius* and *Rhabdalestes* lack a progressive pattern of paedomorphic reductions of the skeleton, laterosensory canal system and fin rays relative to phylogenetically proximate outgroups. These three genera have incongruent distributions in the occurrence of such reductive features rather than a coherent pattern of progressive paedomorphosis. As such, this lineage does not conform to the pattern of progressive paedomorphosis found in the clade leading to *Lepidarchus*.

BIOGEOGRAPHY AND VICARIANCE

The presence of members of the Characiformes in the freshwaters of both Africa and South and Central America has engendered biogeographical interest since the mid-nineteenth century. This distribution has been discussed both within the context of the static continent concept of earth history (e.g. Darlington, 1957) and, more recently, under the framework of the continental drift model (e.g. Lundberg, 1993).

One of the groups of freshwater African and Neotropical fishes repeatedly commented upon in previous biogeographical analyses was the family Characidae of Greenwood *et al*. (1966: 395). As defined by those authors, the Characidae encompassed numerous taxa covering the distributional range of the Characiformes in both the New World and Africa. Also, as later noted by Greenwood (1983: 181) it was one of the few families of freshwater fishes common to the two continents.

Assignment of a taxonomic level (e.g. the Characidae as a family) is somewhat arbitrary. Nonetheless, the external similarity of various characids (*sensu* Greenwood *et al*., 1966) on both sides of the Atlantic was striking. Transfer of the African components from the Characidae to the Alestidae in Géry (1977) and subsequent publications eliminated the single characiform family common to the New and Old Worlds. In actuality, the critical underlying hypothesis of a vicariance event between Africa and New World within what had been previously considered to be the

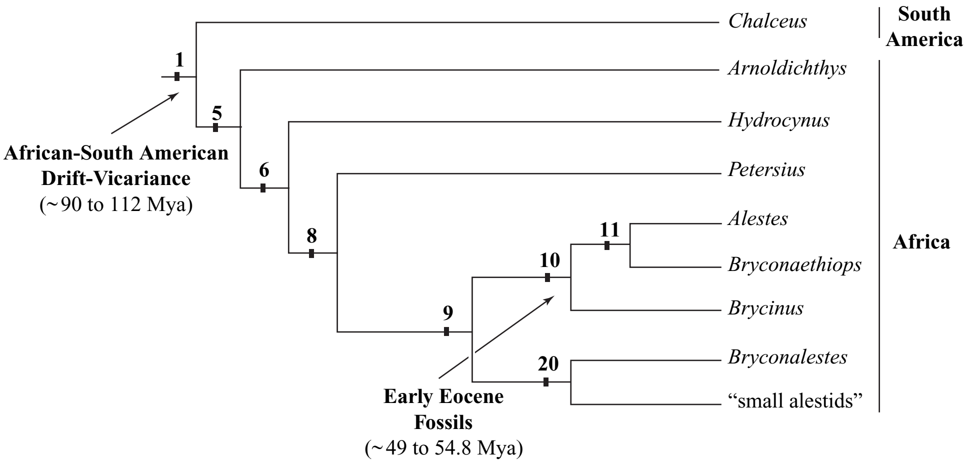

Figure 44. Hypothesis of relationships within the Alestidae, indicating the drift-vicariance hypothesis and the age of the oldest fossil alestids assigned to particular clades in this study.

Characidae was simply shifted to a higher, albeit not rigorously delimited, taxonomic level.

As the members of the Alestidae are inhabitants of freshwaters of much of Africa and South America, and in the absence of a mechanism to account for the dispersal of such fishes across the physiological barrier presented by the intervening Atlantic Ocean, it is most parsimonious to hypothesize that the ancestral component of the Alestidae evolved prior to the separation of South America from Africa. As noted by Lundberg *et al*. (1998: 23) the presence of marine invertebrate fossils indicated 'a continuous, shallow South Atlantic seaway between Africa and South America by late Aptian', approximately 112 Mya.

True ocean depths and habitats between Africa and South America were present by the middle to late Aptian, approximately 105 Mya, albeit perhaps with a limited linkage between what is now West Africa and north-eastern Brazil (Lundberg *et al.*, 1998: 23, fig. 10A and references cited therein). The continents were completely separated by the Turonian period, approximately 90 Mya (Lundberg *et al.*, 1998: fig. 10B). As such the minimum age of the Alestidae, as demonstrated by their presence on either side of the Atlantic is 90 Myr and perhaps of the order of 112 Myr (Fig. 44).

One striking implication of these results is the notable asymmetry in terms of the number of species between the Neotropical alestid genus *Chalceus* with only five species (Zanata & Toledo-Piza, 2004: 107) and the 105, and likely more, African species forming the sister group to *Chalceus* within the Alestidae. These results are either indicative of dramatically different rates of speciation in the two lineages, or large scale extinctions in the New World clade. This pattern of basal taxa within a lineage being notably depauperate in terms of numbers of species relative to their sister group was cited for a variety of freshwater fish taxa by Stiassny & de Pinna (1994).

The correlated restricted geographical distributions for basal taxa reported by Stiassny & de Pinna (1994) does not, however, apply in the case of *Chalceus* vs. the remainder of the Alestidae, given the broad geographical distribution of the species of *Chalceus* within South America. Within the African component of the Alestidae, the sister group to all other Alestids on that continent consists of a single species, *Arnoldichthys spilopterus*, with a restricted distribution in West Africa (Paugy, 1990a: 233, fig. 20.37). This set of attributes fits the scheme proposed by Stiassny & de Pinna (1994) both in terms of the asymmetry of numbers of species between sister groups and in the restriction of the geographical distribution of the basal taxa in the lineage.

Trans-Atlantic relationships within the Characiformes extend beyond the Alestidae. As noted by Vari (1995: 86), the clade consisting of the New World families Lebiasinidae, Erythrinidae and Ctenoluciidae and the African family Hepsetidae predates the complete opening of the intervening Atlantic Ocean. Similarly, the relationships of the clade formed by the African characiform families Distichodontidae and Citharinidae that together form a clade basal within the Characiformes (Vari, 1979; Fink & Fink, 1981) must also lie in some fashion within a clade including numerous New World forms that are now assigned to a series of different families. In his analysis of this situation, Lundberg (1993) pointed out that the Characiformes had an ancestral South American-African distribution that predates the drift of these continents, a concept reiterated by Ortí (1997: 238) and Ortí & Meyer (1997: 94). Within the context of both the phylogenetic hypotheses set forth in those analyses and that for the Alestidae proposed herein, many of the major cladogenic events within the Characiformes predated the separation of the continents.

Numerous authors have commented on the distribution of African freshwater fishes at different geographical scales. Although many of these studies have provided excellent overviews of the diversity and distributions of freshwater fishes in diverse portions of Africa (e.g. Skelton, 1994), they have of necessity focused on questions of degrees of ichthyofaunal similarity or endemism. In his discussion, Reid (1996) noted that the 'ichthyogeography' of African fishes was handicapped by a critical lack of phyletic information on the evolutionary history of the African freshwater fish fauna. Only when such information becomes available would that data in conjunction with information on species distributions permit a full understanding of the historical patterns of fish distribution in Africa.

Attaining that goal has been hindered by the unfortunate reality that there are relatively few species-level phylogenies (e.g. barilin cyprinids; Howes & Teugels, 1989) for groups of African freshwater fishes. Our analysis, focused as it was on phylogenetic questions often above species-level, can provide only some broad outlines for the discussion of such biogeographical questions. Several of the clades do, however, demonstrate distinct patterns that may correlate with the biogeographical areas proposed by many previous authors.

Looking at clade 21 we find that the species of *Bryconalestes* straddle the eastern margins of the Zairean, Lower Guinean, Nilo-Sudanian and Upper Guinean ichthyological provinces (as delimited by Skelton, Tweddle & Jackson, 1991) in West Africa, a pattern presumably indicative of a common history of the ichthyofauna in those regions. The coastal aspects of that pattern are repeated to large part in clade 31, albeit with more of an extension of members of the clade into the central and western portions of the Zairean province, a pattern indicative of a commonality of the history of those two clades. One other clade (clade 14, *Bryconaethiops*) repeats the Zairean-Nilo-Sudanian components of this distribution, although it is situated further within the interior of the continent than is the case for members of clades 21 and 31.

Turning to the rest of the phylogeny of the African components of the Alestidae, we do not find any clear repeated patterns of endemism and nonoverlapping distribution patterns between clades. To a large extent, this lack of resolution is the result of the wide geographical distributions of a number of species in the Alestidae as they are diagnosed at present. Prime examples are *Brycinus macrolepidotus* (highlighted by Reid, 1996: 301), *B. imberi* (Greenwood, 1983: 196) and *Hydrocynus vittatus* (Skelton *et al*., 1991: 222), all of which are species whose ranges encompass many of the recognized ichthyogeographical provinces in sub-Saharan Africa.

Another potential contributing factor to this lack of repeated biogeographical patterns and endemism in the Alestidae is the long evolutionary history of the family (90–112 Myr, see above). The complex geomorphological changes that transpired in Africa during that lengthy time period and the resultant modifications to the river basins and their interconnections would have resulted in progressive changes in the ranges of many species and serve to complicate the interpretation of the underlying historical biogeographical signal.

FOSSIL EVIDENCE

Although no geological benchmarks comparable to the separation of South America and Africa discussed in the previous section permit us to unequivocally date the subsequent cladogenic events within the Alestidae, the fossil record does provide minimal ages for some of the higher level clades within the African component of the family. Fossils identified as characids have been reported from a number of localities in Africa (Greenwood, 1972, 1976; Greenwood & Howes, 1975; Van Neer, 1992; Stewart, 1994, 1997a, b, 2003), Europe (De La Peña Zarzuelo, 1996; Gaudant, 1993, 1996; Monod & Gaudant, 1998) and the Arabian Peninsula (Micklich & Roscher, 1990; Otero & Gayet, 2001). These fossil taxa typically consisted solely of loose teeth and less often of intact components of jaws or whole fishes. These restrictions reduced the degree to which it is possible to incorporate these remains into phylogenetic analyses that were invariably based on evidence from multiple components of the skeleton, along with nonosteological characters.

