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The Neotropical Fish Subfamily Cynodontinae (Teleostei: Ostariophysi: Characiformes): A Phylogenetic Study and a Revision of *Cynodon* and *Rhaphiodon*

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ABSTRACT

Osteological features of cynodontine species and other characiforms were examined in order to investigate the monophyly of the Cynodontinae and the relationships among its species. A number of derived characters corroborated the hypothesis that the Cynodontinae and its three included genera *Cynodon*, *Rhaphiodon*, and *Hydrolycus* are monophyletic. *Hydrolycus armatus* is the sister group of *H. tatauaia*; *H. scomberoides* is the sister group of the clade formed by the latter two species; and *H. wallacei* is the sister group of the clade formed by *H. armatus*, *H. tatauaia*, and *H. scomberoides*. *Rhaphiodon vulpinus* is the sister group to *Cynodon*, and together they are the sister group to the clade formed by *Hydrolycus* species.

Three *Cynodon* Agassiz, 1829, species are diagnosed. *Cynodon gibbus* Agassiz, 1829, occurs in the Rio Amazonas and Río Orinoco basins, and the Rupununi River, Guyana. *Cynodon meionactis* Géry et al., 1999, occurs in the upper Maroni River, French Guiana, and *C. septenarius*, new species, occurs in the Rio Amazonas and its tributaries between the mouths of the Rios Içá and Tapajós, in the Essequibo and Demerara rivers in Guyana, and in the upper portions of the Río Orinoco basin.

Rhaphiodon Agassiz, 1829, is monotypic with *R. vulpinus* being the most widely distributed cynodontine, its distribution extending to the Río Paraná-Paraguay, and Río Uruguay systems.

INTRODUCTION

Fishes of the Cynodontinae Eigenmann, 1907, comprise a group of very distinctive Neotropical characiforms easily recognized by the oblique mouth and highly developed pair of dentary canines in all members of the subfamily. These predators can reach considerable size: *Hydrolycus* species achieve at least 650 mm SL. Although not much valued as food, some species may have some importance in subsistence and commercial fisheries (Mendes dos Santos et al., 1984; Taphorn, 1992).

Cynodontines live in mid- and surface waters of rivers, lakes, and flooded forests in all water types, throughout the Río Orinoco and Rio Amazonas basins, and in the rivers of the Atlantic slopes of the Guianas (fig. 1). *Rhaphiodon vulpinus* ranges southward to the Paraná-Paraguay and Uruguay basins, and *Cynodon gibbus* eastward to the Rio Pindaré in the state of Maranhão, northeastern

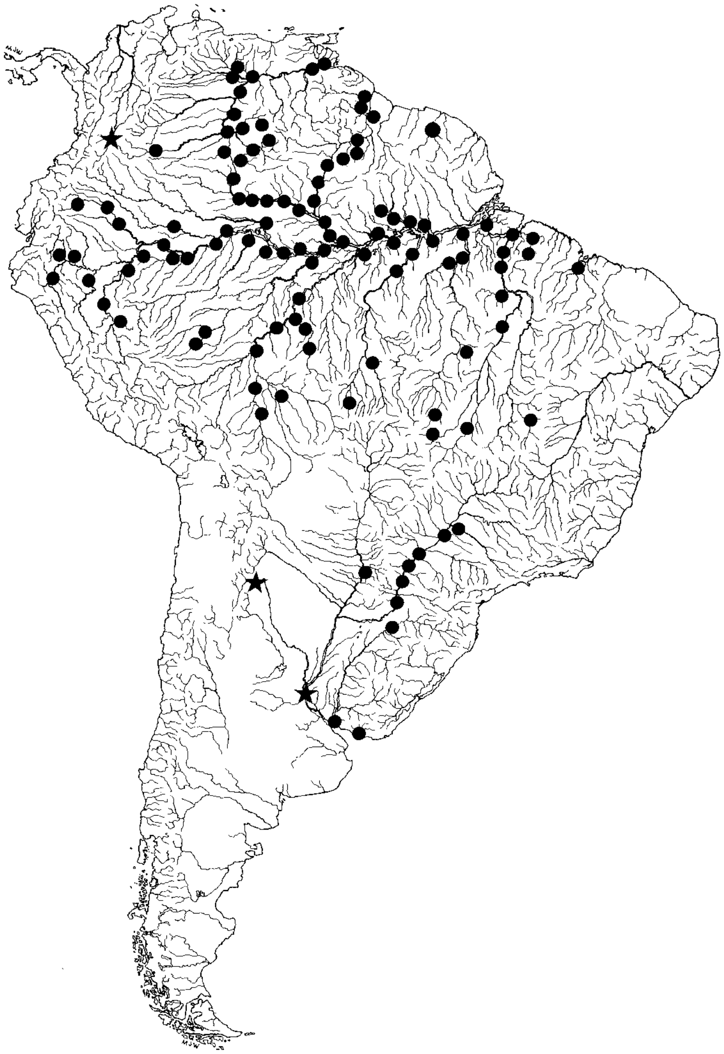

Fig. 1. Map of South America showing geographic distribution of the Cynodontinae; recent species (filled in circles), and fossils (stars). Some symbols represent more than one lot of specimens or locality.

Brazil. No cynodontine has been reported in the Rio São Francisco basin or in the remaining Atlantic coastal drainages south of the Rio Parnaíba in northeastern Brazil. Recent cynodontines are unknown also in the trans-Andean Pacific and Caribbean drainages. Lundberg (1997), however, reported fossil teeth, assigned by him to *Hydrolycus*, from the Miocene La Venta fauna, located in the present Río Magdalena valley of western Colombia. Additional fossil teeth assigned to the Cynodontinae come from the Middle Miocene Anta Formation at the Quebrada de La Yesera, Salta, Argentina (Cione and Casciotta, 1995), and from late Miocene fluvial beds near the city of Paraná, Entre Ríos, Argentina (Cione and Casciotta, 1997) (fig. 1), areas outside the known range of recent cynodontines.

Recognition of the Cynodontinae including *Hydrolycus*, *Cynodon*, and *Rhaphiodon* as a natural group has never been debated, probably as a consequence of the similarities in body shape and general external features shared by all species, combined with their very distinctive appearance relative to other characiforms. Eigenmann (1909: 256) first presented distinguishing features of the Cynodontinae in a key to the family Characidae and later (Eigenmann, 1910: 444) listed the genera he included in that family. Subsequent taxonomic treatments have followed what was proposed by Eigenmann.

The first attempt to diagnose the Cynodontinae based on shared derived features was made by Howes (1976) who focused on features of the cranial musculature. More recently, Buckup and Petry (1994) examined extra-oral series of teeth in the larvae of *Hydrolycus* and *Cynodon*, a feature previously reported only for *Rhaphiodon vulpinus* (Géry and Poivre, 1979), and proposed this feature as a synapomorphy for the Cynodontinae. Lucena and Menezes (1998) proposed six additional characters supporting the monophyly of the subfamily. However, no detailed osteological study has been conducted in an attempt to further corroborate the monophyly of the Cynodontinae and to investigate the hypothesis of the monophyly of *Cynodon*, *Hydrolycus*, and *Rhaphiodon* in conjuction with a study of cynodontine intrarelationships.

The cynodontine genus *Hydrolycus* Müller and Troschel, 1844, has been recently revised (Toledo-Piza et al., 1999) and two new species described, increasing the number of recognized *Hydrolycus* species to four. In the present study, the genera *Cynodon* and *Rhaphiodon* are revised and a new *Cynodon* species is described. As a consequence of the revision of *Hydrolycus*, *Cynodon*, and *Rhaphiodon* eight cynodontine species are recognized compared to the four previously considered valid in the subfamily.

The goals of the present study are: (1) to further examine the hypothesis of the monophyly of the Cynodontinae; (2) to resolve cynodontine intrarelationships and determine whether *Hydrolycus*, *Cynodon*, and *Rhaphiodon* are monophyletic; (3) to determine the recognizable species of *Cynodon* and *Rhaphiodon*, and estimate their geographic distributions.

MATERIALS AND METHODS

PHYLOGENETIC PROCEDURES: The study of phylogenetic relationships of the Cynodontinae was based on examination of morphological features. Osteological characters are defined and described under Character Description and Analysis and summarized in appendix 1. Osteological preparations were cleared and counterstained for cartilage and bone using a modification of the method outlined by Taylor and Van Dyke (1985). Supplemental sources of osteological data include previously cleared-and-stained specimens, (with some stained solely with alizarin), and dry skeletons.

Species listed below followed by an asterisk (*) provided the morphological basis for estimating phylogenetic relationships within the Cynodontinae, and were also used as the basis for illustrations or specific observations noted in the text. Justification for choice of these taxa is provided below. The remaining species listed provided additional observations on characiform osteological characters. Whenever a character is mentioned in the text for an outgroup genus without a species cited, it refers to species listed below, and does not imply that the character is present in all species of the genus.

The species name is followed by institutional catalog number, the number and standard length (SL) of specimens. Head length (HL) is listed for some skeletal preparations. Specimens are cleared and counterstained unless indicated as being dry skeletons (S):

Cynodontinae:

Cynodon gibbus (*): LACM 43295-89, 1, 102.4 mm SL; MZUSP 32857, 1, 149.9 mm SL; MZUSP 32593, 1, 179.0 mm SL.

Cynodon septenarius (*): MZUSP 5415, 1, 174 mm SL; MZUSP 32585, 1, 170.0 mm SL.

Cynodon sp. (*): AMNH 93079, 1, 240 mm SL (S); AMNH 93103, 1, 47.8 mm HL (S); AMNH 32485, 1, 35 mm SL.

Hydrolycus armatus (*): AMNH 55904, 1, 63.2 mm HL (S); AMNH 91342, 1, 450 mm SL (S); AMNH 91343, 1, 124.7 mm HL (S); AMNH 91344, 1, 400 mm SL (S); LACM 43295-36, 1, 135.9 mm SL; MZUSP 32607, 2, 151.0–200 mm SL.

Hydrolycus wallacei (*): MZUSP 32638, 2, 152.0–163.0 mm SL.

Hydrolycus tatauaia (*): MZUSP 32630, 1, 151.0 mm SL; MZUSP 32632, 1, 257 mm SL.

Hydrolycus scomberoides (*): AMNH 40087, 1, 241.0 mm SL (S); MZUSP 26177, 1, 120.6 mm SL; MZUSP 32093, 1, 143.4 mm SL.

Hydrolycus sp. (*H. armatus* or *Hydrolycus tatauaia*): AMNH 56518, 1, 42 mm HL (S); AMNH 56540, 1 (S); AMNH 56541 1(S); AMNH 40122, 3, 95.2–130.1 mm HL (S); AMNH 40048, 1, 117.7 mm HL (S).

Rhaphiodon vulpinus (*): BMNH 1935.6.4: 33-39, 1, 96.8 mm SL; BMNH uncataloged, 1, 114.5 mm SL; LACM 43295-64, 138.4 mm SL; MZUSP 32812, 1, 191 mm SL; USNM 231549, 5, 41.7–50.1 mm SL.

Anostomidae:
Anostomus anostomus: AMNH 43354, 3, 41.4–48.9 mm SL.
Laemolyta taeniata: AMNH 39992, 1, 155.4 mm SL.

Characidae:
Acanthocharax microlepis (*): BMNH 1971.10.17:1444–1460, 1, 68.3 mm SL.
Acestrocephalus sardina (*): AMNH 74567, 2, 63.1–63.2 mm SL; MZUSP 29241, 1, 55.0 mm SL.
Acestrorhynchus falcatus: (*) MZUSP 4572–91, 1, 111.1 mm SL; AMNH 43418, 1, 140.0 mm SL.
Acestrorhynchus falcirostris (*): MZUSP 20592, 1, 115.2 mm SL.
Acestrorhynchus heterolepis: AMNH 93088, 1, 80.9 mm HL (S).
Acestrorhynchus lacustris (*): MZUSP 27893, 1, 129.7 mm SL.
Acestrorhynchus microlepis (*): AMNH 40106, 1, 80.0 mm SL.
Acestrorhynchus nasutus (*): MZUSP 29268, 1, 68.2 mm SL.
Agoniates sp. (*): MZUSP 34332, 1, 121.6 mm SL.
Brycon falcatus (*): AMNH 54976, 2, 94.7–96.9 mm SL.
Chalceus macrolepidotus: AMNH 40059, 2, 69.0–108.3 mm SL.
Charax pauciradiatus (*) MZUSP 20552, 1, 69.1 mm SL.
Galeocharax knerii (*): MZUSP 10542–55, 1, 108.5 mm SL.
Gilbertolus atratoensis (*): BMNH 1924.3.346–48, 1, 91.9 mm SL.
Gnathocharax sp. (*): MZUSP 6819, 1, 26.3 mm SL.
Heterocharax sp. (*): MZUSP 29226, 1, 31.6 mm SL.
Hoplocharax goethei (*): MZUSP 7136–7263, 1, 27.1 mm SL.
Hydrocynus sp.(*): AMNH 88854, 1, 112.5 mm SL (S); USNM 231542, 3, 42.1–63.0 mm SL.
Iguanodectes spilurus: AMNH 40033, 2, 46.5–52.4 mm SL.
Lonchogenys ilisha (*): MZUSP 29265, 1, 48 mm SL.
Mylossoma sp.: AMNH 77395, 1, 89.0 mm SL.
Oligosarcus argenteus (*): MZUSP 37257, 1, 65.7 mm SL.
Roeboexodon gyanensis (*): MZUSP 36587, 1, 45.1 mm SL.
Roeboides sp. (*): AMNH 40198, 2, 51.6 –64.9 mm SL.
Roeboides paranensis: MZUSP 19830, 1, 50.2 mm SL.
Roestes ogilviei (*): MZUSP 9702, 1, 90.7 mm SL.
Roestes molossus (*): INPA 11068, 1, 95.3 mm SL.
Serrasalmus sp.: AMNH 77781, 1, 49.1 mm SL.
Triportheus sp. AMNH 73052, 1, 65.1 mm SL.

Chilodontidae:
Caenotropus maculosus: AMNH 14338, 2, 55.0–69.5 mm SL.

Ctenoluciidae:
Boulengerella cuvieri (*): MZUSP 24162, 1, 137.8 mm SL.
Ctenolucius beani (*): AMNH 11244, 1, 133.6 mm SL.

Distichodontidae:
Distichodus fasciolatus: AMNH 5888, 1, 51.3 mm SL.
Ichthyborus besse: AMNH 57429, 1, 75.0 mm SL.
Ichthyborus quadrilineatus: AMNH 57408, 1, 106.7 mm SL.
Xenocharax spilurus (*): MRAC 80-51-P-610-614, 1, 93.0 mm SL.

Erythrinidae:
Erythrinus erythrinus (*): MZUSP 34350, 1, 67.6 mm SL.
Hoplias cf. *malabaricus* (*): MZUSP 32372, 1, 86.8 mm SL.
Hoplerythrinus unitaeniatus (*): MZUSP 34347, 1, 116.5 mm SL.

Gasteropelecidae:
Gasteropelecus sternicla (*): AMNH 57446, 3, 31.6–39.0 mm SL.
Carnegiella strigata (*): AMNH 74606 1, 34.1 mm SL.

Hepsetidae:
Hepsetus odoe (*): USNM 303782, 2, 38.2–45.6 mm SL; USNM 304407, 1, 124.3 mm SL.

Lebiasinidae:
Lebiasina bimaculata (*): AMNH 5360, 1, 57.6 mm SL.

Pyrrhulina sp. (*): MZUSP 23134, 1, 36.7 mm SL.
Piabucina uruyensis: AMNH 91110, 3, 33.5–63.9 mm SL.

Prochilodontidae:
Prochilodus rubrotaeniatus: AMNH 54845, 1, 86.8 mm SL.

Hemiodontidae:
Hemiodus sp.: AMNH 40105, 3, 57.1–67.9 mm SL.

Hypotheses of relationships were proposed using the cladistic or phylogenetic method first formalized by Hennig (1950, 1966). Detailed explanations about cladistic principles and their operational aspects are available from many sources (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981; Wiley et al., 1991; Swofford et al., 1996).

Parsimony analysis was employed to generate hypotheses of phylogenetic relationships and of character state transformations using the PAUP computer program, version 3.1.1 by D. L. Swofford (1993), and Hennig86 by Farris (1988) associated with Tree Gardener, version 2.2 (Ramos, 1997). The small number of taxa in the analysis permitted the use of the exhaustive search option, which evaluates every possible combination of the taxa in the search for the most parsimonious tree. Autapomorphies were not included in computation of tree statistics.

Multistate characters (3, 4, 18, 20, 22, 41, 45, 46, 51, 62, and 65) were first analyzed as unordered. Then those multistate characters having states that could be ordered sequentially according to their divergence from that putatively primitive condition were analyzed as ordered (3, 4, 18, 20, 41, and 51).

No specific optimization method, i.e., ‘‘accelerated transformation optimization’’ (ACCTRAN) or the ‘‘delayed transformation optimization’’ (DELTRAN), was used to eliminate equally parsimonious alternative hypotheses of character state transformations on a cladogram. Tree manipulations and diagnostics were done with the help of MacClade computer program, version 3 by Maddison and Maddison (1992), and Clados, version 1.2 by Nixon (1992).

Missing entries in the data matrix (represented by ‘‘?’’ in appendix 1) were employed in the present study for two distinct situations: (1) character state not checked due to lack of study material (only one instance represented by character 15 in *Rhaphiodon vulpinus*); and (2) character state inapplicable (coded in some taxa for characters 6, 7, 12, 20, 21, 29, 39, and 65). In order to understand the impact of characters represented by missing entries in the resulting phylogenetic hypothesis, various analysis were performed that included and excluded all of those characters or combinations of them.

Character polarity was determined by outgroup comparison and in one instance (character 39) by using ontogenetic information. Thirty-three characiform outgroup taxa listed above (indicated by stars following the species name) constituted the focus of these comparisons. These taxa were previously proposed as being related to cynodontines either as sister groups or at higher levels of inclusiveness based on the possession of some common features. In addition to the seven cynodontine species examined in the present study those outgroup taxa were checked for all examined characters (*Cynodon meionactis* was not included in the present phylogenetic analysis, see discussion under Comments on *Cynodon meionactis*, following the key to *Cynodon* species, below). In addition to these taxa, a number of other characiforms not directly related to cynodontines (listed above, without asterisk following species names) were examined to assess character distribution and variation within characiforms. The occurrence of character states hypothesized as derived for cynodontines in these more distantly related outgroups is discussed under the appropriate characters. Outgroups presented in the matrix (appendix 1) were restricted to *Roestes*, *Gilbertolus*, and *Acestrorhynchus*, hypothesized to be the closest relatives of cynodontines (Lucena and Menezes, 1998), plus a hypothetical ancestor that summarizes the observations made for remaining outgroup taxa. Justification for outgroup choice is presented under Historical Overview and Comments on Cynodontine Relationships with Other Characiforms.

The Character Description and Analysis section includes a description of each character, its variation within cynodontines, its occurrence in characiform outgroups, and its optimization in the resulting phylogenetic hypothesis. In a few instances characters were observed that show variation within cynodontines and could provide information on cynodontine intrarelationships; however, difficulty in the interpretation of their states complicated the proposition of hypothesis of homology (see Phylogenetic reconstruction for a list of those characters). Various analyses were performed—including, excluding, or testing different codings of such characters—to study their impact on the resulting phylogenetic hypothesis. Problematic characters mentioned above, characters pertinent to the question of cynodontine relationships to other characiforms, and autapomorphic characters are not included in the computation of tree statistics (44 out of the 69 characters were included in the computation of tree statistics), but are included in the Character Description and Analysis section. Some of the characters studied are concerned with the question of cynodontine relationships to other characiforms. Although the question of cynodontine relationships to other characiforms did not constitute the primary objective of the present study, discussions of these characters should be considered pertinent to the present analysis.

TERMINOLOGY: Osteological terminology follows Weitzman (1962) with a few modifications proposed by various authors. Vomer is substituted for prevomer, epioccipital for epiotic, posterior ceratohyal for epihyal; anterior ceratohyal for ceratohyal, and mesethmoid for ethmoid.

SPECIES ACCOUNTS: The taxonomic section of the study is based on analysis of meristic and morphometric characters. Counts and measurements were made on the left side of the specimens, except when the structure being measured or counted was recognizably abnormal or damaged, in which case corresponding data were taken from the right side. Measurements were taken with calipers and data recorded to tenths of a millimeter for distances under 150 mm and to a millimeter for larger distances. All measurements were taken point to point, i.e., not orthogonal to the main body axis. Vertebral counts and pterygiophore insertion relative to neural and hemal spines were examined from radiographs. Counts and measurements are presented in tables and/or in the text and follow Fink and Weitzman (1974) except as noted, with some additions given below: body depth at dorsal-fin origin—immediately anterior to dorsal-fin origin; body depth at pelvic-fin origin—immediately anterior to insertion of the unbranched pelvic-fin ray; dorsal-fin origin to caudal-fin origin—to center posterior termination of the hypural fan (where the principal caudal-fin rays attach to the hypural bones); dorsal-fin origin to adipose-fin origin; pectoral-fin origin to anal-fin origin; dorsal-fin base and anal-fin base—between anterior and posterior termination of fin-ray bases; interorbital width—between borders of frontal bones at anterior tip of supraorbitals; postorbital length—from posterior bony orbital margin to posteriormost termination of opercular bone (without including the fleshy opercular flap); upper jaw length—from tip of snout to distal tip of maxilla; dentary canine length—from base to tip of largest canine tooth in dentary; scales along lateral-line series—counted as longitudinal scale row along perforated lateral-line scales, including those on base of caudal-fin; scale rows below lateral-line—number of longitudinal rows of scales counted from anus to that scale just ventral to (and not including) the perforated lateral scale row. This form of counting scales below the lateral series is found to be more replicable than the traditional form, in which the count is made to the origin of the anal fin. Cynodontines have the scales below the lateral series obliquely arranged, becoming smaller and irregularly organized toward the region of the anal fin, rendering the count inaccurate when taken at the level of the anal-fin origin. Counts taken at the level of the pelvic-fin origin also showed a large degree of inaccuracy. Counting scale rows below the lateral series at the level of the anus, slightly in advance of the anal-fin origin, yielded more replicable counts although some inaccuracy remained. For gill-raker count the limit between the anterior limit of the ceratobranchial and posterior end of the hypobranchial was set at the anterior gill raker in the lower limb of the first gill arch which has its basal portion in contact with the dorsal end of the gill filaments of the same gill arch. Anterior to this point there is a gap between the basal portion of the gill raker and dorsal end of the gill filaments, so that they are not in contact but are separated by skin. When examined in cleared and stained specimens, this point largely corresponds to the limit between the cerato- and hypobranchial of the first gill arch. This system of counting gill rakers is found to be more replicable than counting all gill rakers on the lower limb of the first gill arch (i.e., on both ceratobranchial and hypobranchial) because the anterior rakers could not be easily reached without damage to the specimen (particularly large ones), and rakers on the hypobranchial tend to be smaller and fused to one another to different extents, making the counts susceptible to inaccuracy; vertebral counts: vertebrae incorporated into the Weberian apparatus were counted as four elements and the fused PU1 + U1 was considered a single bone. Measurements of anal-fin length were not included because the tips of the anterior fin rays were damaged in the majority of specimens.

In tables and text, subunits of the head are presented as proportions of head length. Head length and measurements of body parts are given as proportions of standard length. Numbers in parentheses following a particular vertebral count are the number of radiographed specimens with that count. In counts of fin rays, the unbranched fin rays are indicated by lower case roman numerals, and the branched fin rays as arabic numerals.

The Material Examined section of each species account is arranged in the following sequence: total number of specimens examined, and in parentheses, the number of specimens from which counts and measurements were taken, and their range of standard lengths (in mm). The lots are grouped according to country and, within each country, the state or department, followed by institutional abbreviation, catalog number, number of specimens in the lot and their range of standard lengths (the latter two in parentheses), and specific locality data. Institutional abbreviations follow Leviton et al. (1985) and Leviton and Gibbs (1988).

In the key to the species of *Cynodon* below, information on *C. meionactis* is provided by Géry et al (1999), and some of it was recorded differently from the morphometric data in the present study (e.g., orbital diameter) (see Comments on *C. meionactis*, below).

HISTORICAL OVERVIEW AND COMMENTS ON CYNODONTINE RELATIONSHIPS WITH OTHER CHARACIFORMS

Prior to the study of Howes (1976), no author made definitive comments about the relationships of the Cynodontinae. Their ideas about relationships of the group can be inferred only from the classifications they proposed but the extent to which these classifications were intended to reflect close relationships among these groups is unclear. Günther (1864) placed the then-known cynodontines in his suprageneric group Hydrocyonina which also included *Anacyrtus* (= *Charax*), *Hystricodon* (= *Exodon*), *Salminus*, *Hydrocyon* (= *Hydrocynus*), *Sarcodaces* (= *Hepsetus*), *Oligosarcus*, *Xiphorhamphus* (= *Acestrorhynchus*) and *Xiphostoma* (= *Boulengerella*). Regan (1911: 16) included cynodontines within his Characidae together with Erythrininae (*Hoplias*, *Erythrinus*), Lebiasininae (*Lebiasina*, *Piabucina*), Acestrorhamphinae (*Oligosarcus*, *Acestrorhamphus* [= *Oligosarcus*], *Acestrorhynchus*), Sarcodacinae (*Sarcodaces* = *Hepsetus*), Characinae (including many genera assigned to the Characinae, sensu Weitzman, 1962, as well as the African characids), Serrasalmoninae (*Serrasalmo*, *Myletes*, *Pygocentrus*, *Mylesinus*, *Pygopristis*), and Hydrocyoninae (*Hydrocyon*). In his phylogeny of South American characids, Eigenmann (1917: 39) stated that ‘‘another line diverging from the Cheirodontinae has given rise to the Salmininae, Characinae, Acestrorhamphinae, and Cynodontinae, and ultimately the Hydrocyninae.’’ Gregory and Conrad (1938: 321) restricted the array of groups that they considered closely related to the Cynodontinae. They defined a subgroup (their Sarcodacinae) within Regan’s Characidae in which they include Regan’s Sarcodacinae, Acestrorhamphinae, Cynodontinae as well as Xyphostomatidae (*Xyphocharax* [= *Roestes*] and *Luciocharax* [= *Ctenolucius*]). Greenwood et al. (1966: 395) excluded cynodontines from the family Characidae and placed them in their own family, the Cynodontidae. However, no further information was given concerning their relationships with other characiforms.

Géry and Vu-Tân-Tuê (1963: 244) proposed that *Roestes* was closely related to cynodontines. The study of Howes (1976) was, however, the first to present evidence based on shared derived features to support this hypothesis.

A brief comment on the status of the genus *Roestes* is necessary. In a recent review of *Roestes* Günther, 1864, Menezes and Lucena (1998) resurrected the genus *Gilbertolus* Eigenmann, in Eigenmann and Ogle, 1907 (previously considered a junior synonym of *Roestes* by Menezes, 1974) to include *G. alatus*, *G. atratoensis*, and *G. maracaboensis*, all species from the western versant of the Andes. The genus *Roestes* was restricted to those species occurring east of the Andes and includes *R. ogilviei*, *R. molossus*, and *R. itupiranga*. The two genera were diagnosed as a monophyletic unit referred to as the Roestinae. Howes (1976) followed Menezes (1974) in including the species he examined (*alatus*) in *Roestes*. Herein, following Menezes and Lucena (1998), *Gilbertolus* is employed for the species occurring west of the Andes. Therefore, the species included by Howes (1976) in *Roestes* is herein assigned to *Gilbertolus*. Specimens of the species examined by that author were reexamined in the present study and reidentified as *G. atratoensis*.

Howes (1976) proposed seven myological characters that according to him are unique to *Gilbertolus* and cynodontines. Lucena (1993) reevaluated the phylogenetic significance of some of the characters proposed by Howes as supporting a hypothesis of relationships between cynodontines and *Gilbertolus* and proposed another hypothesis in which *Acestrorhynchus* is the sister group to the Cynodontinae. According to Lucena (1993), *Roestes* (based on the examination of *R. ogilviei*) was hypothesized to be the sister group to the group formed by the Heterocharacini (sensu Géry, 1966) and *Gnathocharax*. It is important to mention that Lucena's study was not intended to critically examine the question of cynodontine relationships, but rather to phylogenetically study the family Characidae. Due to the extremely large number of taxa in that family, the author had to limit the total number of taxa examined. The source of the conflict between Howes's (1976) and Lucena's (1993) hypotheses can be partially explained by interspecific variation in the characters pertinent to the hypothesis of relationships between *Roestes*, *Gilbertolus*, and cynodontines in the species examined by these authors.

Lucena and Menezes (1998) conducted a phylogenetic analysis with the objective of investigating the hypothesis of monophyly of *Roestes* and *Gilbertolus*, and reevaluating the hypothesis of their relationships with other characiforms. The two genera were hypothesized to form a monophyletic group referred to as the Roestinae, which was proposed to be the sister group to the Cynodontinae, on the basis of four synapomorphies. In addition, five derived features are shared between the Cynodontinae and *Gilbertolus*, with the primitive condition found in *Roestes*. Under a hypothesis of the monophyly of *Roestes* and *Gilbertolus*, these features have ambiguous interpretations being hypothesized either as synapomorphic for the clade formed by the Roestinae and Cynodontinae with a reversal to the primitive condition in *Roestes*, or as having independent origins in *Gilbertolus* and the Cynodontinae. In the same study Lucena and Menezes (1998) proposed *Acestrorhynchus* as the sister group to the clade formed by the Roestinae and Cynodontinae on the basis of four synapomorphies. In addition, three derived features present in *Acestrorhynchus* and in the Cynodontinae have ambiguous interpretations, being hypothesized either as synapomorphic for the clade formed by *Acestrorhynchus*, the Roestinae, and Cynodontinae with a reversal to the primitive condition in the Roestinae, or as having independent origins in *Acestrorhynchus* and the Cynodontinae. Only *Roestes* (and not *Gilbertolus*) was included in Lucena's (1993) study and the morphological differences between *Roestes* and *Gilbertolus* had yet to be evaluated within a phylogenetic framework. Those factors in combination with the fact that *Acestrorhynchus* and the Cynodontinae share derived features, may account for the results obtained by Lucena (1993).

The Cynodontinae is a highly derived

group characterized by numerous features unique to this assemblage within characiforms (see synapomorphy list under Monophyly of the Cynodontinae below), and finding shared derived characters common to cynodontines and other characiforms has proved to be a difficult task. Furthermore, the systematics of most of the genera traditionally assigned to the Characinae sensu Eigenmann (1910) is poorly known, complicating the interpretation of the phylogenetic significance of many characters. Therefore, the recent study by Lucena and Menezes (1998), focusing on the elucidation of the phylogenetic affinities of *Roestes* + *Gilbertolus* represents a major contribution toward our understanding of the systematics of these taxa. Further testing of the hypothesis of cynodontine relationships, including a better understanding of the significance of the characters with ambiguous interpretations, will come with information from studies of different character systems, and studies focusing on the elucidation of phylogentic relationships of all potentially related genera, especially those traditionally assigned to the Characinae.

The present study confirmed some of the characters proposed by Lucena and Menezes (1998) as derived for the Cynodontinae and *Gilbertolus* and for the Cynodontinae and *Acestrorhynchus*. These are discussed in the Character Description and Analysis section.

Agoniates Müller and Troschel, 1845, has also been hypothesized as probably related to cynodontines. Eigenmann (1912: 317) noted similarities between *Agoniates* and *Hydrolycus scomberoides*. Howes (1976) mentioned that, although he did not examine specimens of *Agoniates* in his myological study of the Cynodontinae and Characinae, there was a possibility that the pattern of dentition, presence of five branchiostegal rays, and length of pectoral fins might constitute derived specializations shared by *Agoniates* and the Cynodontinae. In Lucena's (1993) analysis *Agoniates* was hypothesized to be the sister group to all other members of the Characidae other than the assemblage formed by *Cynodon*, *Rhaphiodon*, and *Acestrorhynchus*.

Agoniates shares with the Cynodontinae the contact between the antorbital and the ventral wing of the lateral ethmoid along its entire lateral edge (character 2 in Character Description and Analysis). A ridge on the lateral surface of the vomer (character 16) is another derived feature shared by *Agoniates* and *Hydrolycus*. An analysis focusing on the relationships of *Agoniates* should be pursued; however, due to the larger number of derived features shared by the Cynodontinae and the characiform outgroups discussed above, the features shared by cynodontines and *Agoniates* are hypothesized herein as having originated independently.

CHARACTER DESCRIPTION AND ANALYSIS

Characters are grouped under separate headings according to the region of the body with which they are associated. The number preceding each character corresponds to that of appendix 1.

ORBITAL REGION

1. Fifth infraorbital

Cynodontines have six canal-bearing bones forming the orbital ring with bony plates that cover part or all of the adductor musculature of the cheek (fig. 2), a condition considered to be primitive for characiforms (Roberts, 1969: 419; Vari, 1979: 301; Fink and Fink, 1981: 315). In *Cynodon*, *Rhaphiodon*, *Hydrolycus scomberoides*, and *H. wallacei* the fifth infraorbital typically reaches the posterior margin of the infraorbital series and the fourth and six infraorbitals are not in contact (fig. 2B). In *Hydrolycus armatus* and *H. tatauaia* the fifth infraorbital is greatly reduced, with the posteroventral margin of the sixth infraorbital in contact with the posterodorsal margin of the fourth infraorbital (fig. 2A).

Different patterns of reduction of infraorbital bones are observed in various characiform groups (Weitzman and Fink, 1983), some having only five infraorbitals (e.g., *Charax*, Lucena, 1987), and others having a reduced or absent fourth infraorbital (e.g., ctenolucids, Vari, 1995). The pattern described above for *Hydrolycus armatus* and *H. tatauaia* is, however, unique among characiforms, and considered synapomorphic for the clade formed by these two species.

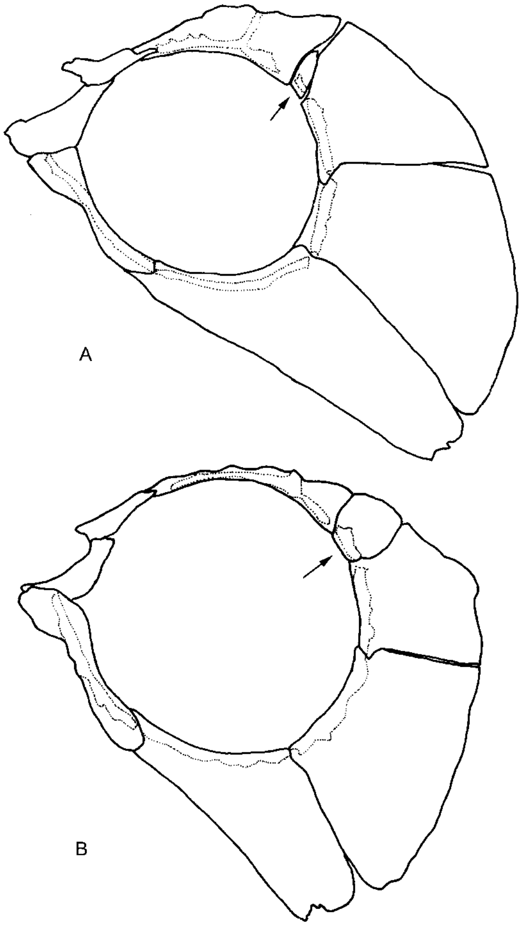

Fig. 2. Infraorbital series, supraorbital and antorbital of (**A**) *Hydrolycus armatus*, MZUSP 32607; and (**B**) *Hydrolycus wallacei*, MZUSP 32638; left side, lateral view, anterior to left. Arrow points to fifth infraorbital.

2. Antorbital-lateral ethmoid contact

All cynodontines have the antorbital bone contacting the lateral margin of the ventral wing of the lateral ethmoid. The antorbital in characiform outgroups having this ossification (a separate antorbital is lacking in ctenolucids and erythrinids, see Vari, 1995: 9) is usually positioned anterior to the ventral wing of the lateral ethmoid with no, or only slight, contact between the dorsalmost portions of these two ossifications.

An extended contact between the antorbital and the lateral edge of the ventral wing of the lateral ethmoid occurs in *Gasteropelecus* and *Agoniates*. In the latter genus the antorbital is well developed (Géry, 1962) with the lateral edge of the ventral wing of the lateral ethmoid anteroposteriorly expanded and forming a distinct lateral surface instead of the narrow edge present in other characiforms. In addition to the antorbital-lateral ethmoid contact, gasteropelecids also share the presence of expanded coracoids with cynodontines. These two taxa do not seem, however, to be closely related as discussed by Weitzman (1954). Gasteropelecids and cynodontines differ significantly in most parts of their osteology, with the former hypothesized to be more closely related to characiforms such as *Astyanax*, *Brycon*, and *Bryconamericus* (Weitzman, 1954: 231). The relationships of *Agoniates* have been discussed in the previous section and the features shared by these taxa are hypothesized as having originated independently. The antorbital bone contacting the lateral margin of the ventral wing of the lateral ethmoid is, therefore, hypothesized as a synapomorphy for cynodontines.

3. Antorbital

The antorbital bone in all *Hydrolycus* species (fig. 3A) is a flat, platelike ossification without an extending process.

The antorbital in *Rhaphiodon* and *Cynodon* (fig. 3B) has a medial, vertically aligned process that extends along the posterior surface of the ventral wing of the lateral ethmoid. In *Rhaphiodon* this process is very narrow, extending only slightly medially from the posterior margin of the antorbital and contacting the posterior margin of the ventral wing of the lateral ethmoid. In *Cynodon* this process is further developed, extending to a greater degree medially, especially in the middle portion of the process.

Flat antorbitals are observed in most characiform outgroups, but in some, the antorbital is not a flat ossification, but presents some degree of elaboration. This was observed in *Acestrorhynchus*, *Gasteropelecus*, *Chalceus*, *Iguanodectes*, and *Xenocharax*. The overall shape of the antorbital in these taxa differs in various ways from that in cynodontines, and therefore does not seem to be directly comparable to that of cynodontines.

The medial process on the posterior margin of the antorbital in *Cynodon* and *Rha-*

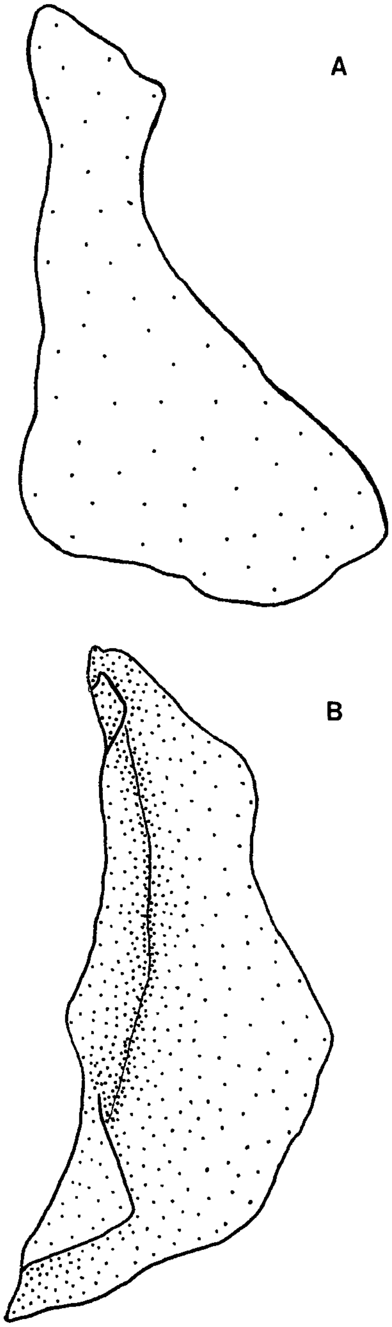

Fig. 3. Antorbital of **(A)** *Hydrolycus tatauaia* MZUSP 32630, and **(B)** *Cynodon gibbus* MZUSP 32587, left side, medial view, anterior to right.

phiodon is hypothesized as derived, as opposed to the condition of a flat, platelike ossification found in *Hydrolycus* and widespread among characiforms outgroups, and is interpreted as synapomorphic for the clade formed by these two genera. The further enlargement of the antorbital process in *Cynodon* is hypothesized as a synapomorphy for that genus.

NEUROCRANIUM

The anterior portion of the neurocranium (mesethmoid-vomer region) of cynodontines is highly modified compared to other characiforms; many specializations are found in the articulation of the premaxilla, maxilla, and ectopterygoid. All ossifications in this area are held together by strong ligamentous tissue. A series of anterior neurocranial features provide considerable morphological information pertinent to the elucidation of the phylogenetic relationships of the Cynodontinae, as detailed below.

4. Mesethmoid

Hydrolycus species have the anterior portion of the mesethmoid, which forms an articular surface for the premaxillae, dorsoventrally expanded, and almost round in shape when examined in lateral view. In *Hydrolycus scomberoides*, *H. armatus*, and *H. tatauaia*, (figs. 4, 5) there is a further expansion of this anterior portion of the mesethmoid compared to *H. wallacei* (fig. 6). This feature was previously noted by Starks (1926: 165) for *Hydrolycus scomberoides* (*H. pectoralis* of that author).

In *Cynodon* and *Rhaphiodon*, the mesethmoid ends in a conical, spinelike process (figs. 7 and 8, respectively), the condition observed in most examined characiform outgroups and considered plesiomorphic (Weitzman, 1962: 19; Roberts, 1969: 405; Vari, 1979: 277). A vertically enlarged anterior mesethmoid was observed in *Mylossoma* and *Roeboexodon guyanensis* among examined outgroups. In the latter species the anterior enlargement of the mesethmoid is accomplished by a vertical expansion of the spine, and is continuous with an expansion of the ventral surface of the mesethmoid, a condition different from that in cynodontines. This vertical expansion of the anterior meseth-

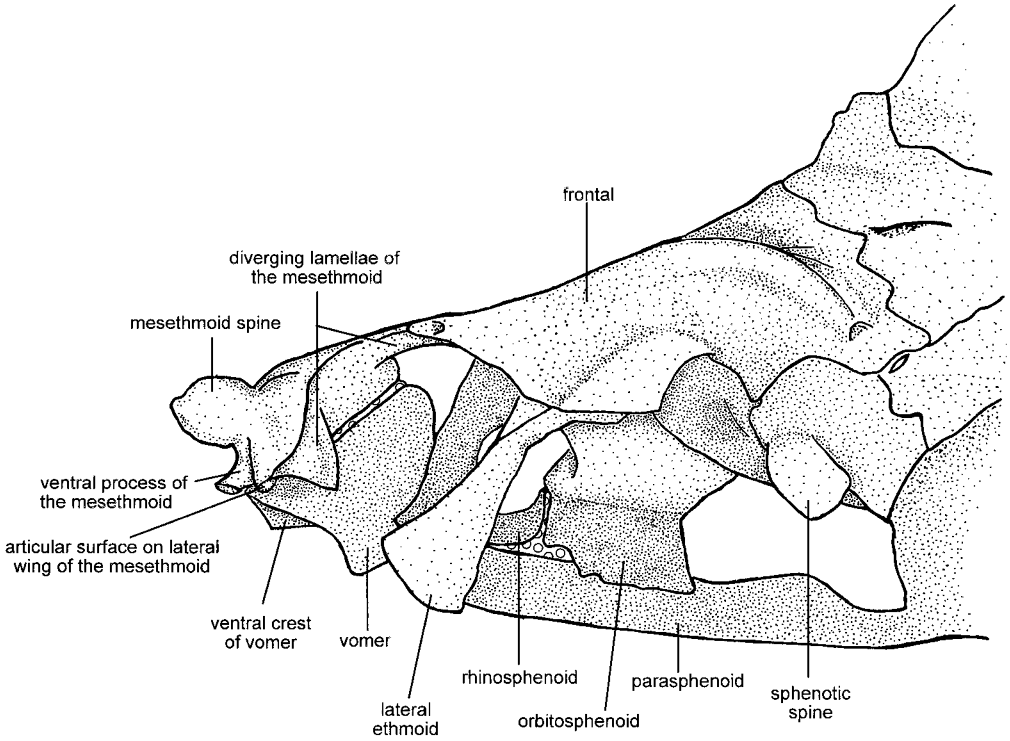

Fig. 4. Anterior and orbital regions of neurocranium of *Hydrolycus scomberoides*, MZUSP 32093; left side, lateral view, anterior to left.

moid in *Roeboexodon guyanensis* results in a bony plate that provides a very broad articular surface for the premaxillae.

Elaboration of the anterior portion of the mesethmoid occurs in a few characiforms e.g., Citharinidae and Distichodontidae, but they represent different modifications from the one described above for *Hydrolycus* (see Vari, 1979: 278–279, for details). The condition observed in *Hydrolycus* is unique among examined outgroups and is most parsimoniously interpreted as a synapomorphy for that clade, with further anterior enlargement of the mesethmoid in *Hydrolycus scomberoides*, *H. armatus*, and *H. tatauaia* hypothesized as a synapomorphy for this clade.

5. Ventral process of the mesethmoid (sensu Starks, 1926: 163)

All cynodontines have a pair of processes projecting from the ventral surface of the mesethmoid (figs. 4–8). These processes arise from the ventral surface of the lateral wings of the mesethmoid to which the premaxillae are attached, and are interposed between the base of the mesethmoid spine anteriorly, and articulation with the vomer posteriorly. The processes bear cartilage pads on their ventral tips. Starks (1926: 163) reported the presence of the ventral processes on the mesethmoid in *Rhaphiodon vulpinus* and *Hydrolycus scomberoides* (*H. pectoralis* of that author). A sheet of thick connective tissue is attached to the tip of these processes and covers the entire ventral portion of the vomer-mesethmoid region. The layer of connective tissue is less dense posteriorly and attaches to the medial portion of the maxilla. In juveniles of *Rhaphiodon* (USNM 231549, 41.7–50.1 mm SL) the processes are represented by two large cartilaginous pads on the ventral surface of the ossified portion of the mesethmoid.