The assignment of such fossils to the Characidae follows the broadly encompassing concept of that family proposed by Greenwood *et al*. (1966). The subsequent progressive restriction of the limits of the Characidae, including the proposal of the Alestidae for the African components of what had been a broadly encompassing Characidae, resulted in the Characidae under this more restrictive definition being an entirely New World family. Such a restricted Characidae is apparently not represented by fossils in either Europe or the Arabian Peninsula (see comments below concerning *Sindacharax*).

The fossil evidence rather indicated that at least some of these European and Arabian Peninsula forms are appropriately assigned to the Alestidae and we herein focus our comparisons of the Old World fossils with Recent members of that family. Some citations of potential members of the Alestidae in the fossil record, such as the report of fossils of the Characidae from the upper Cretaceous of Romania (Grigorescu *et al*., 1985) and of components of the Characiformes from the Cenomanian (Late Cretaceous) of Morocco (Dutheil, 1999), were not accompanied by illustrations, rendering evaluation of the records impossible. In other cases, fossil material considered at one point to represent a member of the Characidae has been subsequently found to be erroneously identified (see De La Peña Zarzuelo, 1991).

The majority of the Old World fossils assignable to the Alestidae are represented by isolated teeth described as having originated from one species, albeit often without any commentary as to the evidence underlying that assumption of the conspecificity of these elements. Whereas various fossil teeth of some of the nominal fossil species closely approximate those of Recent members of the Alestidae, other teeth originally assigned to the same taxon often differ dramatically from the dentition of all examined Recent species of the Alestidae and indeed all Recent characiforms, a difference that renders impossible critical comparisons of such fossil material and Recent species.

We focus our discussion herein on the fossil teeth similar to those of the examined Recent members of the Alestidae, leaving aside those teeth of uncertain phylogenetic affinities that do not correspond to the dentition of the members of that family or indeed the members of the Characiformes that we have examined in this analysis. Prior to delving further into the fossil evidence, it is appropriate to comment on *Mahengecharax carrolli*, recently described as a fossil member of the Alestidae.

Mahengecharax carrolli was proposed by Murray (2003) based on fossils from Eocene deposits of Tanzania and hypothesized by that author to be the sister group to the Recent members of the Alestidae. Our analysis has raised a series of questions concerning the proposed synapomorphies that underpin that phylogenetic alignment. In the interest of brevity we limit the following discussion to those features of particular significance for the hypothesis that *M. carrolli* is a basal alestid.

Perhaps the most problematic aspect of the assignment of *M. carrolli* is the fact that it lacks an unequivocal Weberian apparatus (Murray, 2003: 477) a feature synapomorphic for otophysan ostariophysans, a phylogenetic level considerably above that of the Alestidae. This absence, in and of itself, would lead us to question the usefulness of the fossil taxon for the following historical biogeographical analysis. Above and beyond the uncertainty introduced by this, *M. carrolli* also possesses an autogenous hypural 2 that is separate both from hypural 1 and the compound terminal centrum (Murray, 2003: 477).

Possession of a second hypural fused to the posterior portion of the compound terminal centrum is common to the vast majority of characiforms. Indeed, fusion of those elements is a synapomorphy for otophysan ostariophysans (Fink & Fink, 1981, 1996). Although fusion is secondarily lost in some taxa within the Characiforms, most of the taxa in which it is absent have the first and second hypurals conjoined to form a single plate-like ossification (e.g. Hemiodontidae, Langeani, 1998: 155; see also Roberts, 1974: figs 38, 39). Of particular note concerning the proposed alignment of *M. carrolli* with the Alestidae is the fact that fusion to the centrum is universal among examined members of the Alestidae other than for the diminutive *Lepidarchus* (see Roberts, 1966: fig. 9). In *Lepidarchus*, although hypural 2 is not fused to the compound centrum, it is, however, conjoined with hypural 1, the common condition within the Characiformes for taxa lacking continuity between hypural 2 and the compound terminal centrum. *Mahengecharax carrolli* is, however, of a much larger body size than is the diminutive *Lepidarchus*; in addition the first and second hypurals *Mahengecharax* are separate from each other and the compound centrum, a condition absent in all examined Recent members of the Alestidae.

Murray (2003: 473) further stated that 'the bones of the caudal skeleton clearly indicates that the fossil species is a characiform, and related to living African alestid fishes.' As already noted, the lack of fusion between the second hypural and the compound terminal centrum is a major difference in the form of the caudal skeleton between most members of the Characiformes in general and the Alestidae in particular, vs. *M. carrolli*. Furthermore, the overall form of the hypural complex of the caudal fin of *M. carrolli* (Murray, 2003: fig. 6d), particularly the position of hypurals 1 and 2 vs. hypurals 3 through 6 relative to the longitudinal axis through the vertebral column, differs dramatically from the plan common to all examined members of the Alestidae (compare Murray, 2003: fig. 6d for *M. carrolli* with Fig. 30 of this paper showing the caudal skeleton in *Brycinus macrolepidotus* and with illustration by Brewster (1986: fig. 20) of the caudal skeleton in *Hydrocynus forskahlii*). Indeed, the overall form of the caudal skeleton in *M. carrolli* differs from the morphology common to members of the Characiformes across various levels of the phylogeny of the order (e.g. the characid *Brycon meeki*; see Weitzman, 1962: fig. 15; and the basal distichodontid characiform *Xenocharax spilurus*, see Vari, 1979: fig. 37).

Murray (2003: 477, fig. 6d) identified a bone located in the dorsal portion of the caudal fin of *M. carrolli* as a bony stay and noted (p. 478) that possession is characteristic of alestids. Although a bony stay is not general to, and thus characteristic of, alestids (see character 150), it is indeed common to many members of the family.

The structure identified as a bony stay for *M. carrolli* differs, however, from that present in many members of the Alestidae in several significant attributes. Most notably, the element identified as a dorsal bony stay in *M. carrolli* by Murray (2003: fig. 6d) lies distinctly within the arch of the caudal-fin rays. In the Alestidae, in contrast, the dorsal bony stay is positioned such that the posterior portion of that bone overlaps the anterior surface of the anteriormost procurrent dorsal-fin ray (see Fig. 30). Furthermore, the bone in *M. carrolli* is positioned approximately at the vertical through distal tip of the uroneural whereas the bony stay in those members of the Alestidae that possess the ossification terminates posteriorly distinctly anterior to the vertical through the tip of the uroneural (see Fig. 30 and Brewster, 1986: fig. 20). In light of those differences, we consider the item identified as a bony stay in *M. carrolli* by Murray to be nonhomologous with the bone of that name present in many members of the Alestidae.

Finally, Murray (2003: 477) noted that in *M. carrolli* 'the fourth hypural has a slight hook or expansion on the proximal end such as found in many alestids.' Although we do not question that observation, such a process on the fourth hypural has a much broader distribution across the Characiformes. It is present not only in groups such as the Neotropical Characidae (e.g. *Attonitus, Creagrutus*) but also in taxa such as the Curimatidae (e.g. *Cyphocharax abramoides*), Prochilodontidae (see Fink & Fink, 1981: fig. 23, for condition in *Prochilodus*; Roberts, 1969: fig. 29, for condition in *Ichthyoelephas*) and *Xenocharax* in the Distichodontidae (see Vari, 1979: fig. 37), all of which are hypothesized to be more basal within the Characiformes (Fink & Fink, 1981; Buckup, 1998) than is the Alestidae. This process is sometimes hidden to varying degrees by the adjoining portions of the compound terminal centrum and the uroneurals, but clearly is not limited to, or diagnostic for, the Alestidae; indeed, its presence may be primitive within at least the Characiformes. Thus, the presence of the hook on the fourth hypural in isolation is uninformative as to the relationships of *M. carrolli* at the level of the Alestidae.

In summary, there are major problems with the assignment of *M. carrolli* at both higher taxonomic levels (the Otophysi and Characiformes) and particularly with its placement as to the sister-group to the Recent members of the Alestidae. In light of these problems we do not utilize the species in the following analysis.

What information can be garnered from other fossils identified as characiforms from Old World deposits? In his overview, Gaudant (1993: fig. 2) has the oldest European fossils of the Characiformes identified only to the level of order. The oldest of those records (approximately 53 Myr) is well within the time frame for the existence of the Alestidae based on the trans-Atlantic vicariance model; however, such an ordinal-level identification is uninformative as to the timing of cladogenic events within the Alestidae. Alternatively, publications by De la Peña Zarzuelo (1996), Capetta, Russel & Braillon (1972) and Monod & Gaudant (1998), dealing with some of the oldest reported apparently fossil alestids, all from the Eocene of Europe, are pertinent to the analysis of minimal ages for the subunits of the Alestidae.

Comparison of the figures in De la Peña Zarzuelo (1996: fig. 1) of fossil teeth from the Iberian Peninsula with cleared and stained material of the Alestidae indicates that the tooth illustrated in figure 1D of that study is very similar in terms of both asymmetry and the numbers of cusps to the posterior dentary teeth of the species of *Brycinus*. Although the variation in the form of these posterior dentary teeth within the clade consisting of *Alestes*, *Brycinus* and *Bryconaethiops* renders a generic-level identification of these teeth problematic, an assignment of the fossil teeth to the level of that assemblage of genera is reasonable.

At a minimum this evidence indicates that the ancestor of *Alestes*, *Brycinus* and *Bryconaethiops* (clade 10) had arisen by the time of deposition of the bed from which the fossils originated (Cuisian of the Upper Ypresian, early Eocene) approximately 49–54.8 Mya (Geological Society of America, 1999). The occurrence of fossils assignable to clade 10 by that time period would also indicate that cladogenesis at the levels of clades 5, 6, 8 and 9 predated the early Eocene (Fig. 44) and that the ancestors of the genera *Arnoldichthys* and *Hydrocynus* must have existed as separate lineages by approximately 49–54.8 Mya.

This time frame long predates the oldest reported occurrence of *Hydrocynus* in the fossil record (Late Miocene and Pliocene deposits of Kenya (Stewart, 1994, 2003) and Zaire (Van Neer, 1992) and Pliocene of Egypt (Greenwood, 1972)). It is striking that both *Arnoldichthys*, with a single species (Poll, 1967a) and *Hydrocynus*, with four or five (Brewster, 1986; Paugy & Guégan, 1989), are not speciose notwithstanding their apparently lengthy evolutionary history as separate lineages. This pattern of disparate numbers of species between sister-clades is a continuation of the asymmetrical levels of species numbers at the base of the phylogeny for the Alestidae discussed above for *Chalceus* vs. the African members of the Alestidae.

Capetta *et al*. (1972) reported on fossil characid teeth from the lower and middle Eocene of the south of France and from the Paris basin that they compared to species of *Alestes*, presumably in the older sense of that genus that encompassed the species assigned within this study to *Alestes*, *Brycinus* and *Bryconalestes*. Monod & Gaudant (1998), in turn, proposed that this material represented a fossil species of characiform that they named *Alestoides eocaenicus*. Comparison of the illustrations in those two papers with cleared and stained material of Recent species demonstrates that a subset of the teeth illustrated by Capetta *et al*. (1972; pls. 1, 2) are similar to the premaxillary and dentary teeth of some members of clade 10 in terms of the asymmetry in the form of the teeth, the asymmetry in the distribution of the cusps on the teeth, and in other cases in the 'molariform' overall shape of some of the teeth. Again, there are differences between various details of these fossil teeth and comparable dentition present in extant members of clade 10.

The illustrations in Monod & Gaudant (1998), although based on fossils that originated in the same deposit as the material reported on by Capetta *et al*. (1972), are based on different material. One of the teeth (their fig. 1) is most similar to some of the teeth of the outer row of dentition on the premaxilla of *Alestes macrophthalmus* within the cleared and stained specimens of the Alestidae we examined in this study. The tooth in their figure 5 is also very similar to the second, or perhaps third, dentary tooth in *A. macrophthalmus*, although again differing in certain details of its morphology.

Nonetheless, an alignment of these fossil teeth with *Alestes* is reasonable within the context of our knowledge of tooth forms across the extant members of the Alestidae. Identification of the material of *Alestoides eocaenicus* as closely aligned with *Alestes* supports the hypothesis that not only had clade 10 arisen by the Eocene, as suggested by the evidence from the fossils illustrated in Capetta *et al*. (1972), but furthermore that cladogenesis at the level of clades 11 and 12 predated the early Eocene (Cuisian of the Upper Ypresian, early Eocene; approximately 49–54.8 Mya). As such, the ancestors of *Alestes* and *Bryconaethiops* must have evolved prior to that time period. If future analysis demonstrates that *Alestoides* is most closely related to a subunit of *Alestes*, then it would be appropriate to synonymize *Alestoides* into *Alestes* in order to retain the latter genus as monophyletic.

Fossils assignable to the Alestidae originating in the Arabian Peninsula (Micklich & Roscher, 1990; Otero & Gayet, 2001) are all more recent than the oldest fossils of the family from Europe, having been deposited during the Early Oligocene (28.5–33.7 Mya) or younger time periods (Miocene). Nonetheless, these fossils are interesting in that they document the extension of the fossil occurrence of the Alestidae across the Arabian Peninsula, a region distinctly to the east of the present range of the family in Africa. The available information on *Arabocharax baidensis* (Micklich & Roscher, 1990) is insufficiently detailed to allow us to hypothesize its phylogenetic placement within the Alestidae, but an assignment to that family seems appropriate.

Details of the isolated teeth reported by Otero & Gayet (2001) from deposits in the Arabian Peninsula are more informative on the question of the possible phylogenetic position of the fishes that were the source of some of those teeth. As was the case with the European alestid fossil teeth, some of the fossil teeth illustrated (their fig. 4e–j) are similar to those of Recent species assigned herein to clade 10 within the Alestidae. The teeth in their figure 4e–g are comparable to the dentary dentition present in *Alestes*, *Brycinus* and *Bryconaethiops*, more so to the morphology of these teeth in *Alestes* and *Bryconaethiops*. The teeth in their figure 4i & j are similar to the posteriormost tooth in the inner premaxillary tooth row in *Bryconaethiops boulengeri* among the species that we have examined.

Some of the teeth (Otero & Gayet, 2001: fig. 4k, l) are similar in overall form to the third and fourth teeth of the inner tooth row of *A. macrophthalmus*, although differing in the form of the distal portion perhaps as a consequence of postmortem damage. Notwithstanding these problematic teeth, the evidence from the teeth that are similar to those of *B. boulengeri* indicates that not only had clade 10 evolved by the early Oligocene, a conclusion congruent with the information derived from the European fossils discussed above, but that it also had a much broader historic distribution into regions of the Arabian Peninsula distant from the present distribution of the Alestidae.

The evidence of the fossil record of the Alestidae is strikingly skewed in terms of being informative as to clades 5, 6, 8 and 10–12 to the exclusion of the other higher level clades within the intrafamilial phylogeny (Figs 43, 44). This skewed distribution of the occurrence of fossils within the phylogeny of the Alestidae may, however, represent a sampling bias. The taxa in clade 20 that constitute the bulk of the remaining members of the Alestidae are typically of smaller body size and are either less likely to be preserved in the fossil record, or if they are preserved, are more difficult to unequivocally identify as members of that family. Furthermore, they are primarily distributed in Central and West Africa, areas distant from the known deposits of possible fossil species of the Alestidae in Europe and the Arabian Peninsula.

RELATIONSHIPS OF *SINDACHARAX*

The fossil characiform genus, *Sindacharax,* has been the subject of considerable discussion in the literature (Greenwood, 1972, 1976; Greenwood & Howes, 1975; Stewart, 1997a, b). Although the age of the specimens identified as *Sindacharax* (Pliocene–Miocene) is too recent to be informative as to the timing of higher level cladogenic events within the Alestidae, some biogeographically interesting hypotheses have been advanced as to the possible phylogenetic relationships of this genus.

The first description of fossil material later assigned to *Sindacharax* was by Greenwood (1972) who described it as *Alestes deserti*. The form of the first dentary tooth in *A. deserti*, with a deep indentation along its posterior margin (his fig. 6b) and cusps (his figs 2–4), is comparable to that in the cleared and stained specimens of *Alestes*, *Brycinus* and *Bryconaethiops* examined in our study.

Soon thereafter, Greenwood & Howes (1975: 99) proposed *Sindacharax* to include *A. deserti* of Greenwood (1972) along with *S. lepersonnei*, a species that was first described in the same publication. They compared the dentition of *Sindacharax* to that of the genus *Colossoma* of the Neotropical subfamily Serrasalminae and posed the question of whether *Sindacharax* might be 'the last traces of an Old World Serrasalmine lineage.' Subsequently, Greenwood (1976: 2) described additional material of *Sindacharax*, this time based on jaw bones.

Perceived similarities of the dentition of *Sindacharax* to that of various Neotropical serrasalmines were, in turn, the basis for a hypothesized occurrence of the Serrasalminae, a subfamily known only from South America among Recent species, in both South American and Africa prior to the separation of the two continents as a consequence of continental drift (Ortí & Meyer, 1997: 95). More recently Stewart (2003: 94) reiterated the proposed relationship of *Sindacharax* with the Serrasalminae based on Greenwood & Howes (1975). A necessary corollary of the hypothesized presence of a serrasalmine clade in both Africa and South America in the past was the subsequent extirpation within Africa of the clade of characiforms which included the Serrasalminae following the separation from South America.

Our analysis raises questions as to the association of *Sindacharax* with the Serrasalminae. The morphology of the posterior portion of the premaxilla in *Sindacharax* (see Greenwood, 1976: 2–3, fig. 1A, D), in particular the presence of a premaxillary pedicle, is comparable to that in all members of the African members of the Alestidae (Figs 2, 13, 15; see also Greenwood, 1976: fig. 2C, D) with exception of the basal genus *Arnoldichthys* and the more derived *Lepidarchus*. The latter genus is a diminutive form that demonstrates a number of reductive attributes and the lack of a premaxillary pedicle may be correlated with its reduced body size (see also discussion under 'Miniaturization and Gigantism in the Alestidae', above).

Such an occurrence of the premaxillary pedicle in both the Recent members of the Alestidae and *Sindacharax* and the geographical overlap of the geographical distribution of those taxa brings to the fore the question of association, i.e. that *Sindacharax* might lie with the Alestidae rather than with members of the Neotropical Serrasalminae. It is noteworthy that a pedicle is present in the Serrasalminae in *Colossoma macropomum* (Machado-Allison, 1982: fig. 22B; but not *C. bidens*, Greenwood, 1976: fig. 2A), *Piaractus* (Machado-Allison, 1982: fig. 22A) and *Mylesinus*, all of which are components of one of the major subclades of that family (Machado-Allison, 1983: fig. 1).

It is, however, absent in *Acnodon* (Jégu & Santos, 1990: fig. 10), *Myleus* (Jégu & Santos 2002: fig. 5), *Ossubtus* (Jégu, 1992: fig. 7C), *Tometes* (Jégu *et al.*, 2002a: fig. 6; Jégu *et al.*, 2002b: fig. 6) and *Utiarichthys* (Machado-Allison, 1983: fig. 4C), other components of the same clade within the Serrasalminae. It is also absent in *Pristobrycon* (Machado-Allison, 1983: fig. 5; 1985: fig. 3) and *Pygopristes* and *Serrasalmus* (Machado-Allison, 1985: fig. 3), all of which are members of the second major lineage within the Serrasalminae for which information on the morphology of the upper jaw is available in the literature.