Determination of the element homologous to the ventral processes of the mesethmoid described for cynodontines in characiform outgroups is complicated. Among examined

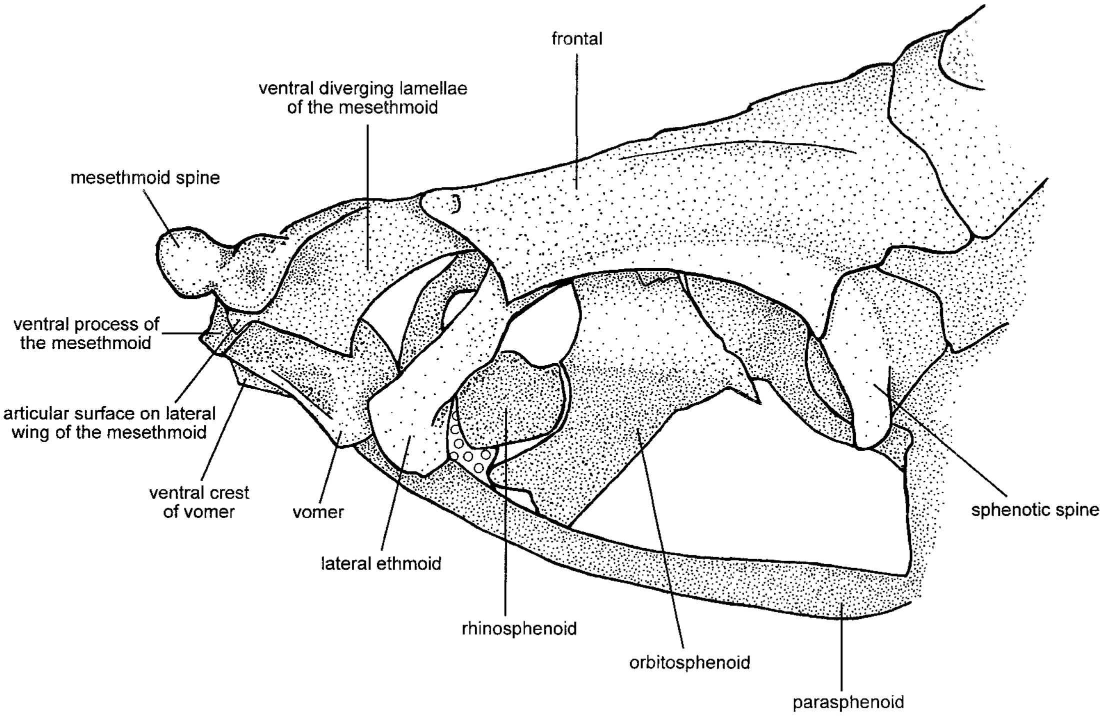

Fig. 5. Anterior and orbital regions of neurocranium of *Hydrolycus armatus*, MZUSP 32607; left side, lateral view, anterior to left.

outgroups, an ossification similar to the ventral processes of the mesethmoid described for cynodontines occurs in erythrinids, *Lebiasina bimaculata*, and *Piabucina* sp. In these taxa the processes occupy the same position on the mesethmoid as the structures in cynodontines, originating ventrally from the lateral groove of the mesethmoid where the premaxillae attach. Such processes in erythrinids and lebiasinids are more laterally oriented than the processes in cynodontines, in which they lie somewhat parallel to each other. The posterior edges of the processes in erythrinids and examined lebiasinids contacts the anterior margin of the vomer (as in *Rhaphiodon* and some *Hydrolycus* species, detailed below). The sheet of connective tissue attached to the margins of these processes in cynodontines was absent in these outgroups. Rather, in the outgroups the cartilage at the tip of the ventral process of the mesethmoid contacts a cartilaginous surface on the anterior portion of the palatine, and ligamentous tissue suspends the maxilla and palatine arch to the ventral process of the mesethmoid. Weitzman (1964: 137) described the mesethmoid of *Hoplias* and *Erythrinus* as being similar to that of *Brycon*. The latter genus lacks the ventral processes of the mesethmoid noted for cynodontines. The two lateral processes in the mesethmoid of *Brycon* were described as the ‘‘lateral ethmoid wing’’ (= lateral wings of the mesethmoid) by Weitzman (1962: 19). Ventral parts of the lateral wings of the mesethmoid in *Brycon* contact the upper portions of the vomer via a synchondral joint (Weitzman, 1962: 19). As noted above, the ventral processess of the mesethmoid in erythrinids also join the anterior margin of the vomer by a synchondral joint. It is not clear whether Weitzman (1964: 137), in mentioning the similarity between the mesethmoid in *Brycon* to that in *Hoplias* and *Erythrinus*, was referring just to the similarity in overall shape or implied also that the lateral processes present in the mesethmoid of these taxa represented the same structure. A lateral wing of the mesethmoid was coded as present for *Hoplias* by Buckup (1991: 213, character 2). It is also not clear whether what was considered the lateral wing of the mesethmoid by Buckup is what it is called here the ventral processes of the mesethmoid or is rather the very narrow lateral extension of the mesethmoid dorsal to these processes where the ascending processes of the premaxilla are connected. In cynodontines a distinct structure can be recognized extending laterally from the mesethmoid onto which the premaxilla and the anterodorsal process of the maxilla attach; that structure seems to correspond to the lateral wing of the mesethmoid as described by Weitzman (1962: 19). A similar element is absent in erythrinids.

Processes on the ventral portion of the mesethmoid bearing some resemblance to those in cynodontines were found in *Prochilodus rubrotaeniatus*, *Caenotropus maculosus*, *Laemolyta taeniata*, and *Hemiodus* sp. among examined outgroups. In the latter two species the anterodorsal portion of the vomer is separated from the ventral portion of the mesethmoid processes by a large cartilage block. In *Prochilodus rubrotaeniatus* and *Caenotropus maculosus* the posterior portions of the processes contact the anterior portion of the vomer and laterally they contact the anterior cartilaginous surface of the palatine. Weitzman (1954: 217) described a ventral process on the mesethmoid contacting the vomer along a broad suture in *Carnegiella vesca*. This process observed here in *Carnegiella strigata*, bears little resemblance to the processes noted above for cynodontines and some characiform outgroups.

Starks (1926: 163), in describing the ventral processes of the mesethmoid in *Rhaphiodon vulpinus*, stated that ‘‘These are the same processes described for *Hoplias* and doubtless the same as those of the cyprinoids that bear the pre-ethmoids.’’ In the description of the ethmoid region of *Hydrolycus pectoralis* (*H. scomberoides*) Starks (1926: 165) stated that ‘‘The pre-ethmoid processes of the mesethmoid are the same.’’ [as in *Rhaphiodon vulpinus*]. For *Distichodus fasciolatus* Starks (1926: 169) noted that ‘‘A nodule of cartilage filling a concavity at the union between the mesethmoid and the vomer doubtless represents the pre-ethmoid.’’ Fink and Fink (1981: 312), in their discussion of ostariophysan interrelationships, mentioned that (their character 4): ‘‘In cypriniforms a cartilage body or endochondral ossification, usually termed the ‘pre-ethmoid’, is tightly articulated between the vomer and mesethmoid. In *Chanos*, **many characiforms** [my emphasis], and some other teleosts a probably homologous cartilaginous or ossified body is present between the palatine, maxilla, and ethmoid.’’

The available evidence precludes an adequate assessment of homologies of the ventral processes of the mesethmoid for cynodontines relative to the condition found in other characiforms. However, all the groups listed above in which relatively similar processes were observed are hypothesized as being more closely related to groups that lack well-developed processes. *Prochilodus rubrotaeniatus*, *Caenotropus maculosus*, and *Laemolyta taeniata* belong to three different monophyletic families that together with the Curimatidae (in which such ventral processes on the mesethmoid are lacking) are hypothesized to form a monophyletic group (Vari, 1983). Erythrinids and lebiasinids share many derived features with *Hepsetus* and ctenolucids, taxa that also lack these processes. All the groups that are potentially related to the Cynodontinae at different levels of inclusiveness (*Roestes*, *Gilbertolus*, and *Acestrorhynchus*—see discussion on section about cynodontine interrelationships) lack processes on the ventral portion of the mesethmoid that resemble to those described for the Cynodontinae. As a consequence, the ventral processes on the mesethmoid as described for the Cynodontinae are hypothesized as synapomorphic for the members of that subfamily.

6. Orientation of ventral processes of the mesethmoid

In all cynodontines except *Hydrolycus wallacei*, the ventral processes of the mesethmoid are ventrally directed at an approximately 90° angle relative to the mesethmoid spine (figs. 4, 5, 7, 8). In *Hydrolycus wallacei* (fig. 6), however, these processes are reoriented into a forward direction at a considerably smaller angle relative to the mesethmoid spine.

This character was coded as a missing entry (meaning inapplicable) in the outgroups since they do not possess ventral processes

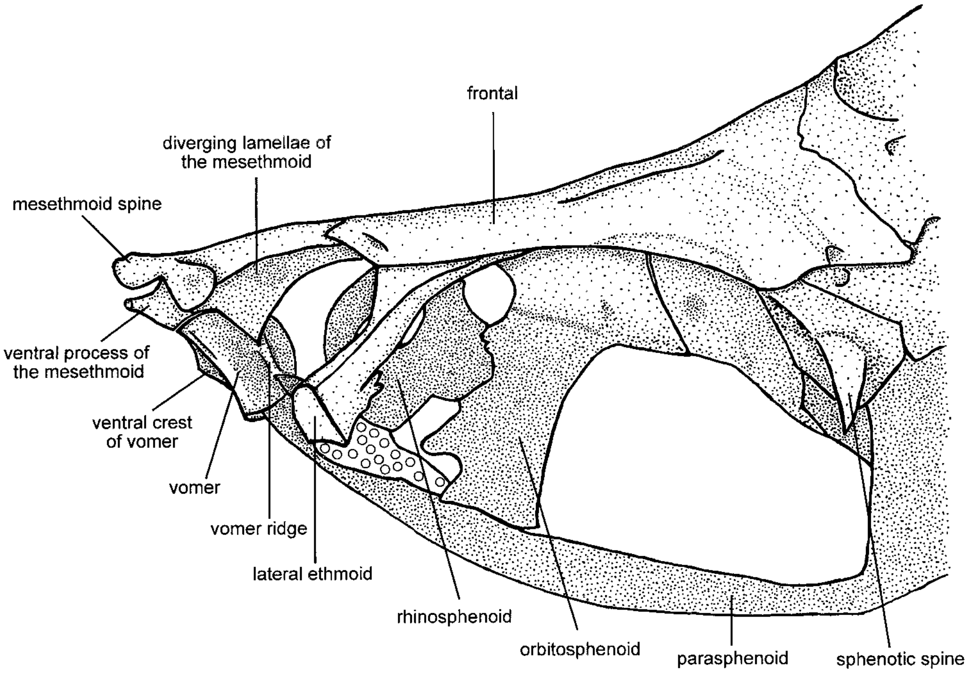

Fig. 6. Anterior and orbital regions of neurocranium of *Hydrolycus wallacei*, MZUSP 32638; left side, lateral view, anterior to left.

on the mesethmoid as described for cynodontines. According to the most parsimonious hypotheses of cynodontine intrarelationships generated in the present study, this character is interpreted as an autapomorphy for *Hydrolycus wallacei*.

7. Vomer–mesethmoid contact

In *Hydrolycus tatauaia*, *H. armatus*, *H. scomberoides*, and *Rhaphiodon vulpinus*, the anterior surface of the vomer contacts the ventral process of the mesethmoid along its posterior surface (figs. 4, 5, 8). In *Cynodon* (fig. 7) the vomer does not directly contact the ventral processes of the mesethmoid; its contact occurs dorsal to the posterior surface of the ventral processes of the mesethmoid, which are free of contact with other ossification. The condition in *Hydrolycus wallacei* is difficult to interpret due to the anterior shift of the ventral process of the mesethmoid (charater 6), and although the vomer does not contact that process along its entire posterior surface as in the remaining *Hydrolycus* species and *Rhaphiodon*, there is contact along the dorsalmost portion of the processes, a condition slightly different from that in *Cynodon*. For this reason the condition in *Hydrolycus wallacei* was coded as a missing entry.

This character was also coded as a missing entry in outgroups since they lack the ventral processes on the mesethmoid. All examined outgroups that have an element similar to the ventral process of the mesethmoid described for cynodontines, have that process contacting the anterior surface of the vomer (e.g. in erythrinids), a condition similar to that in *Hydrolycus tatauaia*, *H. armatus*, *H. scomberoides*, and *Rhaphiodon vulpinus*. However, as noted under character 5 above, homology propositions for the ventral processes of the mesethmoid in cynodontines relative to the condition found in characiform outgroups are not clear, and all taxa that possess similar processes are more closely related to taxa that lack them.

Examination of different ontogenetic stages did not provide information that could be used to determine polarity of this character. In juveniles of *Rhaphiodon* the anterior portion of the vomer is already in contact with the posterior portion of the ventral processes of the mesethmoid, which are cartilaginous at this stage (USNM 231549, 41.7–50.1 mm SL). It was not possible to examine this feature in juveniles of *Cynodon* due to the poor condition of the specimen available (AMNH 32485, 35 mm SL).

The distribution of this character in cynodontines renders any kind of optimization for the character states arbitrary. As a consequence it is impossible to unambiguously propose this character as an additional synapomorphy for any clade under the phylogenetic reconstruction summarized in the cladogram (fig. 20). Tests including and excluding this character from the analysis did not change the resulting hypothesis.

Some modifications of the anterior portion of the neurocranium in cynodontines are associated with the area of articulation with the maxilla. Such modifications occur on the lateral portion of the vomer, lateral wing of the mesethmoid, ventral diverging lamellae of the mesethmoid, and in part, the ventral processess of the mesethmoid. In cynodontines those elements delimit a groove or fossa that provides an area of attachment for the ligamentous tissue of the medially directed anterodorsal process of the maxilla. The series of modifications that contribute to form this fossa and the variation exhibited within cynodontines are detailed under characters 8–10 below.

8. Ventral diverging lamellae of the mesethmoid

Cynodontines have well-developed ventral diverging lamellae of the mesethmoid (sensu Weitzman, 1962: 19). Posteriorly, the lamella of each side contacts the upper central portion of each lateral ethmoid. Anteriorly the lamella of each side is continuous with a portion of the lateral wing of the mesethmoid medial to the region where the maxilla attaches, and extends posteriorly on the lateral surface of the vomer. This results in a well-developed triangular bony plate, with one corner of the triangle pointing toward the posterior margin of the vomer (figs. 5–8) (henceforth the entire element will be referred to as the diverging lamella of the mesethmoid). Together the triangular bony plates from each side clasp the lateral surface of the vomer. The ventral margin of this triangle forms the dorsal limit of a fossa where the maxilla articulates.

Hydrolycus scomberoides has a slightly different condition from the one described above. In this species there is no continuity of the lamella along the ventral surface of the mesethmoid with the portion of the lamella extending from the lateral wing of the mesethmoid (fig. 4).

The diverging lamellae of the mesethmoid are reduced or absent in many characiform outgroups, e.g., erythrinids, lebiasinids, ctenoluciids, and gasteropelecids. Weitzman (1962: 137) stated that the ventral diverging lamellae of the mesethmoid are well developed in the Erythrinidae; however, I agree with Buckup (1991: 214) who regards Weitzman's mention of such lamellae as a misinterpretation of a similar ossification that extends posteriorly from the dorsal surface of the lateral mesethmoid wings. A few *Acestrorhynchus* species (*A. falcirostris* and *A. nasutus*) have a lateral lamella that extends ventrally from the mesethmoids with its anterior portion contacting the vomer and extending posteriorly toward the lateral ethmoid. In the remaining *Acestrorhynchus* species, such a lamella is very reduced and does not reach the vomer ventrally. As in the Erythrinidae it seems that the lamella as described for *Acestrorhynchus* species does not correspond to the ventral diverging lamella of the mesethmoid described by Weitzman (1962: 19). Characiforms with well-developed ventral diverging lamellae of the mesethmoid include *Roestes*, *Gilbertolus*, *Charax*, *Roeboexodon*, the Cynopotaminae (Menezes, 1976), *Acanthocharax*, and *Agoniates*.

A discontinuity between the anterior and posterior portion of the diverging lamella of the mesethmoid is restricted to *Hydrolycus scomberoides* within cynodontines, a condition most parsimoniously interpreted as autapomorphic for this species.

9. Triangular portion of the ventral diverging lamellae of the mesethmoid

The extent to which the triangular portion of the ventral diverging lamella of the mesethmoid (described under character 8) extends along the lateral surface of the vomer varies among cynodontines. In all *Hydrolycus* species and *Rhaphiodon* the triangular

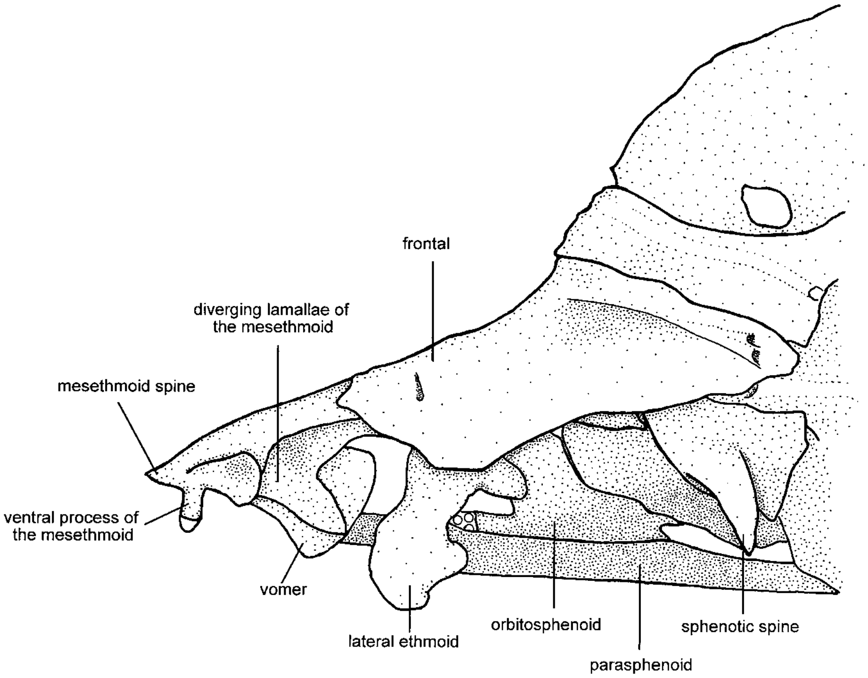

Fig. 7. Anterior and orbital regions of neurocranium of *Cynodon gibbus*, MZUSP 32587; left side, lateral view, anterior to left.

portion of the ventral diverging lamella of the mesethmoid extends laterally over the anterodorsal corner of the vomer, leaving most of the lateral surface of the vomer uncovered (figs. 4–6, 8). In *Cynodon* this lamella is more elongate, extending beyond the midline, and in many specimens reaching the posteroventral edge of the vomer (fig. 7). As a consequence, in *Cynodon* most of the lateral surface of the vomer is covered by the triangular portion of the ventral diverging lamella of the mesethmoid.

At first a direct comparison of the condition of this character in outgroups with that in cynodontines seemed complicated, in view of the high degree of modification of the entire vomer-mesethmoid region in cynodontines. However, closer examination of this feature in outgroups revealed that in some, the portion of the lamella at the ventral surface of the mesethmoid that extends ventrally to contact the anterior portion of the vomer is continuous with the portion extending medially and posteriorly from the lateral wing of the mesethmoid (*Charax*, *Acanthocharax*, *Galeocharax*, *Brycon*, *Roeboexodon*). This portion of the ventral diverging lamella of the mesethmoid in examined outgroups does not extend as far posteriorly on the surface of the vomer, in many cases being very reduced or lacking (e.g., *Roestes*, *Gilbertolus*, and *Agoniates*). Therefore, the triangular portion of the ventral diverging lamella of the mesethmoid covering most of the lateral surface of the vomer is hypothesized as synapomorphic for *Cynodon*.

10. Articular surface on lateral wing of the mesethmoid

The region of the lateral wing of the mesethmoid where part of the ligamentous tissue of the maxilla attaches differs among cynodontines. In *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* this portion of the lateral wing of the mesethmoid has a distinct posteriorly oriented articular surface (figs. 4, 5). Ligamentous tissue from the maxilla converges anteriorly to attach to this articular surface, which forms the anterior boundary for a depression on the lateral surface of the vomer where the maxilla abuts at the level of the synchondral joint between the vomer and ventral processes of the mesethmoid (see character 14 below). In *Cynodon*, *Rhaphiodon*, and *Hydrolycus wallacei*, ligaments from the maxilla attach to the ventral portion of the lateral wing of the mesethmoid without a distinct posteriorly directed articular surface forming an anterior boundary for the area of articulation of the maxilla. As a consequence the depression on the lateral surface of the vomer where the maxilla abuts extends slightly more anteriorly and reaches the posterolateral surface of the mesethmoid. This is more evident in *Hydrolycus wallacei* and *Rhaphiodon* (figs. 6 and 8, respectively) than in *Cynodon* (fig. 7) in which the depression on the vomer is reduced compared to the remaining species.

Ligamentous tissue suspending the upper anterior tip of the maxilla to the lateral wing of the mesethmoid is the typical condition among characiforms (Weitzman, 1962: 19; Roberts, 1969: 405), and also occurs in cynodontines. Comparisons of the portion of the mesethmoid where the maxilla attaches in characiform outgroups and cynodontines is complicated due to the highly modified mesethmoid region of cynodontines. The lateral wings of the mesethmoid in many characiforms outgroups have a laterally oriented cartilaginous cap that is continuous with the cartilaginous surface from the lateral portion of the vomer (e.g., *Roestes*, *Charax*, *Galeocharax*, Heterocharacini), and from which the maxilla is suspended by ligaments. In *Brycon*, *Acestrocephalus*, *Acanthocharax*, and *Acestrorhynchus* the ligamentous tissue from the anterior tip of the maxilla attaches to a small portion of the lateral wing of the mesethmoid that has a ventral to slightly lateral articular surface.

A posterior orientation of the articular surface of the lateral wing of the mesethmoid onto which part of the ligamentous tissue of the maxilla attaches is unique to *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* among examined characiforms; this seems to be the result of the reorientation of the lateral wing of the mesethmoid to a somewhat more vertical position, shifting the surface of the articulation of the ligaments of the maxilla to a more posterior orientation. Such a reorientation of the lateral wing of the mesethmoid is also expressed in the orientation of its articular surface with the premaxilla that is more closely associated with the lateral portion of the ventral processes of the mesethmoid in *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* compared to the condition in *Cynodon* and *Hydrolycus wallacei* (in *Rhaphiodon* the articular surface of the lateral wing of the mesethmoid with which the premaxilla articulates is less pronounced laterally). The condition observed in *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* is hypothesized as a synapomorphy for that assemblage.

The vomer in cynodontines is a massive bone that fills the space between the mesethmoid and lateral ethmoids. It is highly concave ventrally and dorsolaterally, being an inverted Y-shaped bone posteriorly in cross section (see character 13 below) with the angle between the two arms of the Y very acute, and the vertical process that forms a sagittal bony plate elongate, and contacting a similar bony plate of the mesethmoid anteriorly.

An inverted Y-shaped vomer was described for the Erythrinidae and Lebiasinidae by Weitzman (1964: 138). The angle between the two arms of the Y in these families is not, however, as acute as in cynodontines. In erythrinids and lebiasinids the dorsolateral surface of the vomer forms an almost a 90° angle, whereas in cynodontines this angle is much greater. A vomer like that in cynodontines was observed only in *Distichodus fasciolatus*, among examined characiforms, with the overall shape of this ossification being more similar to that of *Cynodon*. Modifications of the vomer that provide information about cynodontine intrarelationships are described below.

11. Ventral crest of vomer

In *Hydrolycus* species and *Rhaphiodon* the ectopterygoid is in close contact with the ventral surface of the vomer and not with the mesethmoid as in *Cynodon* (character 31 below). A close contact between the vomer and the ectopterygoid also occurs in *Acestrorhynchus* and *Hepsetus* but represents a different set of modifications than those found in the Cynodontinae.

The ventral surface of the vomer in *Hydrolycus* species and *Rhaphiodon* bears two longitudinal crests (figs. 4, 6, and 8, lateral view) situated side by side and separated by a longitudinal groove. The ectopterygoid of each side abuts the ventrolateral portion of each crest, which serves as an area of attachment for the ligamentous tissue between these two elements. This crest is developed to varying degrees among cynodontines when present. It is relatively small in *Rhaphiodon* and *Hydrolycus wallacei* and very developed in *Hydrolycus scomberoides*. A crest on the ventral surface of the vomer is lacking in *Cynodon*.