Further analysis demonstrates that the overall form of the premaxilla of *Sindacharax* is, when viewed ventrally, comparable to that of cleared and stained specimens of *Bryconaethiops*. The latter genus typically has, however, one tooth or an area of attachment for such a tooth between the two rows of premaxillary teeth shown by Greenwood (1976: fig. 1A) for *Sindacharax*. We found that this tooth is absent on one premaxilla in one of the five cleared and stained specimens of *Bryconaethiops* examined in this study. Furthermore, that specimen lacks any apparent scar in the expected area of attachment of such a tooth, a condition comparable to that in the illustrated premaxilla of *Sindacharax* (Greenwood, 1976: fig. 1A).

Finally, and most importantly, the pattern of cusps in the dentition of *Sindacharax* (Greenwood, 1972: figs 2-4; Greenwood & Howes, 1975: fig. 22C) has the 'included cusps' that are present in *Alestes*, *Brycinus* and *Bryconaethiops* (see character 64), but absent in the members of the subclade of the Serrasalminae with a posterior pedicle on the premaxilla. As a consequence, it is most parsimonious to hypothesize that the phylogenetic relationships of *Sindacharax* lie with a component of the Alestidae, in particular the clade consisting of *Alestes*, *Brycinus* and *Bryconaethiops*, rather than with the subunit of the Serrasalminae where the pedicle arises homoplastically.

Stewart (1997a) described another species, *S. greenwoodi*, and suggested that it might be most closely related to *Alestes stuhlmanni*, a Recent East African species. The overall form of the premaxilla and arrangement of the dentition on that bone in *S. greenwoodi* is from a ventral view (Stewart, 1997a: fig. 1) comparable to these osteological systems in *Bryconaethiops boulengeri*. This situation parallels that for other nominal species of *Sindacharax*. Although it is difficult to evaluate the reported similarities in form of the dentition of *S. greenwoodi* vs.

A. stuhlmanni based on available data, it is noteworthy that the distribution of the oral teeth differ dramatically in those two species (compare Stewart, 1997a: fig. 1 for *S. greenwoodi* with Paugy, 1986: fig. 18, for *A. stuhlmanni*, respectively) raising doubts about the suggested close relationship between those two species.

The suggestion that *A. stuhlmanni* should possibly be transferred to *Sindacharax* (Stewart, 1997a: 38) is untenable. The shift of a species that Brewster (1986: 190) assigned to '*Alestes sensu stricto*', the *Alestes* of this study, on the basis of two very distinctive synapomorphies (her synapomorphies 19 and 20), would undoubtedly render *Alestes* nonmonophyletic and is thus an inappropriate course of action.

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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 for bone and cartilage, the standard length of the specimens, and abbreviated locality information. Standard length is in millimeters. All listed specimens were cleared and counterstained except where they are indicated as having been examined via radiographs (R) or as whole, alcohol-preserved material (A). Sex of specimens was determined, when possible, by the examination of gonads and/or externally apparent sexually dimorphic features.

ALESTIDAE

Alestes baremoze * (Joannis), MZUSP 60301, 1, 118.6 mm; USNM 230111, 1, 128.2 mm; Niger, middle/upper Niger River, at Niamey. USNM 61312, 1 (R), 174.0 mm, male; Egypt, near Luxor.

Alestes dentex * (Linnaeus), USNM 371017, 1, 139.4 mm; Egypt, Nile River, at Aswan. USNM 371017, 3 (R), 150.2–187.3 mm; Egypt, Nile River, at Aswan.

Alestes liebrechtsii Boulenger, MCZ 50326, 1, 34.9 mm; Zaire, Zaire River, main stream near mouth of Grande-Pukusi River, a few km downstream from Kinganga.

Alestes macrophthalmus * Günther, USNM 42368, 1, 176.3 mm; Angola, Quanza River. USNM 42367, 1 (R), 247.0 mm, female; Angola, Cunga.

Alestopetersius caudalis * (Boulenger), MNHN 1925-0292, 1, 47.4 mm; Congo, Zaire River, Boma.

Alestopetersius hilgendorfi * (Boulenger), ANSP 66421, 1, 57.3 mm; Cameroon.

Alestopetersius leopoldianus (Boulenger), USNM 365946, 1, 22.9 mm; Congo, Benalia Territory, Ngula River.

Alestopetersius smykalai * Poll, MNHN 1991-0905, 1, 35.8 mm; Nigeria, Jamieson River.

Arnoldichthys spilopterus * (Boulenger), USNM 365945, 2, 71.5–74.4 mm; Nigeria, Sapelli, delta of Niger River. USNM 367305, 10 (A), 55.8–72.2 mm, 2 (R), 61.4–72.2 mm, male and female; Nigeria, Uegeli.

Bathyaethiops caudomaculatus * (Pellegrin), USNM 365947, 2, 26.6–30.2 mm, 2 (R), 27.4–30.2 mm; Congo, Stanley Pool.

Brachypetersius altus * (Boulenger), USNM 365948, 1, 47.3 mm; Congo, Boende, Tshuapa.

Brachypetersius gabonensis * Poll, AMNH 230285, 2, 59.1–67.1 mm; Gabon, Moyen-Ogogue, Mikouma River.

Brachypetersius notospilus * (Pellegrin), MNHN 1930-0131, 1, 57.4 mm; Congo, Kouilou.

Brycinus bimaculatus * (Boulenger), MCZ 64825, 1, 72.4 mm; Congo Likouala, Lac Telle. MNHN 1925-0278, 1 (R), 91.7 mm, male; Zaire, Momboyo, Eala.

Brycinus brevis * (Boulenger), USNM 179332, 2, 89.7–106.0 mm; Liberia, St. Johns River, 0.5 mile (0.8 km) downstream of bridge at Sanniquellie District border.

Brycinus carolinae * (Paugy & Lévêque), MNHN 1982-0909, 1, 96.6 mm, 1 (R), 83.8 mm, male; Guinea, Niger River Basin, Niandan.

Brycinus imberi * (Peters), MZUSP 62623, 1, 65.3 mm; South Africa, Kwazulu Natal, Mlamboguena Pan. USNM 176352, 1 (R), 98.8 mm, male; Belgian Congo (= Congo), Stanleyville, Cataract at Wagenia Fishery.

Brycinus kingsleyae * (Günther), AMNH 230304, 1, 63.0 mm; Gabon, Moyen-Ogogue, Lake Zile, near St. Martin village, near Lambarene. MZUSP 22854, 1, 50.0 mm; Gabon, Ivindo River, mouth of the Nounah.

USNM 119129, 1 (R), 123.1 mm, male; Cameroon, So River.

Brycinus lateralis * (Boulenger), USNM 310101, 1, 86.6 mm; Botswana, Xugana, semipermanent flowing river. USNM 309579, 1 (R), 89.1 mm, male; Zambia, Western Province, Central Barotse Village. MZUSP 56427, 1, 63.7 mm; Botswana, Okavango.

Brycinus leuciscus * (Günther), USNM 229887, 2, 73.5–74.0 mm; Republic of Niger, middle/upper Niger River, at Niamey.

Brycinus macrolepidotus * Valenciennes, MZUSP 60303, 1, 58.6 mm; Togo, Mono River, 36 K due E of Ayengre. USNM 310088, 2, 38.5–77.3 mm; Ghana, Dayi River Estuary. USNM 303918, 2, 121.9–123.7 mm; Cameroon, Manyu, Cross River System. USNM 61347, 1 (R), 205.2 mm, male; Egypt. USNM 61348, 1 (R), 239.5 mm, female; Egypt.

Brycinus nurse * (Rüppell), USNM 339724, 2, 107.4–112.4 mm; Nigeria, Mayo Gamgam (Fulani), main river at Gashaka Camp.

Brycinus aff. *nurse* (Rüppell), USNM 304189, 2, 48.4–62.0 mm; Cameroon, Lower Ndian River System, S of Korup to sea coast, river around last banana village. USNM 357074, 1, 75.7 mm; Nigeria, Gashaka Gumpti National Park, Dumpti Lake.

Brycinus aff. *opisthotaenia* (Boulenger), AMNH 230291, 1, 41.9 mm; Gabon, Moyen-Ogogue, Lake Zile, near St. Martin village, near Lambarene.

Brycinus sadleri * (Boulenger), MCZ 145431, 2, 74.6–79.7 mm; Uganda, Lake Victoria, Lake Nawampasa, near Lake Kyoga. MCZ 150700, 2, 63.3–70.7 mm; Kenya, Nyanza, Rachuonuo District, Osodo Beach, S shore of Nyanza Gulf, 65 km S of Kisumu town.

Bryconaethiops boulengeri * Pellegrin, MNHN 1964-0250, 1, 129.2 mm; Congo, Odzala. AMNH 227484, 1, 68.6 mm; Central African Republic, Sangha, Mossapoula Creek Bridge.

Bryconaethiops macrops * Boulenger, MNHN 1979-0382, 1, 106.7 mm; Central African Republic, Congo River basin, Oubangui, Bangui.

Bryconaethiops microstoma * Günther, USNM 339722, 2, 54.9–55.1 mm; Nigeria, Mayo Gamgam (Fulani), main river at Gashaka Camp.

Bryconaethiops sp., USNM 304256, 1, 56.8 mm; Cameroon, Cross River system, main Cross River, downstream of Mamfé.

Bryconalestes derhami * (Géry & Mahnert), MNHN 1980-1192, 1, 63.8 mm; Ivory Coast, Tabou, Olodio.

Bryconalestes intermedius * (Boulenger), USNM 304040, 2, 65.4–72.5 mm; Cameroon, Cross River system, upper tributaries of Manaya River, near Baro Village, N of Korup, upper beaches of Marube River, draining to Bake River.

Bryconalestes longipinnis * (Günther), USNM 310105, 2, 62.7–64.3 mm; Togo, Togo-Kama River, 6 km NW of Sokode on Bassari Road, upstream 3/4 km (due W) of bridge. MZUSP 60307, 1, 64.2 mm; USNM 193937, 1, 76.2 mm; Liberia, Gbarnga District, streams and tributaries to St. John's River.

Chalceus epakros * Zanata & Toledo-Piza, MZUSP 76070, 1, 123. 6 mm; Brazil, Pará, São Luís, Rio Tapajós above Itaituba. MZUSP 30754, 1, 67.9 mm; Brazil, Pará, Pederneiras, Rio Tapajós.

Chalceus erythrurus * Cope, MZUSP 27296, 92.5 mm; Brazil, Amazonas, Costa Japão, Ressaca do Japão, lower Rio Japurá. * MZUSP 20385, 1, 109.6 mm; Brazil, Amazonas, Lago Janauacá. MZUSP 75613, 1 (A), 92.4 mm; Brazil, Amazonas, Janauacá, Lago Murumuru.

Chalceus guaporensis * Zanata & Toledo-Piza, USNM 319294, 1, 124.1 mm; Peru, Madre de Dios, Manu, Parque Nacional Manu, Pakitza, Picaflor Stream, Cana Brava, Trail # 19.

Chalceus macrolepidotus * Cuvier, FMNH 85686, 93.3 mm; Venezuela, Amazonas, 50 km towards Puerto Ayacucho from Puerto Nuevo. USNM 226115, 1, 115.3 mm; Suriname, Nickerie District, Corantijn River at km 180, side channel of main river along Surinamese shore. MZUSP 43291, 1, 207.9 mm; Brazil, Amazonas, Rio Negro, Cantagalo.

Chalceus spilogyros * Zanata & Toledo-Piza, MZUSP 76069, 122.7 mm; Brazil, Pará, Igarapé Jacaré, right margin of Rio Tapajós, near Boim.

Chalceus sp., USNM 231547, 1, 115.0 mm; aquarium specimen.

Clupeocharax schoutedeni * Pellegrin, USNM 365949, 1, 29.0 mm; Congo, Lac Tumba.

Duboisialestes tumbensis * (Hoedeman), USNM 365955, 1, 34.4 mm; Congo, Stanley Pool. USNM 365953, 1 (A), 26.0 mm; Congo, Stanley Pool, M'Bamu, just N of Zete-Moko. USNM 365954, 1 (A), 32.6 mm; Congo, Stanley Pool, Kingabwa beach.

Hemmigrammopetersius barnardi * (Herre), AMNH 19861, 3, 29.7–29.8 mm; Malawi, Shire River, Chikwawa. USNM 365950, 1, 23.7 mm; Malawi, Mpatsanjoka Dambo, road from Senga Bay to Salima, Lake Malawi.

Hemmigrammopetersius intermedius * (Blache & Miton), MNHN 1985-0168, 1, 32.1 mm (R), SL unavailable; Ivory Coast, Niger River Basin, Bage River.

Hydrocynus brevis * Günther, USNM 61350, 1, 140.4 mm; Egypt, near Luxor. USNM 52178, 1 (R), 344.0 mm, male; Bayad, Nile River. USNM 72791, 1 (R), 360.0 mm (possible male); Sudan, Khartoum, Nile River. USNM 52095, 1 (R), 258.6 mm (female); Sudan, Atbara River. USNM 72790, 1 (A), 525.0 mm; Sudan, Khartoum, Nile River.

Hydrocynus cf. *brevis* Günther, USNM 052178, 5 (A), 119.4–345.0 mm; Bayad, Nile River.

Hydrocynus forskahlii * Cuvier, MZUSP 60307, 1, 120.0 mm; Nigeria or Niger. USNM 176314, 2 (R), 279.0 mm (male), 367.3 mm (female); Congo, Kasenyi, Haut Zaire. USNM 84156, 1 (R), 341. 7 mm (female); Lake Tanganyika. USNM 176314, 2, 279.0–367.3 mm; Congo, Haut Zaire, Kasenyi. USNM 230143, 2, 138.2–138.5 mm; no locality data.

Hydrocynus sp., USNM 231342, 3, 39.7–58.4 mm; Upper Volta, Black Volta River at Morno.

Ladigesia roloffi * Géry, USNM 365951, 1, 29.9 mm; MCZ 47674, 1, 24.5 mm; Sierra Leone, Kasewe Forest.

Ladigesia sp., USNM 206409, 1, 22.6 mm; Sierra Leone, Sewe River, at Mattru-Jong, 9 miles (= 14.4 km) N of Mattru.

Lepidarchus adonis * Roberts, USNM 267290, 7, 15.5–19.1 mm; Ghana, Aluku. USNM 205536, 6, 14.1–18.9 mm; Ghana, Western Region, small coastal stream in dense forest 0.5 mile (= 0.8 km) beyond village of Aluku.

Micralestes acutidens * (Peters), MCZ 48248, 2, 46.3–47.8 mm; Central African Republic, Mbomou River, at Gozobangui.

Micralestes cf. *acutidens* (Peters), USNM 369305, 1, 40.7 mm; Zaire (= Congo), Stanley Pool, Congo River Basin.

Micralestes elongatus * Daget, USNM 339718, 2, 50.3–59.6 mm; Nigeria, Mayo Gamgam (Fulani), main river at Gashaka Camp.

Micralestes cf. *elongatus* Daget, MNHN 1985-0165, 1, 69.6 mm; Ivory Coast, Cavally River.

Micralestes humilis Boulenger, USNM 303992, 1, 46.8 mm; Cameroon.

Micralestes lualabae * Poll, AMNH 5805, 2, 54.6–56.4 mm; Congo, Eastern Congo, Stanleyville.

Micralestes occidentalis * (Günther), USNM 205534, 2, 39.6–43.7 mm; Ghana, Western Region, Butre River Basin.

Micralestes sp., * USNM 166885, 2, 34.5–38.0 mm; Egypt, 8 mi (= 12.8 km) NE of Cairo, drainage ditch at El Marg.

Nannopetersius ansorgii * (Boulenger), MNHN 1962-0127, 1, 59.1 mm; Gabon, Kouilou River Basin, Niari River. ANSP 38704, 1, 49.3 mm; West Africa, Mayili, Chiloango River.

Petersius conserialis * Hilgendorf, ZMH 11563, 1 (R), 111.4 mm; Tanzania, Dunda. FMNH 54287, 1 (R), 101.8 mm; Tanzania, Kingani at Dunda. BMNH 1922.4.18.8, 1 (R), 97.3 mm; Tanzania, Rufiji River, Mpanga.

Phenacogrammus aurantiacus * (Pellegrin), MZUSP 22853, 1, 67.0 mm, 1 (R), 78.4 mm; Gabon, Ivindo River Basin, Mivounghe River near Makokou.

Phenacogrammus cf. *interruptus* (Boulenger), AMNH 227592, 1, 44.0 mm; Central African Republic, Sangha, Lossi Creek.

Phenacogrammus major * (Boulenger), MNHN 1979-0279, 1, 71.9 mm; Cameroon, Sanaga River.

Phenacogrammus urotaenia * (Boulenger), MNHN 1985-0596, 1, 63.9 mm; Cameroon, Awout.

Phenacogrammus sp., USNM 176274, 2, 39.8–44.5 mm; aquarium specimens.

Rhabdalestes eburneensis * (Daget), USNM 193974, 2, 43.4–47.5 mm; Liberia, Gbarnga District, streams and tributaries to St. John's River.

Rhabdalestes loenbergi * (Svensson), USNM 310844, 1, 40.1 mm; Ghana, Dayi River, at Befi.

Rhabdalestes cf. *loenbergi* (Svensson), AMNH 228619, 1, 25.7 mm; Central African Republic, Chaine des Bongos, National Park of Manovo Gounda-St. Floris, Gounda River.

Rhabdalestes rhodesiensis * (Ricardo-Bertram), USNM 309583, 1, 39.4 mm; Zambia, Western Province, Kataba Stream on highway between Mongu and Senanga.

Rhabdalestes septentrionalis * (Boulenger), MNHN 1980-1608, 1, 46.7 mm, 1(R), 28.8 mm; Senegal, Gambie, Niereko, Wassadou.

Tricuspidalestes caeruleus * (Matthes), USNM 365952, 2, 29.6–29.9 mm; Congo, Ikela, Tshuapa River.

Virilia pabrensis * (Roman), USNM 229785, 2, 18.8–19.7 mm; Nigeria, pumping station at bridge over Rima River, Illela Road.

CHARACIDAE

Acestrorhynchus microlepis Eigenmann, USNM 225501, 1, 127.7 mm; Suriname, Nickerie District, Corantijn River.

Agoniates anchovia Eigenmann, MZUSP 20130, 1, 113. 7 mm; Brazil, Amazonas, Fonte Boa, Rio Solimões.

Agoniates halecinus Müller & Troschel, MZUSP 34332, 1, 121.6 mm; Brazil, Pará, Belo Monte, Rio Xingu.

Astyanax parahybae * Eigenmann, MZUSP 42870, 1, 65.8 mm; Brazil, São Paulo, Cunha, Córrego do Oriente (or do Jardim), along road to Campos de Cunha.

Attonitus bounites Vari & Ortega, USNM 349701, 1, 42.8 mm; Peru, Departamento de Puno, Provincia Carabaya, Zona Reservada Tambopata Candamo, Rio Candamo.

Brycon alburnus Böhlke, FMNH 57640, 1, 192.5 mm; Ecuador, Río Barranca Alta, Naranjito.

Brycon chagrensis (Kner and Steindachner), FMNH 12384, 1, 180.5 mm; Panama, upper Río Chagres.

Brycon coxeyi Fowler, MEPN 1531, 1, 130.6 mm; Ecuador, Provincia Zamora Chinchipe, Río Nangoritza.

Brycon dentex Günther, ANSP 75932, 1, 86.6 mm; Ecuador, Esmeraldas, Río Quininde near mouth, tributary of Río Esmeraldas.

Brycon falcatus * Müller & Troschel, MZUSP 38255, 1, 116.4 mm; Suriname, Nickerie District, stream 0.5 km from Mataway.