In the majority of examined characiforms (with the exception of *Acestrorhynchus* and *Hepsetus*, see character 31) the ventral surface of the vomer is flat, with no conspicuous elaborations for the attachment of ligaments. In *Agoniates* a median ridge that delimits two fossa for the attachment of ligaments arises from the mesopterygoid. *Gilbertolus atratoensis* possesses two small projections of bone on the ventral surface of the vomer onto which ligamentous tissues from the mesopterygoid and ectopterygoid attach bearing some resemblance to those described for *Hydrolycus* and *Rhaphiodon*. The ectopterygoid does not directly contact these processes in *Gilbertolus atratoensis* as it does in *Hydrolycus* and *Rhaphiodon*. In the specimen of *Roestes ogilviei* examined, the processes are hardly noticeable, and they are absent in the examined specimen of *R. molossus*.

Interpretation of the ventral processes on the vomer of *Hydrolycus* and *Rhaphiodon* is ambiguous under all optimizations of this character. In addition, the slight resemblance of the condition in those cynodontine taxa to that in *Gilbertolus* further complicates any conclusion about the evolution of this feature. Therefore, this character was not hypothesized as synapomorphic for the species that possess it. Analyses that included, excluded, or used different character codings of this character did not affect the resulting phylogenetic hypothesis.

12. Lateral arms of vomer

In all cynodontines the two lateral bony plates forming the two arms of the inverted Y of the vomer are well developed along the posterior portion of the ossification. Some variation in the anterior portion of the vomer is, however, observed among cynodontines. In *Cynodon* these two lateral bony plates are continuous all the way to the anterior portion of the vomer, nearly as far as the articulation with the mesethmoid. As a consequence, in *Cynodon* the vomer in cross section is an inverted Y along its entire length. In all *Hydrolycus* species and *Rhaphiodon* the lateral arms of the vomer gradually diminish in relative size anteriorly, extending only onto the posterior half of the bone. As a consequence, from a ventral view, the concavity of the vomer is only evident posteriorly. Anteriorly the vomer in *Hydrolycus* species and *Rhaphiodon* is not an inverted Y in cross section but rather flat ventrally. As already mentioned, the vomer of *Distichodus fasciolatus*, is similar to that of *Cynodon,* with continuous bony plates along its entire length.

In characiform outgroups that have a shape of the vomer similar to that in cynodontines (e.g., erythrinids, lebiasinines), and those in which the shaft of the vomer has a relatively constant width along its length (e.g., *Hoplocharax*, *Heterocharax*, gasteropelecids) the lateral portion of the vomer usually extends beyond the longitudinal axis of the shaft of the vomer and is continuous along the length of the vomer. In other characiforms the vomer is a relatively flat ossification that extends laterally to varying degrees beyond the margin of the shaft. In most of these groups (e.g., *Roestes*, *Gilbertolus*, *Acestrocephalus*, *Charax*, and *Brycon*), there is an enlarged articular surface at the anterolateral portion of the vomer that widens this portion of the bone. This articular surface is lacking in cynodontines. A direct comparison of the condition in these taxa to that in cynodontines is, as a consequence, further complicated. The condition described for *Cynodon*, is most parsimoniously optimized as derived in the cladogram that resulted from the analysis but it is not at this time proposed as an additional synapomorphy for that genus since the condition in outgroups was coded as a missing entry.

13. Vomer-palatine contact

In all cynodontines the anterior portion of the palatine has a cartilaginous articular surface that abuts a matching articular facet in the posterior edge of the main body of the vomer.

Contact between the vomer and the palatine is relatively common among characiforms. What differs, however, is the type of contact. The anterior cartilaginous surface of the palatine in characiforms typically contacts the anterolateral portion of the vomer by way of a relatively loose type of contact. In ctenoluciids the articular surface of the vomer is situated laterally between the anterior and posterior edges. *Acestrorhynchus* species seem to have a unique condition among characiforms in which the anterior portions of the palatine abuts against two ventral processes in the ventral surface of the vomer. In erythrinids the palatine contacts a ventral process in the mesethmoid through ligamentous attachments. *Prochilodus* has two large articular surfaces located somewhat posteriorly on the vomer in contact with the palatine. However, the shape of the vomer in the latter genus is highly modified relative to that in most characiforms and this makes a direct comparison with the condition observed in cynodontines difficult. *Roeboexodon* also has two large articular surfaces in the vomer that contact the palatine. These articular surfaces although somewhat posterior in the vomer are oriented ventrally, and thus, are not directly comparable to the condition in cynodontines.

An articulation between the vomer and the palatine of the type observed in cynodontines also occurs in the Serrasalminae among examined characiforms and has been hypothesized as a synapomorphy for the latter group (Machado-Allison, 1983: 163). The phylogenetic relationships of the Serrasalminae remain unresolved. Machado-Allison (1983) discussed the problem and mentioned characters in common between serrasalmines and *Brycon*. Lucena's (1993) study on relationships within the Characidae presented evidence supporting a close relationship between serrasalmines, *Chalceus*, *Brycon*, and African characids, taxa lacking such vomer-palatine contact. In *Hepsetus* there is an elongate cartilaginous region at the posterior edge of the vomer that the cartilaginous surface of the anterior portion of the palatine contacts, a condition similar to that in cynodontines. *Hepsetus* is hypothesized as being closely related to the Ctenoluciidae and Erythrinidae, families with a different type of vomer-palatine contact. The vomer-palatine articulation found in these characiforms outgroups is, therefore, most parsimoniously cinsidered as originating independently from that in cynodontines, and therefore, the condition in the latter taxa is hypothesized as synapomorphic.

14. Vomer-maxilla articulation

The maxilla of cynodontines articulates with the lateral surface of the vomer at the anteroventral portion of the latter ossification. In this area of contact the vomer has a shallow depression. Anterodorsally this depression is roofed by the anteroventral portions of the ventral diverging lamella of the mesethmoid (see character 9 above), and the posteroventral portions of the lateral wing of the mesethmoid. The latter serves as an area for ligamentous attachment of the maxilla to the neurocranium (see character 10 above).

In *Hydrolycus* species, the depression on the vomer is more accentuated than in *Cynodon* and *Rhaphiodon*, with the latter exhibiting a condition that is intermediate between that of *Cynodon* and *Hydrolycus*. This feature demonstrates ontogenetic variation. In a small specimen of *Rhaphiodon* (BMNH 1935.6.4: 33–39, 96.8 mm SL) the depression is absent, whereas in a larger individual (MZUSP 32812, 191.0 mm SL) it is obvious. In very large specimens of *Hydrolycus armatus* the depression in the vomer is developed and deep, forming a fossa (examined in a number of dry skeletons, e.g., AMNH 91344SD, 400 mm SL).

The differing degrees of development of the lateral depression in the vomer may be of phylogenetic interest among cynodontines. The ontogenetic variation observed within species, and the continuous variation among species, complicates the definition of discrete character states, making their definition impossible at this time. However, the presence of a varying developed depression on the lateral surface of the vomer associated with the articulation of the maxilla was not encountered outside the Cynodontinae among characiforms and, therefore, is hypothesized as an additional synapomorphy for the subfamily.

15. Ridge on lateral surface of vomer

In large specimens of *Hydrolycus* the lateral surface of the vomer develops a ridge that interrupts the continuity of the concavity on the surface of the bone. Such a ridge is already developed in specimens of *Hydrolycus scomberoides*, *H. wallacei* (fig. 6), and *H. tatauaia* of approximately 150 mm SL. In *H. armatus* it is absent in a specimen 136 mm SL (LACM 43295-36), and in a specimen 151.0 mm SL (MZUSP 32607) is only very slightly developed, represented by a thickening of bone in the area where the ridge is present in larger specimens. It is well developed in an *H. armatus* specimen of 200 mm SL (MZUSP 32607). It was not possible to determine whether such a ridge is present in *Rhaphiodon*. In the largest *Rhaphiodon* specimen prepared for osteological examination (MZUSP 32812, 191 mm SL), a thickening of bone is observed slightly posterior to where the tip of the ventral diverging lamellae of the mesethmoid contacts the vomer. However, it is not continuous along the lateral surface of the bone as in other cynodontines with the ridge. Larger specimens of *Rhaphiodon vulpinus* have to be examined to further investigate the presence of such a ridge in this species. Therefore, this character was, coded as a missing entry for the latter species.

The lateral ridge of the vomer in *Hydrolycus* species forms a link between the tip of the triangular portion of the ventral diverging lamella of the mesethmoid anteriorly, and the process that extends from the lateral ethmoid posteriorly. This entire portion becomes massively developed in very large specimens of *Hydrolycus* (observed in dry skeletons of *H. armatus*), forming a continuous bridge extending from the mesethmoid to the lateral ethmoid. As a consequence, the median vertical plate of the vomer that is continuous with the remaining lateral surface of the vomer in small specimens seems almost a separate ossification occupying a more internal medial position, in the large specimens.

No such ridge on the lateral surface of the vomer was observed in any of the specimens of *Cynodon*. A bridge uniting the lateral ethmoid and mesethmoid is also present in *Cynodon*; however, it is formed by extensions of these two elements that are in direct contact with each other (in *Hydrolycus* these two elements are not in direct contact).

A distinct ridge on the dorsolateral surface of the vomer occurs in *Agoniates* and *Distichodus fasciolatus* among examined characiforms. This ridge is also in contact anteriorly with a process extending from the mesethmoid and posteriorly with a process from the lateral ethmoid. Presence of such a ridge on the lateral surface of the vomer is hypothesized as derived.

The relationships of *Agoniates* have been briefly discussed in the previous section. *Distichodus* is related to members of the Distichodontidae and Citharinidae (Vari, 1979), which lack the ridge on the vomer. The presence of the ridge on the vomer is most parsimoniously hypothesized as an independent acquisition in these outgroups.

The ridge on the dorsolateral surface of the vomer cannot be unambiguously hypothesized as synapomorphic for *Hydrolycus* at this time, pending a better definition of the condition in *Rhaphiodon*.

16. Rhinosphenoid

All *Hydrolycus* species and *Rhaphiodon* have a rhinosphenoid (figs. 4–6, and 8). Such a distinct ossification is absent from *Cynodon*.

The rhinosphenoid was first named and described by Starks (1926: 164) for *Rhaphiodon vulpinus*. In that species and all *Hydrolycus* species except *H. scomberoides*, the rhinosphenoid is a flat, and widely curved rod. Anteriorly it attaches to the midsagittal portion of the lateral ethmoids. Posteriorly it connects the medial portion of the orbitosphenoid (fig. 6). Ventrally, it contacts the parasphenoid through cartilage. It extends dorsally to contact the roof of the braincase just anterior to the fontanel. The dorsal extension of the rhinosphenoid forms a septum between the olfactory nerves as they issue from the anterior portion of the orbitosphenoid. In large specimens of these taxa the dorsolateral portion of each side of the orbitosphenoid develops a process that extends anteriorly and medially to meet the dorsal portion of the rhinosphenoid. As a consequence, two anterior openings for the olfactory nerve are delimited in the orbitosphenoid. The dorsal extension of the rhinosphenoid develops later ontogenetically than the remaining ossification. Specimens of *Hydrolycus armatus* smaller than 151.0 mm SL (fig. 5) and *Rhaphiodon vulpinus* of 96.8 mm SL (BMNH 1935.6.4: 33–39) have only the ventral portion of the ossification developed. Larger specimens (approximately 200.0 mm SL) have the dorsal extension of the rhinosphenoid well developed (compare figs. 5 and 6). A specimen of *Hydrolycus tatauaia* (MZUSP 32630, 151.2 mm SL) has the dorsal extension of the rhinosphenoid well developed.

In *H. scomberoides* the rhinosphenoid is reduced compared to that of the remaining cynodontines with this ossification (fig. 4). The dorsal extension is lacking in all specimens prepared for osteological examination, the largest being 241.0 mm SL (AMNH 40087SD, dry skeleton). The ventral portion of the rhinosphenoid in *H. scomberoides* is also reduced, and consists of a small curved rod filling the space between the orbitosphenoid and lateral ethmoids immediately dorsal to the parasphenoid.

The rhinosphenoid has been reported only among characiforms. Within the order, in addition to cynodontines, it also occurs in many lineages of the Characinae (sensu Weitzman, 1962), such as *Acestrorhynchus*, *Roestes*, *Gilbertolus*, *Agoniates*, *Brycon*, and others.

In *Acestrorhynchus* the rhinosphenoid is in contact with the parasphenoid, a feature that has been considered unique for the genus (Menezes and Géry, 1983). In small specimens this contact is made through cartilage between the two ossifications, whereas in larger specimens the bones are in direct contact. In *Hydrolycus* species and *Rhaphiodon vulpinus* the rhinosphenoid also contacts the parasphenoid through cartilage, with direct contact between the bones in larger specimens.

The absence of a rhinosphenoid is considered derived for *Cynodon,* with the absence of this ossification in other characiform lineages hypothesized as independent events.

17. Lateral ethmoid–orbitosphenoid contact

Cynodon, *Rhaphiodon vulpinus*, and *Hydrolycus scomberoides* have a type of lateral ethmoid–orbitosphenoid contact in which the dorsomedial portion of the lateral ethmoid bears a process extending posteriorly and contacting the anterodorsal portion of the lateral edge of the orbitosphenoid (fig. 7). This process originates dorsal to the olfactory foramen through the lateral ethmoid.

In small specimens of these taxa the anteromedian opening of the orbitosphenoid is open to the orbital cavity and it is covered dorsolaterally by the contact between the lateral ethmoid and orbitosphenoid. In larger specimens of *Cynodon gibbus* (MZUSP 32593, 179.0 mm SL, cleared and stained; AMNH 93079SD, 240.0 mm SL, dry skeleton), the contact between the lateral ethmoid and orbitosphenoid is enlarged by the dorsal growth of these two elements. As a consequence of this expansion and the growth of the ventral lamella of the frontal, the dorsolateral portion of the anteromedian opening of the orbitosphenoid is completely covered. The ventral portion of the lateral ethmoid process extends medially to almost meet the medial outgrowth of the same process of the contralateral ossification (I was unable to determine whether or not the process from each side meets ventromedially). The anteromedian opening for the olfactory nerve is restricted to the ventral portion of the orbitosphenoid. The olfactory foramen of the lateral ethmoid is positioned entirely ventral to the ventromedial portion of the lateral ethmoid process. It appears that the orbital cavity through which the olfactory nerve extends is restricted to a ventral position between the orbitosphenoid and lateral ethmoid.

Contact between the lateral ethmoid and orbitosphenoid is considered a derived condition in characiforms (Vari, 1979: 279) and it seems to have originated independently in the various groups where it occurs, i.e., the African characiforms Distichodontidae, Citharinidae, some *Alestes* species, *Bryconaethiops*, *Hydrocynus*, and the Neotropical groups Anostomidae, Curimatidae, Prochilodontidae, Lebiasinidae, and Parodontidae (Vari, 1979: 279-283). A type of lateral ethmoid-orbitosphenoid contact similar to that of cynodontines occurs in *Piabucina*, *Lebiasina bimaculata*, and *Pyrrhulina* sp. but is less developed in the latter two species.

The contact between the orbitosphenoid and lateral ethmoid in most groups men-

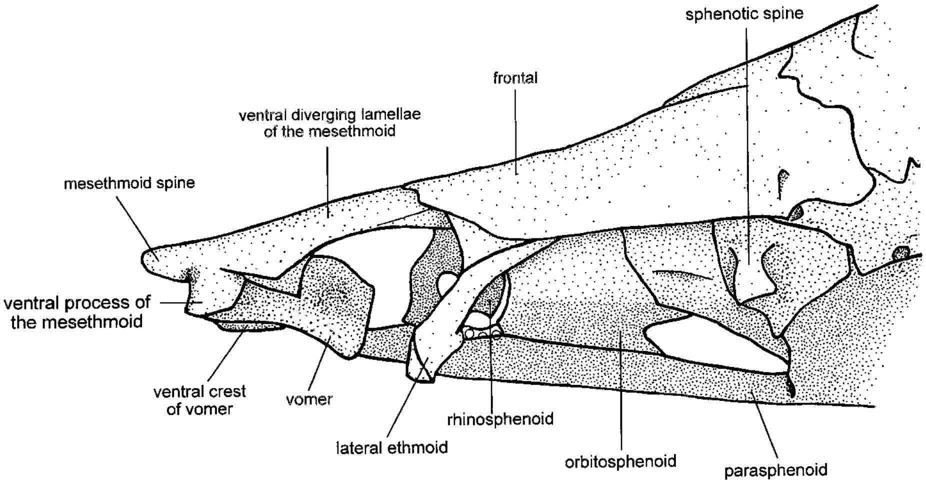

Fig. 8. Anterior and orbital regions of neurocranium of *Rhaphiodon vulpinus*, MZUSP 32812; left side, lateral view, anterior to left.

tioned above is of a different type than that in cynodontines. In distichodontids the lateral ethmoid process that contacts the orbitosphenoid originates from the ventral portion of that element (Vari, 1979: 280). The dorsal contact between these two elements in citharinids that is similar to that in cynodontines, but a second articulation between them is formed mainly by an anterior extension of the orbitosphenoid (Vari, 1979). In the Alestinae and *Hydrocynus* the process between the lateral ethmoid and orbitosphenoid is formed entirely by the latter element and is a bony tube surrounding the olfactory nerve (Roberts, 1969: 441; Brewster, 1986: 191). In Neotropical characiforms, contact between the lateral ethmoid and orbitosphenoid is made by a dorsal and ventral process. In all groups mentioned above, the processes between the lateral ethmoid and orbitosphenoid are associated with varying degrees of coverage of the olfactory bulb and tract.

The contact between the lateral ethmoid and orbitosphenoid is most parsimoniously hypothesized as derived for the clade formed by *Cynodon* and *Rhaphiodon vulpinus* with an independent origin in *Hydrolycus scomberoides*.

18. Orbitosphenoid-parasphenoid distance

All cynodontines have the orbitosphenoid in direct contact with the parasphenoid. However, the distance between the main portion of the orbitosphenoid and the parasphenoid differs among them. *Hydrolycus wallacei, H. tatauaia,* and *H. armatus* have the main portion of the orbitosphenoid well separated from the parasphenoid, with an elongate bony plate extending from the orbitosphenoid ventrally to contact the parasphenoid (figs. 5, 6). In *Cynodon* and *Rhaphiodon vulpinus* the distance between the parasphenoid and orbitosphenoid is greatly reduced and these two elements are in contact just ventral to the main body of the orbitosphenoid (figs. 7, 8). *Hydrolycus scomberoides* has an intermediate condition in which the bony plate contacting these two elements is not as dorsoventrally elongate as in the remaining *Hydrolycus* species (fig. 4), but is relatively more developed than in *Cynodon* and *Rhaphiodon*.

Many characiforms have the parasphenoid and orbitosphenoid remote from each other (e.g., *Brycon, Roestes, Gilbertolus, Charax,* the Heterocharacini, *Acestrocephalus, Acestrorhynchus*, and *Serrasalmus*). Such a separation was listed as one of the distinguishing features for the Characinae (Weitzman, 1962: 48), and also occurs in the Hemiodontinae (Roberts, 1974: 416). An orbitosphenoid close to the parasphenoid occurs in the Ctenoluciidae, Erythrinidae, Lebiasinidae, *Hepsetus* (Roberts, 1969: 406), *Galeocharax,* and the prochilodontids *Semaprochilodus* and

Prochilodus (Roberts, 1973: 217). *Galeocharax* is more closely related to characids such as *Acestrocephalus* (Menezes, 1976) and *Charax* (Lucena, 1993); *Semaprochilodus* and *Prochilodus* are part of a monophyletic assemblage formed by the Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae (Vari, 1983), all with well-separated parasphenoids and orbitosphenoids. The phylogenetic relationships of the clade formed by the Ctenoluciidae, Erythrinidae, Lebiasinidae, and *Hepsetus* (Vari, 1995) have not been the subject of investigation. However, in view of the current evidence for cynodontine relationships with *Gilbertolus*, *Roestes*, and *Acestrorhynchus* (see Historical Overview and Comments on Cynodontine Relationships with Other Characiforms), all of which have the orbitosphenoid well separated from the parasphenoid, the condition in *Cynodon* and *Rhaphiodon* is hypothesized as derived.

The orbitosphenoid close to the parasphenoid is hypothesized as a synapomorphy for the clade formed by *Cynodon* and *Rhaphiodon*, and the intermediate condition present in *Hydrolycus scomberoides* is considered autapomorphic for that species.

19. Dilatator fossa

The dilatator groove in cynodontines has some modifications relative to the condition in other characiforms. These modifications are most probably correlated with the origin of the dilatator operculi muscle in the orbit. The cranial musculature of cynodontines was studied by Howes (1976) who noted that in all cynodontine genera the dilatator operculi muscle has two origins. One is dorsally from the frontal-sphenotic groove, which extends onto the cranial roof, and the other is ventrally from the deep cavity that lies between the frontal and the orbitosphenoid.

The typical form of the dilatator groove in characiforms is one in which the frontal is strongly indented where it overlies the sphenotic, providing a sharp dorsal rim for the dilatator groove. The dilatator operculi originates from the fossa formed by the frontal and sphenotic, and in many cases by the lateral border of the pterotic (Roberts, 1969: 410 for *Brycon*, with discussion of variation of this pattern; Howes, 1976). In characiforms with this pattern, the dilatator muscle does not extend anteriorly onto the dorsal surface of the cranial roof past the posterodorsal margin of the orbit. (Note: different patterns of the dilatator groove occur in the Ctenoluciidae, Erythrinidae, and *Acestrorhynchus* and they represent a set of modifications different from those observed for cynodontines and will not be considered here. See Vari, 1995: 13–15 for details on the patterns the dilatator groove in these taxa.) Only in cynodontines is the dilatator fossa greatly expanded anteriorly, covering most of the dorsal surface of the frontal. An expanded dilatator groove extending onto the dorsal surface of the frontal at the middle of the orbit was reported for *Cynopotamus* (Menezes, 1976: 6). Cynodontines, as described above, have an even more developed dilatator fossa, a condition unique among characiforms and considered synapomorphic.

Different modifications of the neurocranium associated with the expansion of the dilatator fossa are observed within cynodontines. One modification occurs at the posterodorsal edge of the orbit, where the frontal and the dorsal portions of the sphenotic spine overlap to provide the dorsal rim for the dilatator groove. In the usual condition among characiforms, the dorsal portion of the sphenotic spine contacts the ventrolateral margin of the frontal, forming a continuous rim for the dilatator fossa that is developed laterally to varying degrees. This rim is very reduced in cynodontines as a function of two main modifications of this portion of the neurocranium. The first one is a function of the development of the frontal shelf at the posterodorsal edge of the orbit (character 20 below). The second relates to the differing degree of development of the dorsal portion of the sphenotic spine (character 21 below).

20. Frontal shelf at posterodorsal edge of orbit

In most characiforms with a primitive form of the dilatator fossa, the area at the posterodorsal edge of the orbit has developed a lateral shelf that is continuous with the dorsal area of the sphenotic spine. This shelf can vary from moderately to well developed in these groups.