Brycon guatemalensis Regan, USNM 134395, 1, 155.3 mm; Guatemala, Río Hondo.

Brycon insignis Steindachner, MZUSP 42045, 1, 167.0 mm; Brazil, Rio Paraíba?

Brycon aff. *meeki* Eigenmann & Hildebrand, MEPN 3925, 1, 102.8 mm; Ecuador, Esmeraldas, Estero Limoneito, tributary of Río Maria, 5 km from Borbón.

Brycon melanopterus * (Cope), MZUSP 6626, 1, 113.7 mm; Brazil, Amazonas, Manacapuru, Igarapé of Lago Manacapuru.

Brycon oligolepis Regan, FMNH 10259, 1, 136.0 mm; Colombia, Barbacoas.

Brycon opalinus (Cuvier), MZUSP 42443, 1, 105.7 mm; Brazil, Minas Gerais, Olaria, Rio Pari.

Brycon pesu * Müller & Troschel, ANSP 175448, 1, 92.0 mm; Guyana, Siparuni VIII-2, Essequibo River.

Brycon striatulus (Kner & Steindachner), FMNH 56356, 1, 173.5 mm; Colombia, mouth of Río Dagua.

Bryconops alburnoides * Kner, MZUSP 34590, 1, 129.2 mm; Brazil, Pará, Cuminá, Rio Trombetas.

Catoprion mento (Cuvier), USNM 257547, 1, 58.6 mm; Venezuela, Apure, main channel of Río Cunaviche.

Charax pauciradiatus * (Günther), MZUSP 20552, 1, 69.1 mm; Brazil, Pará, Lago Timbiras, Rio Capim.

Cheirodon interruptus * (Jenyns), MZUSP 18894, 1, 40.0 mm; Brazil, Rio Grande do Sul, arroio in Belém Novo, near Porto Alegre.

Chilobrycon deuterodon Géry & de Rham, MUSM 5511, 1, 139.9 mm; Peru, Departamento Tumbes, Provincia Tumbes, Cabo Inga, Río Tumbes, at confluence with Quebrada Cazaderos.

Creagrutus magoi Vari & Harold, USNM 353863, 1, 42.2 mm; Venezuela, Bolivar, Río Chaviripa.

Hollandichthys multifasciatus Eigenmann & Norris, USNM 297983, 2 (A), 77.1–85.1 mm; Brazil, São Paulo, stream crossing SP-98, 94 km NW of Bertioga.

Lignobrycon myersi (Miranda-Ribeiro), MZUSP 40227, 1, 70.0 mm; Brazil, Bahia, Ilhéus, Fazenda Santa Luzia, Rio do Braço.

Piaractus mesopotamicus * (Holmberg), MZUSP 19584, 1, 57.0 mm; Brazil, Instituto de Pesca da SABESP (Pantanal Matogrossense).

Pseudochalceus sp., USNM 327402, 1 (A), 69.3 mm; Ecuador, Esmeraldas. Quebrada Cancare (1°13′N, 78°44′W).

Salminus hilarii * Valenciennes, MZUSP 45257, 1, 160.0 mm; Brazil, Minas Gerais, Rio São Francisco, Represa de Três Marias.

Serrasalmus rhombeus * (Linnaeus), MZUSP 56425, 1, 92.6 mm; Brazil, Amazonas, Rio Solimões, 31.5 km below Juruá.

Tetragonopterus argenteus * Cuvier, MZUSP 18798, 1, 49.0 mm; Brazil, Mato Grosso, Barão do Melgaço, Rio Cuiabá, mouth of Rio Croará.

Triportheus albus * Cope, MZUSP 56426, 1, 118.7 mm; Brazil, Goiás, Minaçu, Serra da Mesa.

Triportheus sp., USNM 258079, 2, 69.1–80.0 mm; Venezuela, Apure, Río Apure.

CRENUCHIDAE

Characidium sp., USNM 305486, 3, 32.3–44.8 mm; Bolivia, Departamento Chuquisaca, Río Camatindi, 8 km N of border of Departamento Tarija.

Crenuchus spilurus * Günther, MZUSP 20310, 1, 33.4 mm; Brazil, Pará, Igarapé Acú, Aveiro. USNM 270132, 4, 37.5–39.0 mm; Venezuela, Amazonas, Caño Loro, where crossed by road from San Carlos de Río Negro to Solano.

CTENOLUCIIDAE

Boulengerella lateristriga (Boulenger), USNM 270331, 1, 145 mm; Venezuela, Amazonas, Caño Urami system, just upstream of Santa Lucia.

Boulengerella sp. USNM 326304, 1, 24.1 mm; Venezuela, Barinas, Río Apure basin.

Ctenolucius beani (Fowler), USNM 293169 1, 143 mm; Panama, Darien, Río Tuira, 0.5 km above Boca de Cupe.

CURIMATIDAE

Cyphocharax abramoides (Kner), USNM 2679521, 110.3 mm; Brazil, Pará, Rio Xingu, Belo Monte.

DISTICHODONTIDAE

Xenocharax spilurus * Günther, USNM 227693, 1, 89.3 mm; Gabon, Lac Ezanga.

ERYTHRINIDAE

Hoplerythrinus unitaeniatus (Spix), USNM 225313, 1, 27.3 mm; Suriname, Nickerie District, small creek entering Corantijn River on E side, approximately 300 m N of Amotopo boat landing.

Hoplias cf. *malabaricus* (Bloch), USNM 226265, 2, 22.8–26.6 mm; Venezuela, Monagas, Río Orinoco, Barrancas. USNM 308914, 1, 19.0 mm; Brazil, Amazonas, Ilha da Marchantaria.

Hoplias microlepis * (Günther), MZUSP 48124, 1, 112.3 mm; Panama, Frijoles, Río Frijoles.

HEMIODONTIDAE

Hemiodus unimaculatus * (Bloch), MZUSP 32501, 1, 92.2 mm; Brazil, Pará, Rio Xingu, Belo Monte.

HEPSETIDAE

Hepsetus odoe * (Bloch), USNM 179331, 1, 107.0 mm; Liberia, St. Johns River, 0.5 mi (= 0.8 km) downstream of bridge at Sanniquellie District border. USNM 303782, 3, 18.7–41.0 mm; Cameroon, Manyu, Cross River system.

APPENDIX 2: CHARACTER STATE MATRIX

Character matrix of 200 characters for the species of the Alestidae and examined outgroup characiforms. Character numbers correspond to those in the text.

Taxon	Characters							
	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Alestidae								
Alestes								
baremoze	0010101000	0000010000	0010000000	1010010001	1010111020	0101101030	1111011110	00011000-1
dentex	0010101000	0000010000	0010000000	1010010001	1010111020	0101101030	1111011110	00011000-1
macrophthalmus	0000101000	0000010000	0010000010	1010010001	1010111020	0101101030	1111011110	00011000-1
Alestopetersius								
caudalis	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
hilgendorfi	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
smykalai	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
Arnoldichthys								
spilopterus	0010101000	0000000100	0000000000	1001121000	1000100020	0001101030	0000000000	01001010-0
Bathyaethiops								
caudomaculatus	0000001000	0010000000	1010000000	1000000000	1010110120	0101001040	1000010110	00001100-1
Brachypetersius								
altus	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
gabonensis	0000001000	0010000100	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
notospilus	0000101000	0010000100	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
Brycinus								
bimaculatus	0001101000	0000000000	0010000000	1010021000	1010110020	0101101020	1111011110	00011000-1
brevis	0001101000	0000000000	0010000000	1110021000	1010110020	0101101020	1111011110	00011000-1
carolinae	0000101000	0000000000	0010000000	1110021000	1010110020	0101101020	1111011110	00011000-1
imberi	0000101000	0000000000	0010000000	1110021000	1010110020	0101101020	1111011110	00011000-1
kingsleyae	0000101000	0000000000	0010000000	1010021000	1010110020	0101101020	1111011110	00011000-1
lateralis	0000101000	0000000000	0010000000	1010010000	1010110020	0101101020	1111011110	00011000-1
leuciscus	0000101000	0000000000	0010000000	1010010000	1010110020	0101101030	1111011110	00011000-1
macrolepidotus	0001101000	0000000000	0010000000	1010021000	1010110020	0101101010	1111011110	00011000-1
nurse	0000101000	0000000000	0010000000	1110021000	1010110020	0101101020	1111011110	00011000-1
sadleri	0000101000	0000000000	0010000000	1010010000	1010110020	0101101020	1111011110	00011000-1
Bryconaethiops								
boulengeri	0010101000	0000010100	0010000000	1010010000	1010111020	0101102030	1111011111	00011000-1
macrops	0010101000	0000010100	0010000000	1010010000	1010111020	0101102030	1111011111	00011000-1
microstoma	0010101000	0000010?00	0010000000	1010010000	1010111020	0101102030	1111011111	00011000-1
Bryconalestes								
derhami	0010101000	0010000000	0010000000	1000010000	1010110120	0101001030	1010011110	00001000-1
intermedius	0010101000	0010000000	0010000000	1000010000	1010110120	0101001030	1010011110	00001000-1
longipinnis	0010101000	0010000000	0010000000	1000010000	1010110120	0101001030	1010011110	00001000-1
Chalceus								
epakros	0000000001	0000000100	0100000000	1001121000	1000100020	0001102000	0000000000	0100100100
erythrurus	0000010000	0000000100	0100000000	1001110000	1000100020	0001102000	0000000000	0100100110
guaporensis	0000000001	0000000100	0100000000	1001121000	0000100020	0001102000	0000000000	0100100100
macrolepidotus	0000010001	0000000100	0100000000	1001110000	1000100020	0001102000	0000000000	0100100110
spilogyros	0000010001	0000000100	0100000000	1001110000	1000100020	0001102000	0000000000	0100100110