In all cynodontines, the frontal shelf at the posterodorsal margin of the orbit is either reduced or absent. The reduction of the posterior frontal shelf is probably associated with the type of insertion of the dilatator operculi muscle which, according to Howes (1976: 215), has two origins, one on the dorsal surface of the frontal and a second from the space between the frontal and orbitosphenoid. A reduction of the frontal shelf would provide a passageway for the muscle to reach the ventral portion of the frontal. A reduced frontal shelf at the posterodorsal margin of the orbit also occurs in *Acestrocephalus sardina*, *Acanthocharax microlepis*, and *Gnathocharax* among examined characiform outgroups. However, the dilatator operculi muscle in these species apparently lacks a ventral origin as in cynodontines (Howes, 1976: 235). This region of the frontal in *Acestrorhynchus* is restructured in a different way, associated with the specialization of the dilatator fossa in this genus (coded as a missing entry for this character).

In *Hydrolycus tatauaia* and *H. armatus* (fig. 5), the frontal shelf at the posterodorsal edge of the orbit, although reduced, is present and is slightly more developed in larger specimens. A further reduction of the shelf of the frontal occurs in *Cynodon*, *Rhaphiodon*, *Hydrolycus wallacei*, and *H. scomberoides* (figs. 4, 6–8). In these taxa the shelf is completely lacking. According to the most parsimonious hypotheses of cynodontine intrarelationships, the lack of the frontal shelf at the posterodorsal edge of the orbit is interpreted as a derived condition, synapomorphic for the Cynodontinae, with a partial secondary reversal to a small shelf in *Hydrolycus tatauaia* and *H. armatus* as a derived character for the clade formed by these two species.

21. Dorsal portion of sphenotic spine

Cynodon, *Rhaphiodon*, and *Hydrolycus scomberoides* have a reduction in the dorsal portion of the sphenotic spine proximal to the main body of the neurocranium such that the sphenotic spine no longer contacts the ventrolateral margin of the frontal (figs. 4, 7, 8). In all other *Hydrolycus* species the dorsal portion of the sphenotic spine extends dorsally to contact the margin of the frontal, a condition similar to that found in most characiform outgroups.

A reduction of the dorsal portion of the sphenotic spine is also common to ctenoluciids, erythrinids, and lebiasinines. However, this reduction is accompanied by a longitudinal expansion of the remainder of the spine, causing a restructuring (Vari, 1995: 14). No such restructuring of the spine occurs in the Cynodontinae and the modification in cynodontines does not seem to correspond to that in the groups mentioned above. Characidiins have a reduced sphenotic in which the sphenotic bone excludes the origin of the dilatator operculi muscle from the lateral margin of frontal, a condition not directly comparable to other characiforms (Buckup, 1991: 216). *Serrasalmus* has a modified sphenotic spine, a feature apparently related to the condition of the levator arcus palatini muscle (Machado-Allison, 1985: 25). Modifications of the sphenotic spine were also described and proposed as a synapomorphy for an assemblage within distichodontids (Vari, 1979: 285–289). Such modifications are different from those described for the Cynodontinae. The reduction of the dorsal portion of the sphenotic spine in cynodontines is hypothesized as synapomorphic for the clade formed by *Cynodon* and *Rhaphiodon* with an independent acquisition in *Hydrolycus scomberoides*.

22. Anterior shelf of frontal

The anterior portion of the frontal shelf in cynodontines also shows some modifications as a consequence of the expansion of the dilatator fossa and the area of attachment of the dilatator operculi muscle.

Hydrolycus armatus has the least modified form of such a shelf among cynodontines relative to the condition in characiform outgroups. Anteriorly the shelf of the frontal in this species covers the dorsal surface of the lateral ethmoids, extending laterally relative to the longitudinal axis of the body. In smaller specimens (LACM 43295-36, 135.9 mm SL; MZUSP 32607, 2 specimens, 151.4–200 mm SL) the anterior portion of the frontal shelf is represented by a very narrow bony platform but is wider in larger specimens. In *Hydrolycus tatauaia* the anterior shelf of the frontal is similar to that in *H. armatus*, although relatively less pronounced. Even the largest specimen of *H. tatauaia* prepared for osteological examination (MZUSP 32632, 257.0 mm SL) has a narrower shelf than smaller specimens of *H. armatus*. In *H. wallacei* the anterior shelf of the frontal is completely absent (largest specimen prepared for osteological examination, MZUSP 32638, 163.0 mm SL). As noted in *H. armatus*, this shelf is considerably more developed in relatively large specimens (examined in dry skeletons preparations, AMNH 91342SD, 450 mm SL). Since *Hydrolycus tatauaia* reaches sizes comparable to that of *H. armatus*, it is possible that the shelf also is more developed in larger specimens of the latter species. *Hydrolycus wallacei* does not seem to reach sizes comparable to the latter two species (largest specimens examined, MCNG 21901, 335 mm SL), but it is possible that specimens larger than those available for study might have the frontal shelf more developed.

Cynodon, *Rhaphiodon*, and *Hydrolycus scomberoides* have the anterior shelf of the frontal relatively more expanded than in *H. armatus*. It also extends more ventrally relative to the longitudinal axis of the body than does the shelf in *H. armatus*. As a consequence a deep groove is formed between the shelf of the frontal and the orbitosphenoid. In *H. scomberoides* the anterior frontal shelf is truncated at the midline of the orbit. Although the anterior shelf of the frontal is expanded in all of the three taxa mentioned above, in each of them the shelf has a different shape. In *Rhaphiodon* the margin of the anterior shelf of the frontal is straight ventrally, whereas in *Cynodon* it has a curved edge. In *Hydrolycus armatus* the area between these two elements is shallower and more open. The different conditions of the anterior shelf of the frontal in cynodontines are partially shown in figures 4–8.

A frontal bone with an expanded platform located lateral to the supraorbital canal and projecting over the lateral ethmoid was noted by Buckup (1991: 215) for some characiforms e.g., *Charax*, *Cynopotamus*, *Tetragonopterus*, *Bryconops*, *Oligosarcus* and *Phenacogaster*. That condition resembles that of *Hydrolycus armatus* within cynodontines and was also noted for *Roestes* and *Gilbertolus*. However, the condition of a relatively expanded anterior shelf of the frontal of *Cynodon*, *Rhaphiodon*, and *Hydrolycus scomberoides* is considered derived. However, proposing this feature as synapomorphic for clades within the Cynodontinae is problematic due to the high degree of variation of the shelf in the three taxa, which complicates ordering them in a sequence that diverge from the putatively primitive condition. Furthermore, in *Hydrolycus wallacei* the shelf is absent, a condition different from that of other cynodontines. Consequently, the various conditions of the anterior shelf of the frontal are herein only hypothesized as autapomorphic for *Hydrolycus scomberoides*, *H. wallacei*, and *Rhaphiodon vulpinus*, with the condition of *Cynodon* considered synapomorphic for the genus.

23. Third posttemporal fossa bordered by epioccipital and exoccipital

All cynodontines possess a vertically ovate posttemporal fossa bordered by the epioccipital and exoccipital. The hypothesized plesiomorphic condition of the posttemporal openings in characiforms consists of a dorsal and a posterolateral fossa on each side of the neurocranium (Vari, 1979: 289; 1983: 37). The dorsal fossa is bordered by the supraoccipital, the parietal, and the epioccipital. The posterolateral fossa is bordered by the pterotic and epioccipital. A third posttemporal fossa bordered by the epioccipital and exoccipital was described for the Citharinidae and Distichodontidae by Vari (1979: 289), who also discusses the presence of such a fossa in cynodontines. Although a third posttemporal fossa also occurs in the families Curimatidae (Vari, 1983: 37), Hemiodontidae, and Parodontidae (Roberts, 1974), and *Hydrocynus* (Brewster, 1986) the fossa in those taxa is contained entirely within the epioccipital (Vari, 1983: 37; Brewster, 1986: 168).

In the present study, a third posttemporal fossa similar to that of cynodontines (i.e. bordered by both the epioccipital and exoccipital) was noted in *Roestes*, *Gilbertolus atratoensis*, *Heterocharax*, *Lonchogenys*, and *Gnathocharax* sp., and it is hypothesized as a derived condition. Whether or not this feature would provide support for a hypothesis of a close relationship between all the taxa involved depends on a detailed analysis of characiform relationships focusing on a higher level of universality.

24. Dorsal posttemporal fossa

Cynodon species lack the dorsal posttemporal fossa that is bordered by the supraoccipital, parietal, and epioccipital in characiform outgroups. The lack of this fossa, (also in the citharinids *Citharinus* and *Citharidium)* was hypothesized as derived by Vari (1979: 289). *Carnegiella vesca* among the Gasteropelecidae has a reduced dorsal posttemporal fossa (Weitzman, 1954: 218). In the present study such a fossa was found to be apparently lacking in the examined specimens of *Gasteropelecus sternicla*. The taxa mentioned above are not closely related to cynodontines, with the relationships of *Citharinus* and *Citharidium* being with the Distichodontidae (Vari, 1979). The relationships of the Gasteropelecidae are not fully resolved, but the family has been hypothesized as being most closely related to some characid lineage close to *Astyanax*, *Brycon*, and *Bryconamericus* (Weitzman, 1954: 231). Therefore, the lack of the dorsal posttemporal fossa is hypothesized as independent in citharinids, gasteropelecids, and *Cynodon* with the condition in the latter genus considered synapomorphic.

25. Basioccipital

In all cynodontine species the portion of the basioccipital that articulates with the vertebral column is flared posteriorly, forming a receptacle for the first centrum. This feature was previously noted by Nelson (1949: 501) for *Rhaphiodon vulpinus*. Ventrally, this posterior projection of the basioccipital is indented and forms two ventral processes. The posterior expansion of the basioccipital becomes even more pronounced in larger specimens in which it covers the first centrum almost completely. The first centrum in these specimens is only seen from a dorsal view, and ventrally from the indented portion of the basioccipital projection. A condition of the craniovertebral joint as described for cynodontines is unique to this assemblage among examined outgroups and hypothesized as a synapomorphy.

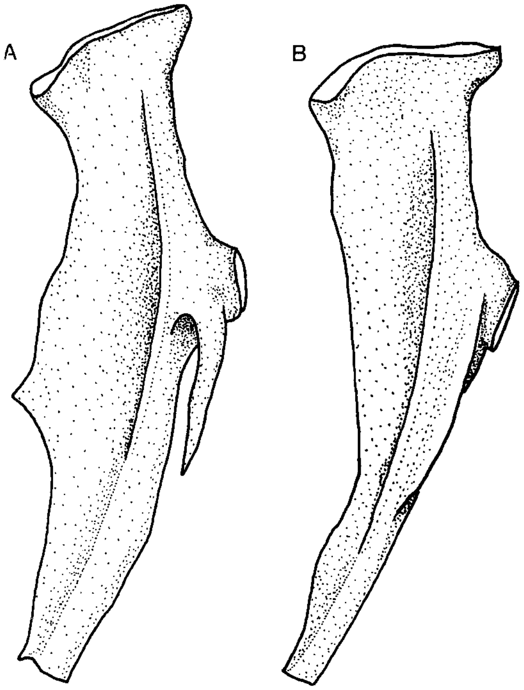

Fig. 9. Hyomandibula of (**A**) *Hydrolycus wallacei*, MZUSP 32638; and (**B**) *Cynodon gibbus*, MZUSP 32587; left side, lateral view, anterior to left.

SUSPENSORIUM AND HYOID ARCH

26. Hyomandibula

In all *Hydrolycus* species and *Rhaphiodon vulpinus*, the shaft of the hyomandibula that rests against the dorsomedial face of the preopercle is largely separate from the main body of the bone and forms a short process that extends ventrally from the condylar articular surface for the opercle (fig. 9A). In *Cynodon*, such a process is absent, and the contact of the hyomandibula with the preopercle is in the form of a groove, extending along the arm of the hyomandibula (fig. 9B),—a condition widespread in characiform outgroups. The condition present in *Hydrolycus* and *Rhaphiodon* is unique among examined outgroups.

Two alternative, equally parsimonious, hypotheses are possible for this character. The first is the acquisition of the process in the ancestor of the Cynodontinae clade, with its subsequent loss in *Cynodon*. Alternatively, the process may have arisen independently in the genera *Hydrolycus* and *Rhaphiodon*.

27. Symplectic

The symplectic in cynodontines is fairly elongate, its posterior portion bearing a bladelike process extending dorsally from its main body and fitting snugly into a groove in the medial face of the lower arm of the hyomandibula (fig. 10A). This groove is roofed over dorsally. As a consequence, the dorsalmost portion of the symplectic is completely enclosed within the hyomandibula, a condition absent in all other examined characiforms.

In most characiforms the contact of the symplectic with the hyomandibula is formed exclusively by a synchondral joint (fig. 10B) (which is also present in cynodontines) lateral to the dorsal extension of the bone.

Erythrinids also have a well-developed symplectic. However, the condition in this family differs from that in the Cynodontinae. In *Hoplerythrinus unitaeniatus* and *Erythrinus erythrinus* the lamellar process of the symplectic extends toward and contacts the metapterygoid (a slight contact of a lamellar process of the symplectic with the metapterygoid was also observed in *Boulengerella lateristriga* among ctenoluciids). The symplectic process and the hyomandibula are in slight contact along their margins. The symplectic in *Hoplias* (fig. 10C), in addition to contacting the metapterygoid, extends dorsally to also contact the medial surface of the hyomandibula. Although there is a shallow groove in the portion of the hyomandibula where the dorsal process of the symplectic fits, this groove is never roofed over dorsally as in cynodontines. Erythrinids are more closely related to ctenoluciids, lebiasinids, and *Hepsetus* (Vari, 1995), taxa which lack an extended contact between the symplectic and the hyomandibula, so that the development of an intimate contact between these two elements in cynodontines and erythrinids is most parsimoniously hypothesized to be an independent acquisition.

Given its unique nature within characiforms, the condition observed in the Cynodontinae is proposed as synapomorphic for the subfamily.

Ontogenetic variation in this character was observed in *Rhaphiodon vulpinus*. Specimens of 41.6–48.5 mm SL (USNM 231549) have the process on the symplectic extending dorsally. But at these sizes the groove on the hyomandibula, into which the process fits in larger specimens, is absent. In a larger specimen (BMNH 1935.6.4: 33–39, 95.3 mm SL) the groove and the dorsally situated roof associated with it are both present. At this stage the symplectic process fits in the groove of the hyomandibula but does not extend all the way into the roofed portion. In a larger specimen, MZUSP 32812 (191.0 mm SL), the process on the symplectic extends all the way into the roofed portion of the groove in the hyomandibula.

28. Metapterygoid teeth

Metapterygoid teeth are found in all *Hydrolycus* species and *Rhaphiodon vulpinus*. Of the two cleared and stained specimens of *H. scomberoides* examined (MZUSP 26177, 120.6 mm SL, MZUSP 32093, 143.4 mm SL), only the smaller has metapterygoid teeth, which are also present in one dry skeleton of *H. scomberoides* examined (AMNH 40087, 241.0 mm SL). It is unlikely that this is a function of ontogenetic change of this feature since the intermediate-size specimen (143.4 mm SL, mentioned above) lacks teeth on the metapterygoid. Rather it seems that there is intraspecific variation in the presence of these teeth in *H. scomberoides*. All examined specimens of *Cynodon* species lack metapterygoid teeth.

The metapterygoid teeth are found mainly on the dorsal half of the ossification, distributed in patches of different sizes. Some specimens have a broad patch of metapterygoid teeth and in others the patches are very small. The teeth are arranged in separate tooth plates fused with the metapterygoid or can be individually coalesced directly with that bone.

Within actinopterygians, toothed metapterygoids have been reported only for *Amia* and *Polypterus* (Arratia and Schultze, 1991) and were described as separate tooth plates that fuse to each other and with the metapterygoid and appear late in ontogeny.

The presence of teeth in the metapterygoid of *Hydrolycus* species and *Rhaphiodon vulpinus* is a unique condition in characiforms

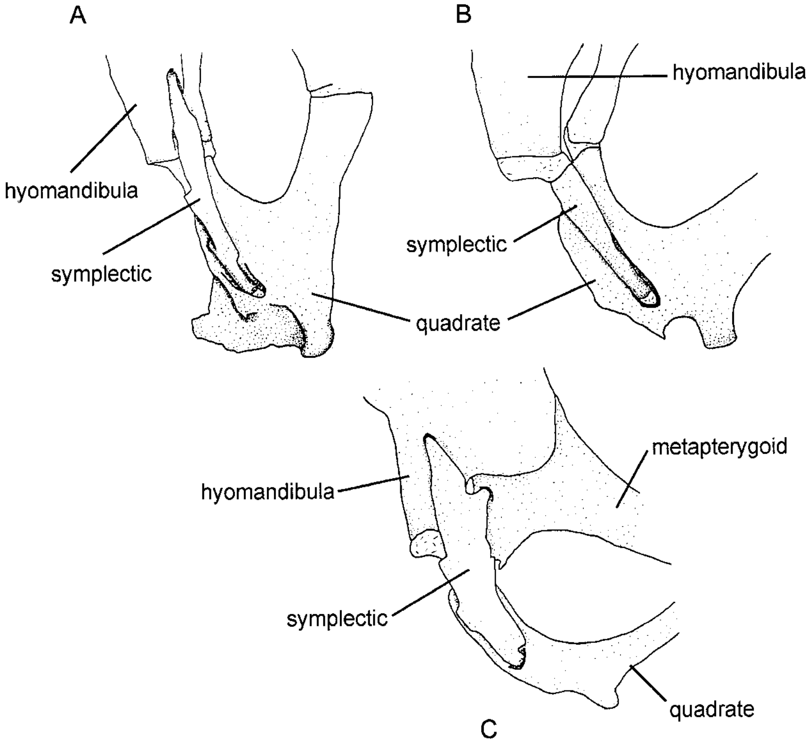

Fig. 10. Symplectic and adjoining bones of (**A**) *Hydrolycus armatus*, MZUSP 32607; (**B**) *Acestrorhynchus lacustris*, MZUSP 27893; and (**C**) *Hoplias* sp., MZUSP 32372; left side, medial view, anterior to right.

and there are two equally parsimonious explanations for the distribution of this character. The first is the acquisition of metapterygoid teeth in the ancestor of the Cynodontinae, with its subsequent loss in *Cynodon*. Alternatively, metapterygoid teeth may have had independent origins in *Hydrolycus* and *Rhaphiodon vulpinus*.

29. Mesopterygoid teeth

Cynodontines possess a broad patch of very small teeth that almost entirely cover the buccal surface of the mesopterygoid.

These teeth are present only in a few characiforms: they were observed in a few (but not all) *Acestrorhynchus* species and in *Lebiasina bimaculata* (coded as absent by Vari, 1995: 7). Within ctenoluciids, Vari (1995: 24) mentioned the presence of mesopterygoid teeth in *Boulengerella lateristriga* and *B. maculata*. Such dentition was also observed in one specimen of *B. cuvieri* (MZUSP 24162, 138 mm SL). Among erythrinids, such teeth were found in this study in *Hoplerythrinus unitaeniatus* and *Hoplias* sp. In the latter species (MZUSP 32372, 86.8 mm SL) there is only a very small patch of teeth on the lower surface of the mesopterygoid of the left side of the head. On the right side there are only two teeth loosely attached to the mesopterygoid. According to Vari (1995: 7) and Oyakawa (personal commun.) mesopterygoid teeth are absent from *Hoplias*. It is possible that there is interspecific and/or ontogenetic variation in this feature within *Hoplias*, *Boulengerella cuvieri*, and *Lebiasina bimaculata*. Within the Characinae (sensu Eigenmann, 1909), mesopterygoid teeth were observed in one specimen of *Roeboides* sp. (AMNH 40198, 64.9 mm SL) in the form of a toothplate attached to the mesopterygoid bone. A smaller specimen from the same lot (51.6 mm SL) and one specimen of *R. paranensis* (MZUSP 19830) lack mesopterygoid teeth. Teeth on the mesopterygoid were absent in all specimens of *Roeboides* examined by Lucena (1993: 116). In addition, mesopterygoid teeth have also been reported in *Crenuchus* (Buckup, 1991: 265).

Mesopterygoid teeth are a feature that varies among taxa that have been proposed as closely related to cynodontines: they are absent in *Roestes* and *Gilbertolus*, but present in most *Acestrorhynchus* species. Therefore, the presence of teeth in the mesopterygoid cannot be unequivocally proposed as an additional synapomorphy for the Cynodontinae at this time.

The presence of teeth in other characiform groups mentioned above (except *Acestrorhynchus*) is most parsimoniously interpreted as an independent acquisition relative to cynodontines.

30. Ectopterygoid teeth

All cynodontines have very small teeth arranged in a patch covering most or all of the medial surface of the ectopterygoid bone (fig. 11).

Teeth on the ectopterygoid occur in diverse characiforms including *Acestrorhynchus* (Menezes, 1969: 35), the Ctenoluciidae (Vari, 1995: 23), various lebiasinids, the Erythrinidae (Weitzman, 1964: 144-145), *Oligosarcus* (Menezes, 1969: 12,15), the Serrasalminae (Machado-Allison, 1983: 169, and 1985: 33 for ontogenetic variation), the Characidiinae (Buckup, 1993: 241), *Crenuchus* (Buckup, 1991: 265), and *Xenocharax*. Weitzman (1964: 134) suggested that the presence or absence of ectopterygoid teeth may be of little phylogenetic importance, because of considerable intraspecific variation and variation among closely related species.

However, the morphology and pattern of teeth arrangement in the ectopterygoid bone seem to provide some information about relationships in a few characiform groups. Within ctenoluciids, for instance, Vari (1995: 23) reported differences in ectopterygoid teeth patterns between *Ctenolucius* and *Boulengerella* and hypothesized that the condition of very small teeth was derived for the latter genus. The serrasalmids *Serrasalmus* and *Pristobrycon* have cuspidate ectopterygoid teeth (Machado-Allison, 1985: 33) as opposed to the conical teeth present in the majority of characiforms. These were hypothesized by that author as a synapomorphy for these genera (*Oligosarcus* was herein observed to also have cuspidate ectopterygoid teeth). Within erythrinids, the size and distribution of teeth on the ectopterygoid bone also differ. No differences in pattern of ectopterygoid teeth were observed in cynodontines. All members of the group have a broad patch of very small teeth covering most of the ventral surface of that bone, a condition similar to that described by Vari (1995: 23) for *Boulengerella*. In the remaining characiform outgroups in which mesopterygoid teeth are present, they are usually larger relative to the condition observed in cynodontines and *Boulengerella*. The latter genus is, however, more closely related to *Ctenolucius* (Vari, 1995) which has a different pattern of ectopterygoid teeth. The condition of the ectopterygoid teeth in *Boulengerella* and cynodontines is most parsimoniously interpreted as independent acquisitions, with the condition in the latter taxa hypothesized as synapomorphic.

31. Ectopterygoid-metapterygoid contact

In all cynodontines the posterior portion of the ectopterygoid is firmly attached to the anteroventral portion of the metapterygoid. Among characiforms such an ectopterygoid-metapterygoid contact was observed only in *Hepsetus*. In the examined outgroups the posterior portion of the ectopterygoid contacts only the anterodorsal portion of the quadrate, a condition that also occurs in cynodontines. *Hepsetus* is more closely related to the Erythrinidae and Ctenoluciidae (Vari, 1995); therefore, this additional contact of the posterior portion of the ectopterygoid to the anteroventral portion of the metapterygoid is most parsimoniously interpreted as an independent acquisition in *Hepsetus* and the Cynodontinae, with the condition in cynodontines hypothesized as synapomorphic.

32. Ectopterygoid-mesethmoid contact

All cynodontines have longitudinally elongate ectopterygoids extending well beyond the anterior portion of the palatine, and constituting the anteriormost portion of the palatine arch. Longitudinally elongate ectopterygoids are not unique to cynodontines, also occurring in ctenoluciids, *Hepsetus* and *Acestrorhynchus*.

The type of contact between the ectopterygoid and the area near the vomer-mesethmoid joint is distinct in *Cynodon* from that in *Hydrolycus* and *Rhaphiodon*. In *Cynodon* the anterior tip of the ectopterygoid contacts the posterior portion of the mesethmoid just dorsal to the ventral processes on the latter ossification. Although *Hydrolycus* and *Rhaphiodon* also have an elongate ectopterygoid, this ossification is in close contact with the ventral surface of the vomer (see character 11) and its anteriormost tip does not contact the mesethmoid in the same way it does in *Cynodon*.

Typically in characiforms the ectopterygoid is connected to the area near the vomer-mesethmoid articulation by a sheath of connective tissue; however, these elements are not in direct contact, e.g., the Heterocharacini, sensu Géry (1966), Cynopotaminae, Menezes (1976), *Roestes*, *Gilbertolus*, *Charax*, *Agoniates*, lebiasinids, and gasteropelecids. In all of these taxa the palatine bone constitutes the anteriormost portion of the palatine arch, with the tip of the ectopterygoid lying posterior to it.

In *Acestrorhynchus* species the ventral surface of the vomer is anteriorly expanded over the ventral surface of the mesethmoid and bears two ventral process to which the palatine and the ectopterygoid abut. The ectopterygoid contacts the vomer along the area of contact between the mesethmoid and vomer. Within erythrinids, *Hoplias* has a tooth-bearing ossification connected to the anterior end of the ectopterygoid. The anterior tip of this ossification contacts the ventral process of the mesethmoid. However the identity of this ossification is unclear (Weitzman, 1964: 146; Roberts, 1969: 417). In *Hepsetus* the region occupied by the mesethmoid and vomer is a single ossification and the ectopterygoid inserts into two grooves in the anteroventral surface of this element (Roberts, 1969: 406). In all these taxa the ectopterygoid is not in direct contact with the mesethmoid. Among examined characiforms a direct contact between these two elements was observed in *Ichthyborus quadrilineatus* and *I. besse* species more closely related to the Citharinidae-Distichodontidae clade (Vari, 1979). The type of attachment of the ectopterygoid to the vomer and mesethmoid in these *Ichthyborus* species is unique to those taxa and is of a different type than that in cynodontines. The condition observed in *Cynodon* is hypothesized as derived for cynodontines and synapomorphic for the genus.

33. Branchiostegal rays

All cynodontines have five branchiostegal rays. Among examined characiforms outgroups, five branchiostegal rays is also present in erythrinids (Weitzman, 1964: 147), the characidiin *Characidium fasciatum* (Buckup, 1992: 1069), and among hemiodontids in some species of *Hemiodus* and *Bivibranchia* (Roberts, 1974: 417, 420). Five branchiostegal rays were also noted for *Crenuchus* (Buckup, 1991; Vari, 1995), *Piaractus nigripinis* (Roberts, 1969: 422), and *Thoracocharax* (Weitzman, 1960). Géry (1962: 271) mentions that *Agoniates ladigesi* has five branchiostegal rays, of which the anterior two rays are rudimentary. The specimen of *Agoniates* sp. examined in the present study has, however, only four well developed branchiostegal rays.

The presence of four branchiostegal rays is the most common condition in characiforms. Five branchiostegal rays are present in the groups discussed above. A few groups have only three branchiostegal rays (e.g., pyrrhulinines, Weitzman, 1964: 150; and some anostomids of the genera *Pseudanos* and *Anostomus*, Winterbottom, 1980: 39).

A high number of branchiostegals has been considered the primitive condition (McAllister, 1968: 68, 176). All the taxa mentioned above that possess five branchiostegal rays have been hypothesized as being more closely related to characiforms with four branchiostegal rays (see references above). Therefore, at the level of inclusiveness of the present study, the presence of five branchiostegal rays is most parsimoniously interpreted as being derived and having independent origins. The presence of five branchiostegal rays is, as a consequence, proposed as a synapomorphy for the Cynodontinae.

34. Branchiostegal rays on posterior ceratohyal

All cynodontines have two branchiostegal rays on the posterior ceratohyal. This condition is present only in *Acestrorhynchus* and *Ctenolucius* (Vari, 1995: 25) among examined outgroups. All other characiforms have only a single ray on the posterior ceratohyal.

Ctenolucius is more closely related to *Boulengerella* and other taxa with one branchiostegal ray on the posterior ceratohyal (Vari, 1995) and, therefore, the presence of two branchiostegal rays in the posterior ceratohyal is interpreted as derived at the level of inclusiveness of the present study, and hypothesized as being independently acquired in *Ctenolucius* and cynodontines.

In view of the evidence pointing toward phylogenetic relationships between *Acestrorhynchus* and the Cynodontinae, the presence of two branchiostegal rays in the posterior ceratohyal cannot be unambiguously proposed as an additional synapomorphy for the Cynodontinae at this time.

JAWS AND DENTITION

35. Dentary canines

Cynodontines possess a single row of conical teeth in the upper and lower jaws. The teeth are variable in size with small conical teeth alternating with larger canines. One of the anterior dentary canines is enlarged relative to the remaining teeth and extends into the upper jaw when the mouth is closed (see character 36). Enlarged dentary canines are not restricted to cynodontines among characiforms. Relatively pronounced dentary canines also occur in *Acestrorhynchus*, *Hydrocynus*, *Hepsetus*, *Ichthyborus*, the Heterocharacini, the Erythrinidae, and the Cynopotaminae. In some of these taxa, the canines can get relatively stout, especially in large specimens (e.g., *Hydrocynus* and *Hoplias*); however, they are relatively shorter than in cynodontines. In most of these taxa the enlarged canines are not restricted to a single tooth but there are instead a number of relatively large canines of similar size along the dentary and also in the upper jaw (e.g., *Hydrocynus*, *Hoplias*, and *Galeocharax*). In cynodontines one of the anterior dentary canines is always considerably larger than the remaining teeth. A similar canine enlarged to the same degree relative to the remaining comparable teeth is observed in *Roestes*, *Gilbertolus*, and *Agoniates*.

Within cynodontines, a further increase in the relative size of the dentary canine occurs in *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus*. In these species the dentary canine is much more developed than in *Cynodon*, *Hydrolycus wallacei*, and *Rhaphiodon*, in which only the dorsalmost tip of the dentary canine extends dorsally to reach the snout opening. However, in *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* it extends far dorsally into the snout opening. The highly developed dentary canines of *H. tatauaia*, *H. scomberoides*, and *H. armatus* represent a unique condition within characiforms synapomorphic for this assemblage.

36. Foramen in anterior portion of snout for dentary canine

The highly developed dentary canine in cynodontines extends dorsally into the upper jaw. The anterior portion of the snout has been restructured, resulting in an opening through which the dentary canine fits when the mouth is closed. A large opening in the anterior portion of the snout is delimited anteriorly and laterally by the premaxilla, posteriorly and posteromedially by the ascending process of the maxilla, and anteromedially by the vomer-mesethmoid (fig. 11). This opening lies just ventral to the nasal openings in the neurocranium, and the tips of the highly enlarged dentary canine of *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* extend through the nasal openings when the mouth is closed.

The arrangement of the bones in the anterior part of the snout in characiform outgroups with enlarged canines differs from that described for cynodontines. In *Roestes*, *Gilbertolus*, and *Agoniates* the enlarged dentary canine extends dorsally to fit in a space delimited anteriorly and laterally by the premaxilla and the ascending process of the maxilla, and medially by the palatine. The most pronounced difference from the condition observed in cynodontines is that the ascending process of the maxilla passes posterior to the dentary canine in cynodontines while in *Roestes*, *Gilbertolus*, and *Agoniates* this process lies anterior to the dentary canine. The ascending process of the maxilla in those three taxa rests on the posterior surface of the premaxilla, the typical condition

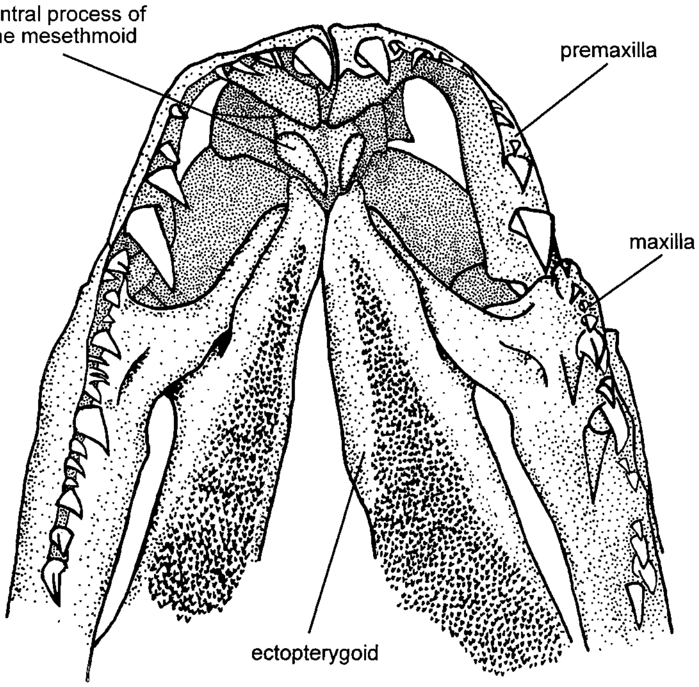

Fig. 11. Upper jaw, ectopterygoid and anterior portion of neurocranium of *Hydrolycus scomberoides*, AMNH 40087, dry skeleton, ventral view, anterior to top.

in characiforms (e.g., *Brycon*, Weitzman, 1962: 32). In cynodontines the ascending process of the maxilla has shifted posteriorly and is not in close association with the premaxilla, leaving an intervening space through which the dentary canine passes.

In *Acestrorhynchus* (Menezes, 1969) and *Hepsetus* the upper jaw has a different modification to receive the canine teeth from the dentary. These two genera have relatively elongate premaxillae, which usually bear two foramina in *Acestrorhynchus* and one in *Hepsetus* through which the dentary canines passes when the mouth is closed. *Hydrocynus* has wide spacing of teeth in both jaws (Brewster, 1986: 187) with the teeth on the upper jaw being intercalated by teeth from the lower jaw when the mouth is closed. The enlarged teeth on the anterior portion of the snout lie outside the mouth when it is closed, and they fit into shallow grooves between the teeth of the opposing jaw.

The condition of the foramen for the dentary canine in the anterior portion of the snout, with the ascending process of the maxilla shifted posteriorly, not contacting the premaxilla, and forming the posterior and lateromedial portion of the foramen, is unique for cynodontines among examined characiforms and hypothesized as synapomorphic.

37. Replacement tooth trenches

There is considerable variation in the morphology of the replacement tooth trenches in characiforms. Monod (1950) and Roberts (1967) described different types of replacement tooth trenches in the order. According to Roberts, cynodontines, *Hepsetus*, *Salminus*, and the Ctenoluciidae have ‘‘shallow replacement trenches at the base of the functional tooth rows, and the replacement teeth lie right at the base of the functional teeth and are readily observed.’’ The majority of other characiforms were described as having more deeply excavated replacement tooth trenches with the replacement teeth lying considerably below the bases of the corresponding functional teeth (Weitzman, 1962: 33; Roberts, 1967: 233). In cynodontines, all teeth in the mandibular replacement trench are horizontally aligned, with the tip of the replacement teeth projecting posteriorly. In the upper jaw, including the premaxilla and maxilla, there is no conspicuous trench, but the replacement teeth are also horizontally and posteriorly directed. In the majority of examined characiform outgroups, including *Roestes*, *Gilbertolus*, *Acestrorhynchus*, the Heterocharacini, and *Charax*, the replacement teeth are placed more deeply in the trench and angled vertically to slightly posterodorsally relative to the functional teeth.

Horizontally and posteriorly directed teeth in the replacement trench also occur in *Hepsetus* (Monod, 1950; Brewster, 1986: 187) and *Hydrocynus* (Roberts, 1967: 233; Brewster, 1986: 187). The morphology of the replacement tooth trench in the latter genus differs from that of *Hepsetus* and the Cynodontinae (Brewster, 1986: 170–171). In the Ctenoluciidae the replacement teeth are also positioned at a 90° angle relative to the functional teeth, in a horizontal relative to the longitudinal axis of the body, and not vertically or slightly angled as in the majority of characiform outgroups. The replacement teeth are very small with their tips somewhat posteriorly directed. *Hepsetus* and ctenoluciids are hypothesized as being more closely related to erythrinids and lebiasinids (Vari, 1995), families with replacement tooth trenches more similar to that described for the majority of characiforms. The similar conditions shared by *Hepsetus* and cynodontines are most parsimoniously hypothesized as independent acquisitions, with the cynodontine condition considered synapomorphic.

BRANCHIAL ARCHES

38. Gill-rakers

All gill-rakers on the leading portion of the first ceratobranchial in cynodontines consist of small, flat bony plates with very small spines covering their entire lateral surface (fig. 12A, B). This condition is present only in *Acestrorhynchus* (Menezes, 1969) among examined outgroups.

Within characiforms a variety of different forms of gill-rakers occurs along the length of the first ceratobranchial, in addition to that described above for cynodontines and *Acestrorhynchus*. In the majority of characiforms the first ceratobranchial has conical, elongate gill-rakers with or without teeth. Erythrinids, ctenoluciids, and *Hepsetus* (Roberts, 1969: 423) and genera assigned to the Cynopotaminae (Menezes, 1976) have elongate gill-rakers along most of the first ceratobranchial, with a few anterior reduced rakers, similar in shape to those described for cynodontines and *Acestrorhynchus*.

Roberts (1969: 423) considered the condition present in *Rhaphiodon* and *Acestrorhynchus* as primitive for characiforms based on the similarity of the gill-rakers in these groups and some primitive actinopterygians (e.g., *Polypterus*, *Lepisosteus*, and *Esox*). However, given the widespread occurrence of elongate gill-rakers along the first ceratobranchial in different characiform lineages, the first ceratobranchial covered with spiny gill-rakers over its entire length in cynodontines and *Acestrorhynchus* is most parsimoniously interpreted as being derived at the level of inclusiveness of the present analysis.

In view of the evidence pointing toward phylogenetic relationships between *Acestrorhynchus* and the Cynodontinae the presence of spiny gill-rakers cannot be unambiguously proposed as an additional synapomorphy for the Cynodontinae at this time.

39. Spines on gill-rakers

The differences in the spines on the free dorsal margin of the gill-raker within the Cynodontinae are noteworthy. Enlarged spines on the free dorsal margin of the gill-rakers of the first ceratobranchial were observed in *Cynodon* and *Hydrolycus wallacei* (fig. 12A). These spines are considerably larger than the remaining spines. Usually one of the spines is distinctly larger, with its length more than half of the vertical length of the bony plate of the gill-raker. Enlarged spines are more evident on the gill-rakers situated toward the posterior end of the first ceratobranchial. *Hydrolycus tatauaia*, *H. scomberoides*, *H. armatus*, and *Rhaphiodon* share a different condition (fig. 12B) in which the spines are not very developed relative to the remaining spines on the surface of the gill-raker, being only slightly larger than the latter.

Acestrorhynchus species, the only other characiform taxa that have short, flattened gill-rakers covering the entire first cerato-

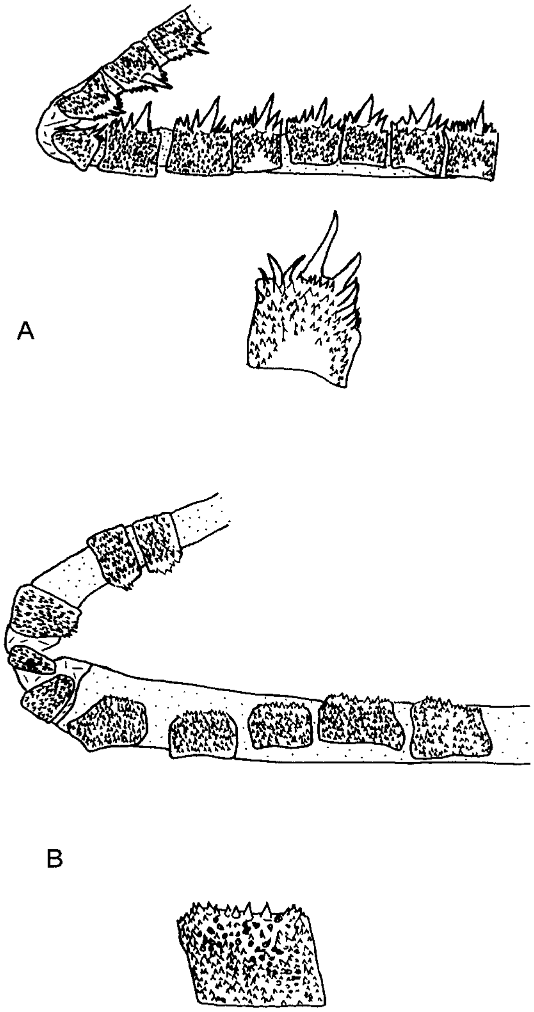

Fig. 12. Posterior portion of first gill arch with enlarged gill raker of (**A**) *Cynodon septenarius*, MZUSP 32585, and (**B**) *Hydrolycus armatus*, MZUSP 32607; lateral view, right side, anterior to right.

branchial, have considerably enlarged spines on the free upper edge of the gill-rakers. In all examined species except *A. falcirostris* and *A. nasutus* there are one or more prominent spines larger than the others. The latter two species lack a single, more prominent spine on the dorsal margin of the gill-rakers, with all spines on the free upper edge of the gill-raker being rather similar in size (Menezes, 1969: 61,74-75). Nevertheless, the spines on the free upper edge of the gill-raker in these species are also considerably larger than the ones on the surface of the gill-rakers. In view of the current hypothesis of relationships between *Acestrorhynchus* and cynodontines, the presence of relatively enlarged spines on the dorsal margin of the gill-rakers of the latter species could be proposed as the primitive condition. Ontogenetic information provides additional support for this hypothesis. In juveniles of both *Cynodon* (AMNH 32485SW, 35 mm SL), *Rhaphiodon* (USNM 231549 41.7–50.1 mm SL), and *Hydrolycus* (MCNG 3204, 25.6–38.6 mm SL) the spines on the free upper edge of the gill-raker are conspicuously enlarged. In larger specimens of *Rhaphiodon* they become smaller relative to the remaining spines on the surface. Therefore, the condition observed in juveniles, provides information about the direction of the character transformation, with the condition observed later in their development, i.e., spines on the free edge of the gill-raker not conspicuously enlarged relative to those on its surface, considered derived.

This character is most parsimoniously hypothesized as synapomorphic for the clade formed by *Hydrolycus tatauaia*, *H. scomberoides*, and *H. armatus* with an independent origin in *Rhaphiodon*.

40. First hypobranchial

The anterior portion of the first hypobranchial in cynodontines is anteroventrally prolonged into a prong-shaped process that extends from the ventrolateral margin of the main body of the bone (fig. 13). The anterior articular cartilaginous surface of the first hypobranchial is situated on the tip of this process.

In examined characiform outgroups, the first hypobranchial is either a flattened (e.g., Erythrinidae, Lebiasinidae, *Roestes*, *Gilbertolus*, *Gnathocharax*, *Charax*, and *Brycon*) or an elongate ossification (e.g., *Acestrorhynchus*, ctenoluciids, and *Hepsetus*) that varies from straight to slightly slanted anteroventrally, but which typically lacks the conspicuous elaboration noted above for cynodontines. Such unelaborated ossifications were also observed among African characiforms (e.g., *Xenocharax* and *Distichodus fasciolatus*), hypothesized as primitive members of the order (Fink and Fink, 1981). Unelabo-

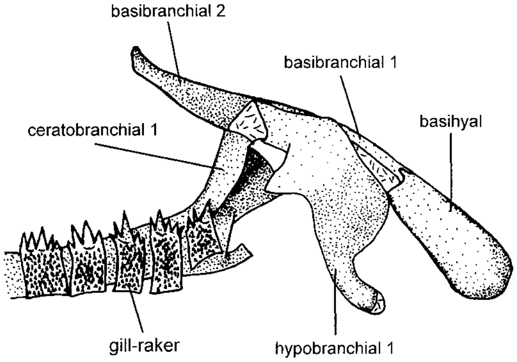

Fig. 13. Basihyal, first hypobranchial, first and second basibranchials, and anterior portion of first ceratobranchial of *Cynodon gibbus*, MZUSP 32587; lateral view, right side, anterior to right.

rated hypobranchials have been hypothesized as plesiomorphic (Vari, 1983: 11). Certain anostomids (*Laemolyta taeniata*, *Anostomus anostomus*), prochilondontids (*Prochilodus*), and *Serrasalmus* have some kind of anterior elaboration on the first hypobranchials. However, none of these groups shows the degree of elaboration presented by cynodontines. In all these groups, the anterior process of the first hypobranchial is much shorter and less curved than in cynodontines. In *Serrasalmus*, in addition, the process is dorsoventrally flattened with no associated articular surface.

The condition observed in cynodontines is unique within characiforms and hypothesized as synapomorphic.

41. First ceratobranchial

The first ceratobranchial in cynodontines has its anterior portion curved dorsally, forming a distinct angle relative to the longitudinal axis of the remaining portion of that ossification. In *Hydrolycus* and *Rhaphiodon*, the angle and the extension of this projection is only slightly pronounced, but it is clearly distinct from the condition observed in characiform outgroups in which the first ceratobrachial is straight over its entire length. A condition similar to that observed in *Hydrolycus* and *Rhaphiodon* was observed only in the cynopotamine genus *Galeocharax*.

The dorsally directed projection of the first ceratobranchial is particularly well developed in *Cynodon* (fig. 13), in which genus the projection is about twice as long as in *Hydrolycus* and *Rhaphiodon* and the angle of the projection relative to the remaining portion of that ossification is much more pronounced. A straight, elongate first ceratobranchial with no anterior projection is considered a primitive condition for characiforms (Vari, 1983: 11). *Galeocharax* is hypothesized to be more closely related to taxa with straight first ceratobranchials (e.g., *Acestrocephalus*, and *Charax*; Menezes, 1976, Lucena, 1993) and, therefore, the dorsally directed first ceratobranchial in *Galeocharax* is most parsimoniously hypothesized as an independent acquisition from that in cynodontines.

The dorsally directed first ceratobranchial of cynodontines forming an angle relative to the longitudinal axis of the remaining portion of that ossification is considered a synapomorphy for cynodontines with its further enlargement in *Cynodon* considered a synapomorphy for the genus.

ANTERIOR VERTEBRAE

42. First vertebra

Cynodon species possess two processes on the ventral portion of the first centrum that lie just dorsal to the ventral processes of the basioccipital (see character 25), and are directed posteriorly and slightly laterally. These processes were observed in all examined cleared and stained specimens and dry skeletons of *Cynodon* species, including a juvenile (AMNH 32485, 35.0 mm SL) in which two small bony projections are present on the ventral surface of the first centrum.

In one specimen of *Hydrolycus wallacei* (MZUSP 32638, 152.2 mm SL; this feature could not be examined in the other available specimen) two small bumps of bone are present in the same region of the ventral processes as in *Cynodon* but are much less developed. Weakly developed processes were also observed in larger specimens of *Hydrolycus armatus* (AMNH 91342, 450 mm SL), but were lacking in one specimen of *Hydrolycus* sp. (AMNH 40048, 117.7 mm HL). Ventral processes on the first centrum are lacking in the examined specimens of *H. tatauaia*, *H. scomberoides*, and *Rhaphiodon vulpinus*.