	Characters							
	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Clupeocharax								
schoutedeni	0000000000	00101-0010	-01001-000	1000010000	1010110100	0101000---	----000100	00000000-0
Duboisialestes								
tumbensis	0000001000	0010000000	1010000000	1000010000	1010110120	1101001040	1000010110	00001100-1
Hemmigrammopetersius								
barnardi	01--001000	0010000000	10100-1000	1000010000	1010110120	0101001140	1000000110	00001000-1
intermedius	01--001000	0010000000	10100-1000	1000010000	1010110120	0101001140	1000000110	00001000-1
Hydrocynus								
brevis	0000101100	00000000-1	0011000000	1010021011	0010111021	0110110---	----111110	111-1000-2
forskahlii	0000101100	00000000-1	0011000000	1010021011	0010111021	0110110---	----111110	111-1000-2
Ladigesia								
roloffi	01--001000	01-11-0000	1010000000	1000010000	1100110120	0101001140	1000010110	00001000-1
Lepidarchus								
adonis	11--0-0010	11-11-1-10	-01001-000	1000000100	1101000100	0001000---	----000100	00000000-0
Micralestes								
acutidens	01--001000	0010000000	1010000000	1000010000	1010110120	0101001030	1000011110	00001000-1
elongatus	01--001000	0010000000	1010000100	1000010000	1010110120	0101001030	1000011110	00001000-1
lualabae	01--001000	0010000000	1010000000	1000010000	1010110120	0101001030	1000011110	00101000-1
occidentalis	01--001000	0010000000	1010000000	1000010000	1010110120	0101001030	1000011110	00001000-1
sp.	01--001000	0010000000	1010000000	1000010000	1010110120	0101001030	1000011110	00001000-1
Nannopetersius								
ansorgii	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
Petersius								
conserialis	0000101000	0000000000	?010??????	1????200??	1?????1?20	0101001040	100001111?	000?1000-1
Phenacogrammus								
aurantiacus	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
major	0000001001	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
urotaenia	0000001000	0010000000	1010000000	1000010000	1010110120	0101001040	1000010110	00001100-1
Rhabdalestes								
eburneensis	01--001000	0010000000	1010000000	1000010000	1010110120	0101001030	1000011110	00001000-1
loenbergi	01--001000	0010000000	1010000000	1000010000	1010110120	0101001140	1000010110	00001000-1
rhodesiensis	01--001000	0010000000	1010000000	1000010000	1010110120	0101001140	1000010110	00001000-1
septentrionalis	0000001000	0010000000	1010000100	1000010000	1010110120	0101001130	1000010110	00001000-1
Tricuspidalestes								
caeruleus	0000000000	00101-0010	-01001-000	1000010000	1010110120	0101001140	?000000100	00000000-0
Virilia								
pabrensis	01--001000	0010000000	10100-2000	1000010000	1010110120	0101001140	1000010110	00001100-1

APPENDIX 2. *Continued*

	Characters							
Taxon	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890
Outgroup								
Astyanax parahybae	01--010000	0000000100	0110000000	0000000000	1000100020	0001001020	0000000000	0100100100
Brycon falcatus	0000110000	0000000100	0110100000	0000000000	1000100020	0001102001	1000000000	0100100100
Brycon pesu	0000110000	0000000100	0110100000	0000021000	1000100020	0001102001	1000000000	0100100100
Bryconops alburnoides	0000010000	0010000100	0110000000	0000000000	1000101020	0001001000	0000000000	01001000-0
Charax pauciradiatus	01--010000	00?0000100	0110000000	1000000010	1000100000	0001000---	----000000	0200100100
Cheirodon interruptus	01--010000	0000000?00	0110000000	0000010000	1000100020	0001000---	----000000	0100100100
Crenuchus spilurus	01--000000	0000000??0	00??000000	0000110000	1000100020	0001000---	----000000	01001000-0
Hemiodus unimaculatus	0000100000	0000000??0	00??000000	0000000001	1010000020	0001000---	----0?000?	0000000100
Hepsetus odoe	0000110000	0000000100	00??0??000	1000021010	0000000000	000100?---	----000000	0200100100
Hoplias microlepis	11--0-0000	0000000100	0010000000	1000121010	0000000000	0001000---	----000000	0200100100
Piaractus mesopotamicus	0000010000	0000000100	0110000001	1000000000	1000100020	0001101010	10000?0000	01001000-0
Salminus hilarii	0000110000	0000000100	0110100000	10000?0010	0000101000	0001001000	0000000000	0200100100
Serrasalmus rhombeus	0000010000	00?0000100	0110?00001	1000000010	100-100020	0001000---	----0?0000	01001000-?
Tetragonopterus argenteus	01--010000	0000000100	0110000000	0000000000	1000100020	0001001000	0000000000	0100100100
Triportheus albus	0000110000	0000000100	0110100000	0000000000	1000100020	0001102000	0010000000	0100100100
Xenocharax spilurus	0000000000	0000000??0	00??000000	1000000000	1000100010	0000001000	0000000000	0100000100

	Characters							
		1	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
	8888888889	9999999990	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Alestidae								
Alestes								
baremoze	0111010100	0110011011	0110001100	0110010001	0011300000	0000101111	1110110111	0001100000
dentex	0111010100	0110011011	0110001100	0110010001	0011300000	0000101111	1110110111	0001100000
macrophthalmus	0111010100	0110011011	0110001100	0110010000	0011300000	0000101110	0110010111	000?100000
Alestopetersius								
caudalis	01010000-0	0010011011	0110001100	0111010000	0101300000	1000110210	0101000110	0010011000
hilgendorfi	01010000-0	0010011011	0110001100	0111010000	0101300000	1000110210	0101000110	0010011000
smykalai	01010000-0	0010011011	0110001100	0111010000	0101300000	1000110210	0101000110	0010011000
Arnoldichthys								
spilopterus	01000010-0	0000001010	0110001100	0110100000	0101100000	0000001210	020000010?	0000000000
Bathyaethiops								
caudomaculatus	0101000110	0010011011	0100001100	0111010000	0101300001	1000110210	0?01000110	0010011000
Brachypetersius								
altus	0111000110	0010011011	0110001100	0111010000	0101300000	1000110210	0101000110	0010011000
gabonensis	0100000?10	0010011011	0110001100	0111010000	0101300001	1000110210	0100001110	0010000000
notospilus	0100000110	0010011011	0110001100	0111010000	0101300000	1000110210	0100000110	0010000000
Brycinus								
bimaculatus	0111010100	0110011011	0110001100	0110010000	0001300000	0000001110	0100001111	0000000000
brevis	0111010100	0110011011	0110101100	0110010000	0101300000	0000001110	0100001111	0000000000
carolinae	0111010100	0110011011	0110101100	0110010000	0001300000	0000001110	0100001111	0000000000
imberi	0111010100	0110011011	0110101100	0110010000	0001300000	0000001110	0100001111	0000000000
kingsleyae	0111010100	0110011011	0110001100	0110010000	0001300000	0000001110	0100001111	0000000000
lateralis	0111010100	0110011011	0110101100	0110010000	0001300000	0000001110	0100001111	0000000000
leuciscus	0111010100	0110011011	0110001100	0110010000	0001300000	0000001110	0100001111	0000000000
macrolepidotus	0111010100	0110011011	0110001100	0110010000	0111300000	0000101110	0100001111	0000000000
nurse	0111010100	0110011011	0110101100	0110010000	0001300000	0000001110	0100001111	0000000000
sadleri	0111010100	0110011011	0110101100	0110010000	0001300000	0000001110	0100001111	0000000000
Bryconaethiops								
boulengeri	0111010100	0110011011	0110001100	0111010000	0001300000	0000001100	0100000111	0000000000
macrops	0111010100	0110011011	0110001100	0110010000	0001300000	0000001100	0100000111	0000000000
microstoma	0111010100	0110011011	0110001100	0110010000	0001300000	0000001100	0100000111	0000000000
Bryconalestes								
derhami	0111010100	0010011011	0110001100	0111010000	0001300000	1000001210	0100001111	0000000000
intermedius	0111010110	0010011011	0110001100	0111010000	0001300000	1000001210	0100001111	0010000000
longipinnis	0111010100	0010011011	0110001100	0111010000	0001300000	1000001210	0100001111	0000000000
Chalceus								
epakros	1100001100	0000001010	0000001000	0110101000	0011100000	0000001110	0100000110	0000000000
erythrurus	1100001100	0000001010	0000001000	0110101000	0011100000	0000001110	01000001?0	0000000000
guaporensis	1100001100	0000001010	0000001000	0110101000	0011100000	0000001210	0100000110	0000000000