Ventral processes on the first centrum are lacking in all examined characiform outgroups and their presence in cynodontines is considered a derived feature. In the present study only well-developed processes on the ventral surface of the first centrum in *Cynodon* species will be considered due to the lack of more specimens of *Hydrolycus wallacei* and *Hydrolycus tatauaia* for examination. Additional specimens could show that the presence of bony projections on the ventral portion of the first centrum is more widespread among cynodontines. However, the relatively more highly developed condition of these processes which is unique to *Cynodon*, can be considered a synapomorphy for this genus.

43. Neural complex of Weberian apparatus

In all cynodontine species the neural complex of the Weberian apparatus does not directly contact the posterior surface of the neurocranium. In the primitive condition among characiphysans (Fink and Fink, 1981: 324) the neural complex is tilted anteriorly and articulates with the posterior margin of the neurocranium. Among cynodontines the neural complex has a more vertical orientation relative to the longitudinal axis of the body, resulting in a gap between its anterior margin and the posterior margin of the neurocranium. At the anterior edge of the neural complex there is a short process onto which attach ligaments arising from the posterior edges of the supraoccipital crest and exoccipital.

The lack of contact of the neural complex with the posterior portion of the neurocranium in cynodontines is unique among examined outgroups, and is considered a synapomorphy for the group.

In all cynodontines the transverse processes of the second and third vertebrae contact each other in an interdigitating pattern that forms an immovable articulation, a condition unique within examined characiforms. Such an interdigitating articulation is primarily the consequence of two modifications of the transverse processes of the second and third vertebrae described below (characters 44 and 46).

44. ‘‘Transverse process’’ of second vertebra

The second vertebra of cynodontines bears a lateral process designated as the ‘‘transverse process’’ by Nelson (1949). This process is highly developed and slightly posterodorsal oriented. It is bifurcated distally into two short processes that clasp the transverse process of the third neural arch (figs. 14–16).

The presence of a ‘‘transverse process’’ on the second centrum is not unique to cynodontines among examined characiforms. Such a process also occurs in erythrinids, ctenoluciids, *Hepsetus*, Heterocharacini, *Gnathocharax, Roestes*, *Gilbertolus*, and in some *Acestrorhynchus* species. However, in all of these taxa the process is only slightly developed and is represented only by a small prominence of bone situated ventral to the intercalarium and the transverse process of the third neural arch. There are ligamentous attachments between the latter process and the ‘‘transverse process’’ of the second vertebra. In erythrinids the process is enlarged relative to that in the remaining examined outgroups and although it contacts the transverse process of third neural arch, it does not bifurcate distally as it does in cynodontines.

The modification of the ‘‘transverse process’’ of the second vertebra in cynodontines is a unique condition among examined characiforms and hypothesized as a synapomorphy for that clade.

45. Lateral process of second vertebra

The lateral process of the second vertebra is highly modified in cynodontines. In the usual characiform condition the process is an elongate element extending laterally and somewhat anteriorly with no modifications of its distal portions (see Weitzman, 1962: 36 for *Brycon meeki*).

Within cynodontines a number of differences from the generalized characiform condition are observed. *Cynodon* and *Hydrolycus* species (figs. 14 and 15, respectively) (except *Hydrolycus scomberoides*, see further comments on the condition of this species below) have the lateral process shortened laterally and greatly expanded dorsoventrally. It extends slightly anteriorly proximally and then turns posteriorly distally. Ventrally, at its tip, there is a broad surface for the attachment of ligamentous tissue connecting with the pectoral girdle. The posterolateral margin of the process ends in two

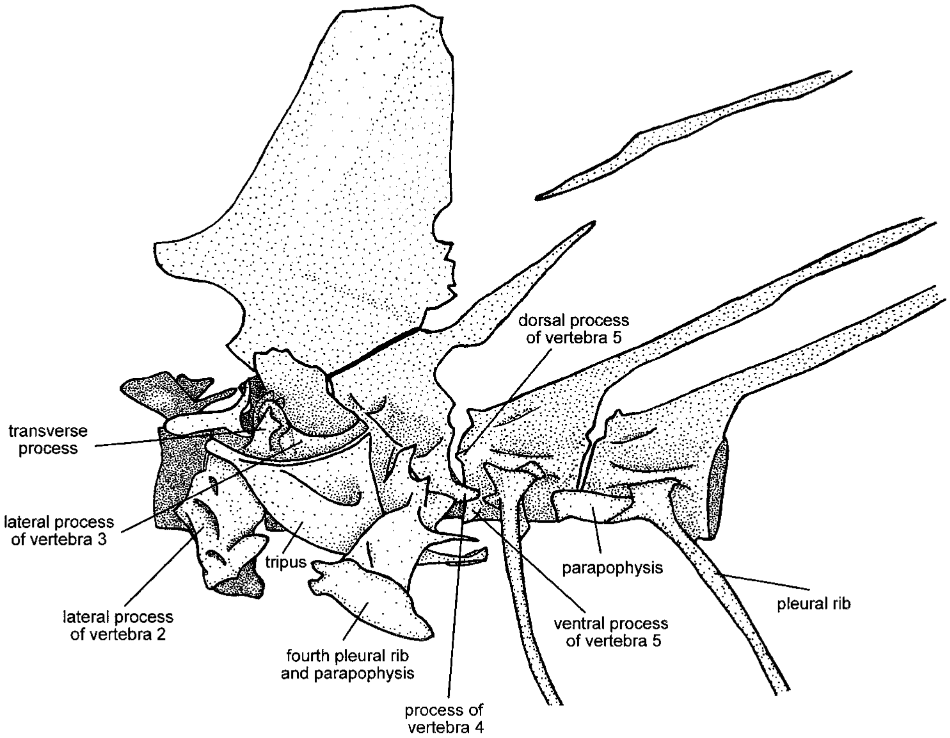

Fig. 14. Weberian apparatus of *Cynodon gibbus*, MZUSP 32587; left side, lateral view, anterior to left.

short processes. Ligamentous tissue attaches to the posterior margin between the two processes and extends to the lateral process of the fourth vertebra. The anteromedial portion of the lateral process of the second vertebra is in contact with the posterior margin of the basioccipital.

Hydrolycus scomberoides has a slightly different condition from that described above. In this species the lateral process of the second vertebra is dorsoventrally flattened and posteriorly directed. The distal tip of the process has a broad surface for the attachment of ligamentous tissue connecting with the pectoral girdle as described for *Cynodon* and the remaining *Hydrolycus* species. However, instead of being directed ventrally, this broad surface in *H. scomberoides* is directed laterally. Anteriorly the lateral process contacts the posterior margin of the basioccipital. The posterolateral margin is a simple structure without processes that serves as an area of attachment for the ligamentous tissue from the process of the fourth vertebra.

The lateral process of the second vertebra is highly modified in *Rhaphiodon vulpinus* (fig. 16) relative to both the primitive characiform condition and the condition in the remaining cynodontines. The condition in *R. vulpinus* has been previously briefly described by Weitzman (1962: 36) and was illustrated by Nelson (1949: 517). In a dorsal view there is a triangular-shaped flat sheet of bone extending laterally and posteriorly under the tripus. Ventrally a short process extends anteriorly, and overlapping the ventral portion of the first centrum. A longer process extends posteriorly and slightly laterally under the ventral portion of the centrum of the third vertebra.

The highly modified lateral process of the second vertebra in cynodontines is a unique condition among characiforms and is interpreted as synapomorphic for the subfamily with the conditions in *H. scomberoides* and *Rhaphiodon vulpinus* constituting autapomorphies for these species.

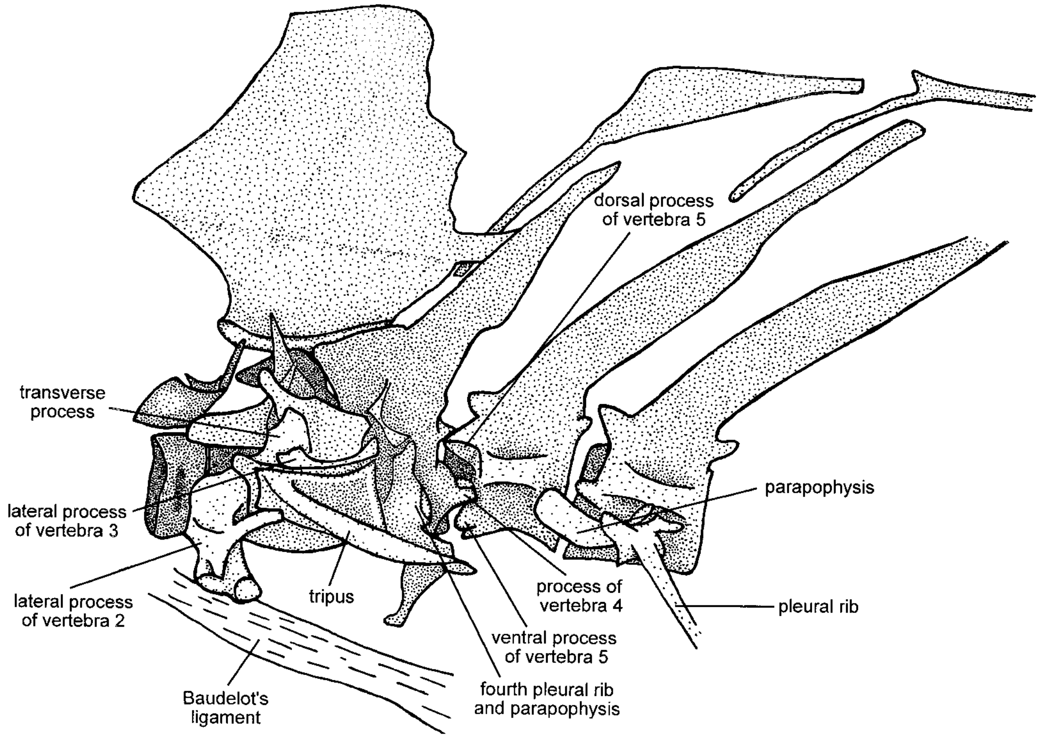

Fig. 15. Weberian apparatus of *Hydrolycus armatus*, MZUSP 32607; left side, lateral view, anterior to left.

46. Lateral process of third vertebra

All cynodontine species except *Hydrolycus wallacei* possess a lateral process on the third vertebra in addition to the typical characiform transverse process of the third neural arch. This additional process abuts the lateral portion of the ‘‘transverse process’’ of the second vertebra that extends posteriorly to contact the third vertebra. In *Rhaphiodon*, *Hydrolycus tatauaia*, and *H. armatus*, the process is relatively well developed, originating just ventral to the lateral portion of the ‘‘transverse process’’ of the second vertebra, and is more evident in larger specimens. A slightly different condition occurs in *Cynodon* and *Hydrolycus scomberoides*. In these species the process is relatively shorter than in *Rhaphiodon*, *Hydrolycus tatauaia*, and *H. armatus* and apparently originates posteriorly to the portion of the ‘‘transverse process’’ of the second vertebra that contacts the transverse process of the third neural arch (fig. 14), rather than ventral to that process as in *Rhaphiodon*, *Hydrolycus tatauaia*, and *H. armatus* (figs. 15 and 16). This process is lacking as a separate element in the two examined cleared and stained specimens of *Hydrolycus wallacei*. Among examined characiform outgroups only *Ctenolucius* has a process similar to that described for *Rhaphiodon*, *Hydrolycus tatauaia*, and *H. armatus*.

The explanations for the distribution of this character are equivocal under any type of optimization used. It is my opinion that this ambiguity is partly a consequence of the poor understanding of the anatomy of this process. A better understanding of this feature would come from a more detailed examination of this element by means of finer dissections at the region of the third vertebra, examination of different ontogenetic stages of this features in specimens having the two different conditions described above, and examination of additional specimens of *Hydrolycus wallacei* to confirm the absence of the process in this species. It was not possible to carry out a more detailed study of this char-

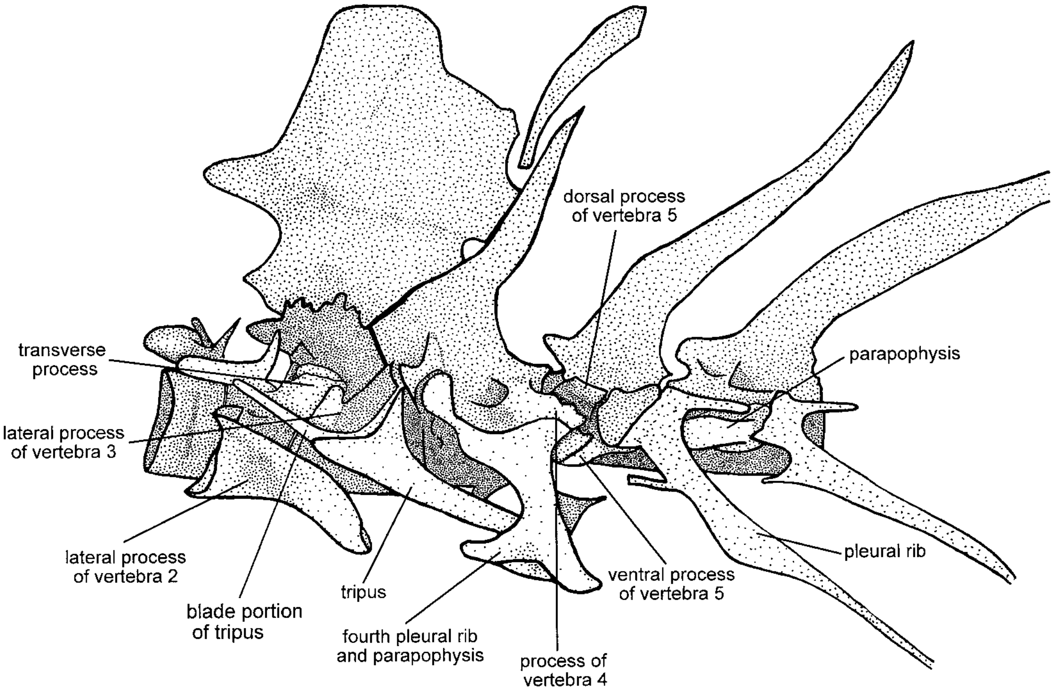

Fig. 16. Weberian apparatus of *Rhaphiodon vulpinus*, MZUSP 32812; left side, lateral view, anterior to left.

acter at this time. Therefore, the additional lateral process on the third vertebra will not be hypothesized as a derived feature at any level for the present analysis.

The contact between the ‘‘transverse process’’ of the second vertebra with the processes of the third vertebra described under characters 44 and 46 forms the interdigitating articulation mentioned above. In large specimens of *Hydrolycus armatus* (e.g., AMNH 40048, 117.7 mm HL) an additional process originates at the posteroventral portion of the second vertebra and extends posteriorly to abut the lateral process of the third vertebra, contributing an additional element to this pattern of the articulation.

The transverse process of the third neural arch is shorter in cynodontines than in examined characiform outgroups. Some variation in the shape is observed within the group, with *Hydrolycus* species (especially *H. armatus* and *H. wallacei*) having a slightly more elongate process. Variation in this feature among cynodontines will not be taken into further consideration at this time because of the difficulty of unambiguously establishing discrete units to account for this variation.

47. Tripus

The tripus of *Rhaphiodon vulpinus* is anteroposteriorly elongate (fig. 16). The blade portion of the tripus is particularly elongate anteriorly, with its tip almost reaching the posterior of the neurocranium. The tripus in the remaining cynodontine species is similar to that of characiform outgroups in which the blade portion of the tripus does not (or only slightly) extend anteriorly of the main body of the tripus. An anteroposteriorly elongate tripus was described for ctenoluciids by (Vari, 1995: 27), in which, the elongation is accomplished by a continuity between the anterior portion of the ossification and the posterior section that terminates in the transformator process. The anterior bladelike portion of the tripus is not elongate in ctenoluciids as it is in *Rhaphiodon vulpinus*. In the latter species the posterior section that terminates in the transformator process is not continuous with the anterior portion of the tripus (see character 48 below).

The anteriorly elongate blade portion of the tripus in *Rhaphiodon vulpinus* is unique among examined characiforms and hypothesized as autapomorphic for the species.

48. Transformator process of tripus

The posterior section of the tripus that terminates in the transformator process is distinct in *Rhaphiodon vulpinus* from that in other cynodontines and among characiform outgroups. In the typical characiform condition the transformator process of the tripus is a thin curved process continuous with the posterior portion of the tripus with no modifications medially (Fink and Fink, 1981: 331). In *Rhaphiodon vulpinus* the posterior portion of the tripus is almost horizontally aligned. In the region medial to the lateral portion of the fused fourth pleural rib plus parapophysis the tripus becomes much thinner and is medially directed at an approximately 90° angle with the anterior portion of that ossification. The transformator process of the tripus in *Rhaphiodon vulpinus* ends in an enlarged rectangular bony plate (figured by Nelson, 1949: fig. 5F, labeled as ‘‘T’’). The structure of the transformator process in *Rhaphiodon vulpinus* is unique among examined characiforms and considered autapomorphic for the species.

49. Fourth pleural rib + parapophysis

The fused fourth pleural rib + parapophysis in *Cynodon* and *Rhaphiodon* differs notably from that of *Hydrolycus*. In the latter genus the fused pleural rib and parapophysis extends laterally in a flat, thin dorsoventrally oriented process (fig. 15). This condition is similar to the condition observed in characiform outgroups and is described and figured by Weitzman (1962: 36, 68).

In *Cynodon* and *Rhaphiodon* the process is greatly enlarged, extending anteriorly and ventrally, and covering the posterolateral portion of the tripus (figs. 14 and 16). The distal end of the process is greatly enlarged, forming a broad articular surface for the attachment of ligamentous tissue. Such a process was previously described for *Rhaphiodon vulpinus* by Nelson (1949: 500), who termed the enlarged distal portion of the process a basal plate. This basal plate contacts the medial portion of the pectoral girdle in the region where the cleithrum articulates with the supracleithrum. A lateral process of the fourth vertebra as described for *Cynodon* and *Rhaphiodon* is a unique condition within examined characiforms and hypothesized as derived.

A heavy mass of connective and ligamentous tissue stretches from the distal portions of the processes of the second and fourth vertebrae, and extends to the pectoral girdle in the region of the articulation of the cleithrum and supracleithrum. An understanding of connections between the elements of the Weberian apparatus and the pectoral girdle in cynodontines necessitates a much more detailed study of these connections in order to isolate the different ligaments and their origins and insertions, a task not feasible at this time.

Lesiuk and Lindsey (1978) in their study on head bending in *Rhaphiodon vulpinus* mentioned that the attachment of the Weberian apparatus to the dorsal tip of the cleithrum constrains the movement of the latter element. The cleithrum is not rigidly attached to the bones of the Weberian apparatus, allowing a rotation of the girdle with respect to the skull through an arc of approximately 10°.

The highly modified fused fourth pleural rib and parapohysis of *Cynodon* and *Rhaphiodon* is unique among characiforms and is hypothesized as synapomorphic for these two genera.

50. Dorsal articulation between fourth and fifth vertebrae

All cynodontines have an articulation between the fourth and fifth vertebra that is unique among examined characiforms. The posteroventral portion of the fourth vertebra in cynodontines has a process extending posterolaterally, with ligamentous attachments originating from both its dorsal and ventral surfaces. Ligaments from the dorsal surface of the process of the fourth vertebra attach to a process extending anteriorly and laterally from the dorsal portion of the fifth centrum (figs. 14–16). Ligaments from the ventral surface of the process of the fourth vertebra attach to the anteroventral portion of the fifth vertebra, which also bears another process (see character 51 below).

Although modifications of the fourth and fifth vertebrae to form an articulation is found in some examined outgroups, the condition differs from that in cynodontines. For instance, *Agoniates*, *Triportheus*, and *Brycon* have an expansion of the posteroventral portion of fourth centra extending to the anteroventral portion of the fifth vertebra. The contact with the fifth vertebra is only from the dorsal surface of the process of the fourth vertebra. The process in these taxa is only a thin lamella of bone that extends posteriorly from the vertebra, a condition different from that in cynodontines in which the process is enlarged and has a lateral extension. There is no modification of the fifth vertebra. *Caenotropus* has a process originating at the posterior portion of the fourth vertebra that contacts a groove on the anterior portion of the fifth vertebra. *Serrasalmus* has a process similar to that of cynodontines (enlarged with an dorsal articular surface) but originating at the posterior region of the fourth centrum, in a more dorsal position than that in cynodontines. This process contacts a process originating from the neural arch of the fifth vertebra.

The articulation between the fourth and fifth vertebra in cynodontines is apparently related to the ability of these fishes to rotate the head upward, as described by Lesiuk and Lindsey (1978) in *Rhaphiodon vulpinus*. These authors observed that upward rotation of the head in this species occurs at the articulation between the fourth and fifth vertebrae (indicated by arrows in their figures 1C, 1D and 1E). Upward rotation of the head is yet to be studied in the remaining cynodontine species. Although the articulation between the fourth and fifth vertebra in *Rhaphiodon vulpinus* is more developed than that of the remaining cynodontine species (see character 51 below), the presence of such an articulation in the remaining species may imply that they may demonstrate at least some degree of head rotation relative to the vertebral column.

The type of articulation between the fourth and fifth vertebra in cynodontines is unique among characiforms and hypothesized as synapomorphic.

51. Ventral articulation between fourth and fifth vertebrae

In addition to the process at the dorsal portion of the fifth centrum mentioned above, cynodontines possess another process situated at the anteroventral portion of the fifth vertebra which is, in turn, laterally expanded, extending ventral to the lateral process of the fourth centrum that forms the articulation between the fourth and fifth vertebrae (figs. 14–16). The ligamentous tissue from the ventral surface of the process of the fourth vertebra attaches to this lateral process of the ventral portion of the fifth vertebra. The latter process is more evident in larger specimens, in which it is more pronounced laterally and extends more ventrally to contact the process of the fourth vertebra. In *Hydrolycus scomberoides* the process seems to be less pronounced than in the remaining cynodontines, hardly apparent in a 143.4 mm SL specimen (MZUSP 32093), and small in a 241.0 mm SL specimen (AMNH 40087). In specimens of the other cynodontine species within the size range of those of *H. scomberoides*, the process of the fifth vertebra is more developed. It is possible to see that there is a slight lateral expansion on the fifth vertebra relative to the same portion of the sixth vertebra which lacks such a process. Therefore, this feature is regarded as present in *H. scomberoides*.

In *Rhaphiodon vulpinus* the ventral process of the fifth vertebra is further enlarged relative to that of other cynodontines, being as well-developed as the other process of the fifth vertebra that articulates dorsally with the process of the fourth vertebra. The process is more conspicuous when observed either from a ventral and/or lateral view (fig. 16). It is already evident in a 50.1 mm SL specimen (USNM 231549), and very conspicuous in a 96.8 mm SL specimen (BMNH 1935.6.4: 33–39).

The presence of the ventral process of the fifth vertebra is unique to cynodontines among characiforms and hypothesized as a synapomorphy for this taxa, with its further enlargement in *Rhaphiodon vulpinus* hypothesized as autapomorphic for this species.

52. Pleural ribs

The fifth and to a certain extent the sixth and seventh pleural ribs of *Rhaphiodon vulpinus* are modified relative to that of remaining cynodontines and examined characiform outgroups. The fifth pleural rib in that species is very short relative to the more posterior ribs and has a flattened proximal portion and a very slender distal portion. A process arises from the medial portion of the rib and extends medially in the region ventral to the fifth centrum. Another process arises at the dorsal tip of the rib and extends posteriorly to the sixth vertebra (fig. 16). These features of the fifth rib are present also in the sixth and seventh ribs, although they are not as conspicuous and show some variation in different specimens. The more posterior ribs are similar to those of other cynodontines and characiform outgroups.