APPENDIX 2. *Continued*

Taxon	Characters							
		1	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
	8888888889	9999999990	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Chalceus								
macrolepidotus	1100001100	0000001010	0000001000	0110101000	0011100000	0000001110	0100000110	0000000000
spilogyros	1100001100	0000001010	0000001000	0110101000	0011100000	0000?01110	01000001?0	0000000000
Clupeocharax								
schoutedeni	01000000-1	-010010011	011001-100	0101010000	0101300001	1001-10210	0101000110	00--01101?
Duboisialestes								
tumbensis	01010000-0	0010011011	0110001100	0111010000	0101300000	1000110210	0101000110	0010011000
Hemmigrammopetersius								
barnardi	01010000-0	0010011011	0110001100	0111010000	0101300001	1001-01210	0100000111	0010001000
intermedius	01000000-0	0010011011	0110001100	0111010000	0101300000	0000101210	0100000111	0010000000
Hydrocynus								
brevis	01000000-0	1000001111	10?1001101	0110010001	1011300000	0000101110	0100000111	0000100000
forskahlii	01000000-0	1000001111	10?1001101	0110010001	1011300000	0000101110	0100000111	0001100000
Ladigesia								
roloffi	01000000-0	0010011011	010001-100	0211010000	0101311011	0000100210	0000000110	----011111
Lepidarchus								
adonis	00-00000-1	0001–1011	010001-100	0101101000	01012111?1	0100100210	0001000100	----011111
Micralestes								
acutidens	0101000110	0010111011	0110001100	0111010000	0101300000	1000101210	0100000111	0011000000
elongatus	0101000110	0010111011	0110001100	0111010000	0111300000	1000101210	0100000111	0010000000
lualabae	0101000110	0010111011	0110001100	0111010010	0111300000	0000101210	0100000111	0011000000
occidentalis	01010000-0	0010011011	0110001100	0111010000	0001300000	0000101210	0100000111	0011000000
sp.	0101000100	0010011011	0110001100	0111010000	0101300000	1000101210	0100000111	0011000000
Nannopetersius								
ansorgii	0101000110	0010011011	0110101100	0111010000	0101300000	1000110210	0101000110	0010011000
Petersius								
conserialis	01?10?00-0	0?10??????	?????011??	?1??01??00	000130000?	??00???110	?1000011?1	00000?0000
Phenacogrammus								
aurantiacus	0101000110	0010011011	0110101100	0111010000	0101300001	1000110210	0101000110	0010011000
major	0101000110	0010011011	0110101100	0101010000	0101300000	1000110210	0101000110	0010011000
urotaenia	0111000110	0010011011	0110101100	0111010000	0101300000	1000110210	0101000110	0010011000
Rhabdalestes								
eburneensis	01010000-0	0010011011	0110001100	0111010000	0101300000	1000101210	0100000111	0010000000
loenbergi	01010000-0	0010011011	0110001100	0111010000	0101300000	1000101210	0100000111	0010000000
rhodesiensis	01010000-0	0010011011	0110001100	0111010000	0101300001	1011-01210	0100000111	0010000000
septentrionalis	01010000-0	0010011011	0110001100	0111010000	0101300000	0000101210	0100000111	0010000000
Tricuspidalestes								
caeruleus	0100000110	0010010011	011001-100	0101010100	0101311001	1000100210	0101000110	11--011111
Virilia								
pabrensis	0100000110	0010011011	0110001100	0111010000	0101300001	1000101210	0100000111	0010000000

	Characters							
		1	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
	8888888889	9999999990	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Outgroup								
Astyanax								
parahybae	01001000-0	0000000000	0000000010	1100010000	0100210000	0000000210	0200000000	0010000000
Brycon								
falcatus	0100100110	0000000000	0000000010	0110100000	0000210000	0000101210	0200000010	0000000000
pesu	0100100100	0000000000	0000001010	0110100000	0000210000	0000101210	0200000010	0001000000
Bryconops								
alburnoides	01001000-0	0000000000	0000000010	0111000000	0001210000	0000101110	0200000010	0000000000
Charax								
pauciradiatus	01001000-0	0000000000	0000000010	1100000000	0101210000	0000000210	0200000000	0010000000
Cheirodon								
interruptus	01000000-0	0000000000	0000000010	1110010000	0100210000	0000100310	0201000000	0010001000
Crenuchus								
spilurus	01000000-0	0000000000	001001-000	0001100000	0100010000	0000-00110	0100000100	0010000000
Hemiodus								
unimaculatus	00-----0-0	0000000000	0000001100	0010101000	0000200000	0000001010	0200000110	0000000000
Hepsetus								
odoe	01000000-0	0000000000	0000001000	0000000000	0000410000	0011-01110	0100000100	000-011000
Hoplias								
microlepis	01000000-0	0000000000	000001-100	0010000000	0100010000	00001?-211	0100000000	0000000000
Piaractus								
mesopotamicus	0110000100	0000000000	0000000010	0010010000	0000010000	0000001210	0200000010	0000000000
Salminus								
hilarii	01000000-0	0000000000	0000000010	0110000000	0000210000	0000101210	0200000010	0000000000
Serrasalmus								
rhombeus	01000000-0	0000000000	0000000010	0110010000	0001010000	000000131-	0200000010	0010000000
Tetragonopterus								
argenteus	01001000-0	0000000000	0000000010	1100010000	0100210000	0000001210	0200000000	0000000000
Triportheus								
albus	0100100100	0010000000	0000000100	0111--0000	0011210000	0011-00311	1200000010	0000000000
Xenocharax								
spilurus	00-00000-0	0000000000	0010000000	0110010000	0000000000	0000-0000?	0200000000	000-000000

APPENDIX 2. *Continued*

Taxon	Characters			
	1111111111	1111111111	1111111111	1111111112
	6666666667	7777777778	8888888889	9999999990
	1234567890	1234567890	1234567890	1234567890
Alestidae				
Alestes				
baremoze	0001000000	0100000000	0000000000	1000011001
dentex	0001000000	0100000000	0000000000	?000011001
macrophthalmus	0001100000	0100000000	0000000000	1000011001
Alestopetersius				
caudalis	0001000000	0100001000	0000000100	1000000000
hilgendorfi	0001000000	0100001000	0000000100	1000000000
smykalai	0001000000	0100001000	0000000?00	?000000000
Arnoldichthys				
spilopterus	0000000111	1100000000	0000000010	1100000000
Bathyaethiops				
caudomaculatus	00--000000	0100000000	0000000100	?000000000
Brachypetersius				
altus	0001000000	0100000000	0000000100	1000000000
gabonensis	0001000000	1100000000	1000000100	1000000000
notospilus	0001000000	0100000000	1000000?00	1000000000
Brycinus				
bimaculatus	0001000100	1100000010	0000000000	1000010000
brevis	0001000100	1100000000	0000000000	?000010000
carolinae	0001000100	1100000010	0000000000	1000010000
imberi	0001000100	1100000010	0000000000	1000010000
kingsleyae	0001000100	1100000010	0000000000	1000010000
lateralis	0001000000	1110000010	0000000000	1000010000
leuciscus	0001000000	1110000010	0000000000	1000010000
macrolepidotus	0001000100	1100000000	0000000000	1000010000
nurse	0001000100	1100000010	0000000000	1000010000
sadleri	0001000000	1110000010	0000000000	1000000000
Bryconaethiops				
boulengeri	0000000000	0100001000	0000001000	1000011000
macrops	0000000000	0100001000	0000001000	1000011000
microstoma	0000000000	0110001000	0000001000	?000011000
Bryconalestes				
derhami	0001000000	0100001100	0000000010	1000000000
intermedius	0001000000	0100001100	0000000010	1000000000
longipinnis	0001000000	0100001100	0000000010	1000000000
Chalceus				
epakros	0001010111	1110000000	0000000000	0000000000
erythrurus	0001010111	1100000000	0000000000	0000000000
guaporensis	0001010111	1110000000	0000000000	0000000000
macrolepidotus	0001010111	1100000000	0000000000	0000000000

	Characters			
Taxon	1111111111 6666666667 1234567890	1111111111 7777777778 1234567890	1111111111 8888888889 1234567890	1111111112 9999999990 1234567890
Chalceus				
spilogyros	0001010111	1100000000	0000000000	0000000000
Clupeocharax				
schoutedeni	01--000000	0100000000	0000000100	1000000000
Duboisialestes				
tumbensis	00--000000	0100001000	0000000100	1000000000
Hemmigrammopetersius				
barnardi	01--000000	0111000000	0111010001	?000000000
intermedius	01--000000	0111000000	0111010001	?000000000
Hydrocynus				
brevis	0001000000	0100000000	0000000000	1000011000
forskahlii	0001000000	0100000000	0000000000	1000011000
Ladigesia				
roloffi	01--001-00	0101000000	0000100000	1000000000
Lepidarchus				
adonis	11----2---	--00000000	0000000100	1011100110
Micralestes				
acutidens	0001000000	1111100000	0000000000	1000000000
elongatus	0001000000	0111000000	0000000000	1000000000
lualabae	0001000000	0111000000	0000000000	1000000000
occidentalis	0001000000	1111100000	0000000000	1000000000
sp.	0001000000	0111000000	0000000000	?000000000
Nannopetersius				
ansorgii	0001000000	0100011101	0000000100	1000000000
Petersius				
conserialis	?001000000	0100000010	00000??000	10000?0000
Phenacogrammus				
aurantiacus	01--000000	0100001000	0000000100	1000000000
major	01--000000	0100001000	0000000100	1000000000
urotaenia	01--000000	0100001000	0000000100	1000000000
Rhabdalestes				
eburneensis	0001000000	0111000000	0111010001	1000000000
loenbergi	0001000000	0111000000	0111010001	1000000000
rhodesiensis	0001000000	0111000000	0111010001	1000000000
septentrionalis	0001000000	0111000000	011???000?	1000000000
Tricuspidalestes				
caeruleus	01--000000	0100000000	0000000100	1000000000
Virilia				
pabrensis	01--000000	0111000000	0121010001	1000000000

APPENDIX 2. *Continued*

	Characters			
Taxon	1111111111 6666666667 1234567890	1111111111 7777777778 1234567890	1111111111 8888888889 1234567890	1111111112 9999999990 1234567890
Outgroup				
Astyanax				
parahybae	0000000000	0010000000	0000000000	0000000000
Brycon				
falcatus	0010100000	0000000000	0000000000	0000010000
pesu	0010000100	0000000000	0000000000	0000010000
Bryconops				
alburnoides	0000000000	0010000000	0000000000	0000001000
Charax				
pauciradiatus	0000000000	0000000000	0000000000	0000000010
Cheirodon				
interruptus	01--000000	0000000000	0000000000	0000000010
Crenuchus				
spilurus	01--000000	1000000000	0000000000	0000000000
Hemiodus				
unimaculatus	0000000000	0000000000	0000000000	0000001000
Hepsetus				
odoe	0000000100	0100000000	0000000000	0000000000
Hoplias				
microlepis	0000000100	1100000000	0000000000	0000000000
Piaractus				
mesopotamicus	0000000000	0000000000	0000000000	0000000000
Salminus				
hilarii	0010000000	0000000000	0000000000	0000010000
Serrasalmus				
rhombeus	0000000000	0000000000	0000000000	0000000000
Tetragonopterus				
argenteus	0000000000	0000000000	0000000000	0000000000
Triportheus				
albus	0010000000	0100000000	0000000000	0000000000
Xenocharax				
spilurus	0000000000	0-00000000	0000000000	0000010000