The fifth rib in the remaining cynodontine species is slightly shorter than the more posterior ribs. It is slender along its entire length and possesses a very short medially directed process dorsally, which is less developed than that in *Rhaphiodon*. The posterodorsal process present in *Rhaphiodon* is absent from the remaining cynodontines. A process on the medial portion of the fifth rib (similar to those of *Cynodon* and *Hydrolycus*) also occurs in some characiform outgroups (e.g., *Gilbertolus*, *Roestes*, *Acestrorhynchus*, *Agoniates*, *Gnathocharax*, and the Heterocharacini), and was described and figured by Roberts (1969: 426, figs. 46, 47); see also Buckup (1991: 226), and Lucena (1993: 56) for distribution of this feature in characiforms. In these taxa, however, the rib is not conspicuously flat in its proximal half as in *Rhaphiodon* and is approximately the same length as the more posterior ribs.

The structure of the fifth rib of *Rhaphiodon vulpinus* is unique among examined characiforms and regarded as autapomorphic for this species.

53. Parapophyses

The parapophyses of all precaudal vertebrae posterior to the fifth vertebra in cynodontines are longitudinally elongate, with the parapophysis of one vertebra extending anteriorly and articulating with the vertebra anterior to it. The first enlarged parapophysis is that of the sixth vertebra (figs. 14, 15), gradually becoming less pronounced in vertebrae posterior to it.

The parapophyses of the vertebrae of other examined characiforms are also somewhat elongate, having a process extending from the portion of the parapophysis that articulates with the vertebral centrum. The condition observed in cynodontines seems to be the result of an enlargement of that process of the parapophysis associated with articulation at a more ventral portion of the centrum. In outgroups the lateral fossae with which the parapophyses of the anterior precaudal vertebrae articulate have a more central position on the centrum. The process extending from each parapophysis is oriented slightly anteroventrally, reaching the anteroventral portion of the vertebra but not extending beyond it to reach the anterior vertebra. The fossae of the posterior precaudal vertebrae gradually shift to a more ventral position on the lateral portion of the centrum with the process of the parapophysis also decreasing in size. In cynodontines the lateral fossae with which the parapophyses of the anterior precaudal vertebrae articulates are in a more ventral position on the centrum than that in examined outgroups and the process of the parapophysis is oriented anteriorly and not ventrally.

In addition to cynodontines an articulation between the parapophysis of one vertebra to the vertebra anterior to it was observed only in *Hydrocynus* among examined characiform outgroups. *Hydrocynus* is hypothesized as being the sister group to certain *Alestes* (Brewster, 1986: 192), a genus lacking an articulation between the parapophysis of one vertebra and the vertebra anterior to it as described for cynodontines and *Hydrocynus*. As a consequence, this feature is hypothesized as an independent acquisition in *Hydrocynus* and the Cynodontinae and considered synapomorphic for the latter taxa.

54. Baudelot's ligament

In all cynodontine species (except *Rhaphiodon vulpinus*) Baudelot's ligament is strong and attaches to the ventral portion of the enlarged lateral processes of the second vertebra (fig. 15). This constitutes a third point of attachment of this ligament in addition to the typical characiform attachment anteriorly to the basioccipital and the posteriorly to the pectoral girdle. *Rhaphiodon* has a somewhat different condition from the remaining cynodontines. In *Rhaphiodon* Baudelot's ligament is not as well developed and although it contacts the lateral process of the second vertebra ventromedially, it is not attached to that process as it is in the remaining cynodontines. The condition in *Rhaphiodon* largely resembles that of characiform outgroups.

Two alternative, equally parsimonious, hypotheses are possible for this character. The attachment of Baudelot's ligament with the lateral process of the second vertebra may be hypothesized as synapomorphic for the Cynodontinae, with a secondary loss of the attachment in *Rhaphiodon vulpinus*, or as independently acquired in *Cynodon* and *Hydrolycus*.

PECTORAL GIRDLE

55. Postcleithrum 2

A lack of postcleithrum 2 is common to all cynodontines. Among characiforms a lack of this ossification also occurs in *Gilbertolus*, *Gnathocharax* (Lucena, 1993), *Ctenolucius*, *Boulengerella lateristriga*, *B. maculata* (Vari, 1995: 26), *Hepsetus* (Roberts, 1969: 426; Vari, 1995: 27), and the Gasteropelecidae (Weitzman, 1954: 226).

Three postcleithra along the posterior margin of the pectoral girdle are plesiomorphic for characiforms (Roberts, 1969: 426; Vari, 1983: 35; 1995: 26), and the lack of postcleithrum 2 is considered a derived character. The reduction in the number of postcleithra occurs also within other ostariophysan lineages including some gonorhynchiforms, cypriniforms, and siluriforms and it was interpreted (see Fink and Fink, 1981: 334) as specializations that evolved independently in these lineages.

In view of the current evidence for a close relationship between the Cynodontinae and *Gilbertolus* plus *Roestes*, the lack of postcleithrum 2 might represent a derived condition for these taxa (with a reversal in *Roestes*). The lack of this element could also be alternatively considered an independent loss in *Gilbertolus* and the Cynodontinae.

56. Postcleithrum 3

Cynodontines also lack postcleithrum 3, a feature that is shared with various other characiforms: *Gilbertolus*, *Roestes*, *Gnathocharax*, ctenoluciids (Vari, 1995: 26), *Iguanodectes* (Lucena, 1993: 115), *Hepsetus* (Roberts, 1969: 426), gasteropelecids (Weitzman, 1954: 226), and *Chilodus* (Vari et al., 1995: 9).

This feature was hypothesized as a synapomorphy for the clade formed by cynodontines, *Gilbertolus*, and *Roestes* by Lucena and Menezes (1998).

57. Coracoid

The posterodorsal portion of the coracoid in all cynodontine species is perforated by a very large foramen (figs. 17, 18) situated just ventral to the insertion of the radials of the pectoral fin and the articulation with the mesocoracoid. The presence of a posterodorsal foramen in the coracoid was previously noted by Starks (1930: 169) and Nelson (1949: 507) for *Rhaphiodon vulpinus*. A condition similar to cynodontines was observed only in *Gilbertolus* among examined outgroups.

In some characiform outgroups (e.g., *Roestes*, *Acestrorhynchus*, *Heterocharax*, *Agoniates*, *Boulengerella*, *Hydrocynus*, *Hemiodus*, *Brycon*, *Oligosarcus*, and *Triportheus*) a foramen of various sizes is present at the region ventral to the articulation with the mesocoracoid and sometimes extending posteriorly ventral to the insertion of the radials of the pectoral fin. Although present in the characiforms mentioned above, in none of these groups is the posterodorsal foramen of the coracoid as enlarged as in the Cynodontinae and *Gilbertolus*. Therefore, the condition in these taxa is hypothesized as derived. In *Roestes* the posterodorsal foramen of the coracoid is intermediate in size between that of *Gilbertolus* and cynodontines, and that of the remaining characiforms in which it is present. However, there is also variation in the size of the foramen in the remaining characiform outgroups, rendering the definition of discrete states to account for this variation problematic.

Lucena and Menezes (1998) also noted the presence of the enlarged coracoid foramen in cynodontines and *Gilbertolus*; however, their

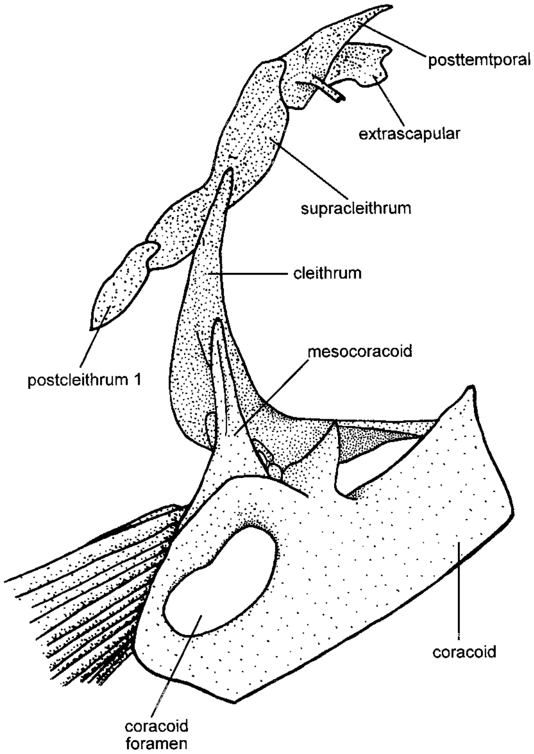

Fig. 17. Left pectoral girdle of *Hydrolycus armatus*, MZUSP 32607; medial view, anterior to right.

interpretation of this character was ambiguous because of its absence in *Roestes*.

58. Size of coracoid

Cynodontines possess relatively enlarged coracoids, a feature shared with a number of other characiforms such as the Gasteropelecidae, *Triportheus*, *Agoniates*, and *Gnathocharax*. In addition, Weitzman (1954: 230) and Roberts (1969: 426) mentioned the presence of enlarged coracoids, in *Pseudocorynopoma* and *Clupeacharax*, respectively. The shape of the expanded coracoids differs in all the examined characiforms outgroups that possess them. They are more developed in the Gasteropelecidae and *Triportheus* than in the Cynodontinae. In the Gasteropelecidae they are fan-shaped with a rounded ventral profile (Weitzman, 1954); whereas in *Triportheus* and *Gnathocharax* the expansion occurs mainly in the posterior portion of the ossification. In cynodontines the enlargement of the coracoid occurs at the vertical plane of the longitudinal axis of the body, with the ventral profile of the coracoid being straight (fig. 17) as in characiform outgroups in which this ossification is not enlarged. *Agoniates* has an expanded coracoid similar in shape to that of cynodontines.

All the taxa mentioned above differ significantly in the rest of their osteology and it seems that expanded coracoids originated independently in all of them, as hypothesized by Weitzman (1954: 228-231). More recently Castro and Vari (1990) provided a detailed discussion about the presence of enlarged coracoids in characiforms and the appropriateness of using that feature to propose relationships. These authors also proposed an independent origin of expanded coracoids in most of these groups, based on the evidence indicating closer relationships of these taxa to species or species groups without expanded coracoids. Taxa proposed as closely related to the Cynodontinae (*Roestes*, *Gilbertolus*, *Acestrorhynchus*) do not have expanded coracoids. The presence of this feature in cynodontines is hypothesized as synapomorphic for the group.

59. Fusion of coracoids

In all cynodontines the coracoids are closely applied to each other along their entire midline. In *Cynodon* species and *Rhaphiodon vulpinus* the contralateral coracoids are fused even more along a large portion of the area of contact, with the region of the fusion between the two ossifications densely corrugated. All attempts to separate the left and right elements resulted in breaking of one coracoid in the region of the corrugated area. Fusion of the contralateral coracoids and the corrugated pattern is present in juveniles of *Rhaphiodon vulpinus* (USNM 231549, 50 mm SL), but not evident in a 35 mm SL specimen of *Cynodon* (AMNH 32485). In *Rhaphiodon vulpinus* a triangular-shaped area in the anterior portion of the conjoined coracoid is formed only by one coracoid. This region is located ventral to the dorsal margin of the ossification that forms the ventral edge of the large foramen formed by the cleithrum and coracoid. This feature occurs in all examined osteological preparations of *Rhaphiodon vulpinus* and was previously noted by Nelson, 1949: 507.

Although all *Hydrolycus* species have the two portions of the coracoids in very close contact and very difficult to separate, they are not fused to one another, at least not to the degree observed in *Cynodon* and *Rhaphiodon*. It was possible to separate completely the opposite coracoids in all specimens in which this was attempted. In some very large specimens of *Hydrolycus* a small area in the anteriormost portion of the coracoids seemed fused, and one of the sides was damaged in the area of the fusion when the bones were separated. In other large specimens, however, the two coracoids were completely separate and intact. A slight corrugated pattern was observed in one specimen of *H. scomberoides*, but the contralateral coracoids were not fused.

Within characiforms, fused and corrugated coracoids have been reported only in the Gasteropelecidae (Weitzman, 1954), a taxon not closely related to the Cynodontinae, as discussed above.

The condition of partially fused and corrugated coracoids described for *Rhaphiodon* and *Cynodon* is hypothesized as a synapomorphy for these genera.

60. Mesocoracoid

The mesocoracoid in cynodontines is greatly enlarged relative to the condition in the majority of examined outgroups. The typical condition of the mesocoracoid in characiforms is that of a short ossification attached to the cleithrum, scapula, and coracoid (e.g., *Brycon*, Weitzman, 1962: 41, 76). Within cynodontines the mesocoracoid occupies a larger portion in the medial portion of the pectoral girdle and has broader articular surfaces with the surrounding bones (fig. 17). It is attached to the cleithrum along a vertical crest at the medial portion of this latter ossification, with the dorsal tip of the mesocoracoid extending dorsally to at least half the length of the vertical portion of the cleithrum. In the typical characiform condition the dorsal tip of the mesocoracoid does not extend to the midpoint of the vertical portion of the cleithrum. The articulation of the mesocoracoid with the coracoid in cynodontines extends more posteriorly on this latter ossification compared to the typical characiform condition, extending along the posterodorsal surface of the coracoid just dorsal to the insertion of the pectoral-fin radials. An enlarged mesocoracoid similar to that of cynodontines occurs only in *Gilbertolus* among examined outgroups. In *Agoniates* and *Gnathocharax* the articulation of the mesocoracoid with the cleithrum is somewhat broad with the dorsal tip of the mesocoracoid reaching the midpoint of the vertical portion of the cleithrum. The articulation with the coracoid, however, is similar to the typical characiform condition. Therefore, the overall enlargement of the mesocoracoid is not comparable to that in the Cynodontinae and *Gilbertolus*.

Lucena and Menezes (1998) also noted the enlarged mesocoracoid in cynodontines and *Gilbertolus*. However, as with character 58, above, the interpretation of the distribution of this feature was ambiguous considering its absence in *Roestes* and given the hypothesis of monophyly of *Roestes* plus *Gilbertolus* they proposed.

61. Scapula

The scapular foramen in the Cynodontinae is almost entirely exposed when examined from lateral view (fig. 18). In the majority of examined characiform outgroups the scapular foramen is covered laterally by the cleithrum and not exposed in lateral view. The condition observed in cynodontines seems to be the result of a posterior shift of the articulation of the scapula and mesocoracoid relative to the medial surface of the cleithrum. In cynodontines the enlarged mesocoracoid articulates with the cleithrum on the middle of the medial surface of this ossification and the articulation of the scapula is with the posteroventral portion of the medial surface of the cleithrum. In the typical characiform condition the articulation of the mesocoracoid and scapula is more anterior on the medial surface of the cleithrum (Weitzman, 1962: fig. 19; Roberts, 1969: figs. 48–52) and as a consequence the scapular foramen is completely covered by the posterior portion of the cleithrum. The insertion of the pectoral girdle is also shifted posteriorly as a result of the posterior shift of the articulation of the scapula with the cleithrum, so that a vertical through the base of the unbranched pectoral-fin ray is situated posterior to a vertical

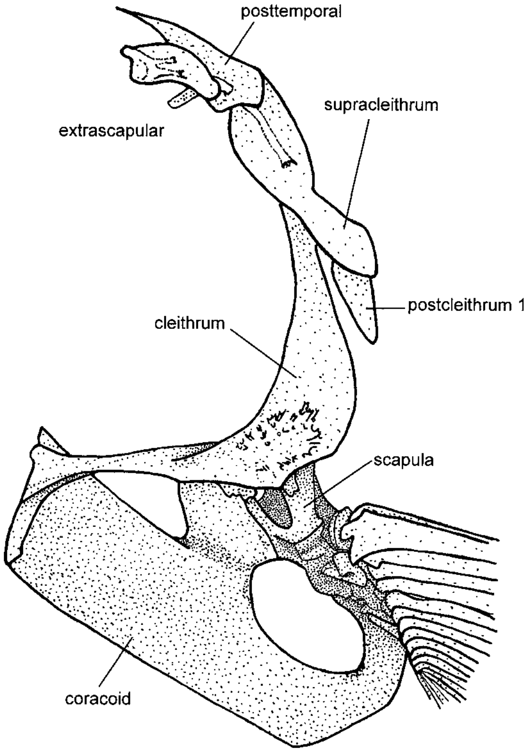

Fig. 18. Left pectoral girdle of *Hydrolycus armatus*, MZUSP 32607; lateral view, anterior to left.

through the posteriormost margin of the cleithrum.

A posterior shift of the articulation of the scapula and mesocoracoid with the consequent exposure of the scapular foramen and posterior shifting of the articulation of the pectoral girdle occurs also in *Gilbertolus* among examined outgroups (Lucena and Menezes, 1998). In the Gasteropelecidae the scapular foramen is also exposed from lateral view. However, in that family the pectoral girdle shows a high degree of modification (Weitzman, 1954: 225), including changes in the overall shape of the cleithrum. Thus, the condition in gasteropelecids on the one hand, and that in cynodontines and *Gilbertolus* on the other, seems to be the consequence of different modifications of the pectoral girdle. In addition in the Gasteropelecidae, the base of the unbranched pectoral-fin ray is located at the vertical through the posterior margin of the cleithrum and not posterior to it, as in the Cynodontinae and *Gilbertolus*. This feature also has an ambiguous interpretation following the same arguments mentioned above for characters 57 and 60.

62. Cleithrum

The anterior portion of the cleithrum in cynodontines ends in a vertically elongate process that articulates with the anterior portion of the enlarged coracoids (fig. 18). This feature is also present in characiform outgroups with enlarged coracoids such as *Triportheus* and *Agoniates*, but is absent from the Gasteropelecidae. In the remaining examined characiform outgroups the anterior portion of the cleithrum that contacts the anterior portion of the coracoid is continuous with the posterior part of the cleithrum along the entire vertical margin of the latter ossification. Lucena's (1993) study on the family Characidae provided some support for a hypothesis of the relationships of *Agoniates*. As discussed previously under Historical Overview and Comments on Cynodontine Relationships with other characiforms, additional studies are needed in order to test that hypothesis, but in view of the larger number of derived features shared by cynodontines and other characiforms (e.g., *Gilbertolus*, Lucena and Menezes, 1998), the features shared by *Agoniates* and cynodontines are most parsimoniously interpreted as homoplastic. The relationships of *Triportheus* are not fully resolved, but evidence discussed by Castro and Vari (1990) points toward a possible relationship between *Triportheus* and some lineage within *Brycon*, a group that does not possess a cleithrum ending in a vertically elongate process. Therefore, the condition in cynodontines is, hypothesized as synapomorphic.

Within cynodontines, the condition in *Rhaphiodon vulpinus* differs from that of *Cynodon* and *Hydrolycus*. In the latter two genera the anterodorsal tip of the cleithrum that contacts the coracoid is pointed anteriorly and in some cases slightly upturned. This anterodorsal projection is lacking in *Rhaphiodon vulpinus* in which the anterior portion of the cleithrum ends in a continuous curve. In the present analysis the condition of the anterior portion of the cleithrum in *Rhaphiodon* *vulpinus* is most parsimoniously interpreted as autapomorphic for the species.

The cleithrum shows some differences among cynodontines, the most pronounced occurring at the posteroventral margin. In *Rhaphiodon vulpinus* the posteroventral margin of the cleithrum is fused to and continuous with the scapula. This species lacks a free margin continuous along the entire posterior and ventral margins of the cleithrum.

In all *Hydrolycus* and *Cynodon* species the entire posterior and ventral margins of the cleithrum are continuous, with the posteroventral margin of the cleithrum not being fused to and continuous with the scapula. The condition in *Hydrolycus* and *Cynodon* is widespread for characiforms, with the condition in *Rhaphiodon* occurring only in gasteropelecids, among examined outgroups, and hypothesized as independently acquired.

The margin of the cleithrum dorsal to the level of insertion of the pectoral fin is slightly indented in *Cynodon* and *Hydrolycus* species, with the portion of the bone just anterior to the insertion of the unbranched pectoral-fin ray slightly expanded. The expanded portion is pointed in *H. scomberoides*, whereas in *Cynodon* and in the remaining *Hydrolycus* species, this portion of the bone is rounded. However, the establishment of unambiguously discrete states for this feature was complicated because of variation of this portion of the ossification in the examined cynodontines. As a consequence this feature is not proposed as an additional character of phylogenetic interest.

PELVIC FINS

63. Pelvic fin insertion

The pelvic fin in *Hydrolycus scomberoides* is distinctly dorsal of the ventral profile of the abdomen. As a result the ventral profile of the abdomen continues without interruptions to the anus. In other cynodontines the pelvic fin is inserted at the ventral profile of the abdomen, which is thus interrupted by the pelvic-fin insertion, the typical condition among characiforms.

In serrasalmines the pelvic fins are inserted slightly dorsal to the ventral profile of the body, this being more evident in *Mylossoma* sp. The condition in serrasalmines is associated with the modification of the scales at the ventral profile of the body resulting in a serrated ventral keel. The pelvic fin inserts at the dorsal portion of the modified scale of the ventral keel, a condition different from that of *Hydrolycus scomberoides*.

The pelvic fin inserted dorsal to the ventral profile of the abdomen in *Hydrolycus scomberoides* is hypothesized as autapomorphic for this species.

ANAL FIN

64. Anal-fin rays

Cynodon species have 61–80 branched anal-fin rays. All other cynodontines combined have 27–50 branched anal-fin rays. The high number of branched anal-fin rays in *Cynodon* is unusual among characiforms. The clade formed by ctenoluciids, erythrinids, lebiasinids, and *Hepsetus* has very short anal fins with 13 or fewer rays. The majority of other characiforms have up to 38 branched anal-fin rays (see Lucena, 1993: 61, 118 for the distribution of this feature among characiform taxa). Characiforms with relatively more branched anal-fin rays include *Stethaprion crenatum* (36–42; Reis, 1989: 57); *Piabucus caudomaculatus* (36–38; Vari, 1977: 3), and *Charax* (33–56, Lucena, 1987); *Roestes* and *Gilbertolus* (38–47 and 40–48 respectively, Menezes and Lucena, 1998). The presence of 60 or more branched anal-fin rays is unique to *Cynodon* among characiforms and hypothesized as derived.

CAUDAL FIN

65. Hypurals

Cynodon and *Hydrolycus* species have hypurals 1–3 fused into a single unit that is articulated with the $PU_1 + U_1$ (fig. 19). In *Rhaphiodon* only hypurals 2 and 3 are fused into a single unit that is articulated with $PU_1 + U_1$. Although the dorsal margin of hypural 1 is in very close contact with the unit formed by the fusion of hypurals 2 and 3, it still remains a separate ossification. Although not articulated with the $PU_1 + U_1$, the anterior end of hypural 1 extends in a thin process directed toward $PU_1 + U_1$. In one specimen of *Rhaphiodon vulpinus* (LACM 43295-64, 138.4 mm SL) hypural 1 is articulated with $PU_1 + U_1$, and it is somewhat fused to hypurals 2 and 3. In the largest examined cleared and stained specimen of *Rhaphiodon vulpinus* (MZUSP 32812, 191 mm SL) hypural 1 was free from the unit formed by hypurals 2 and 3.

In all juvenile cynodontine specimens available for osteological examination *Rhaphiodon vulpinus*: (USNM 231549, 41.7–50.1 mm SL) and *Cynodon* sp. (AMNH 32485SW, 35 mm SL) all six hypurals consist of separate elements. Hypurals 2 and 3 are still not fused in one specimen of *Rhaphiodon vulpinus* (BMNH 1935.6.4: 33–39, 96.8 mm SL). Hypurals 1–3 are already fused in a specimen of *Cynodon gibbus* (LACM 43295-89, 102.4 mm SL).

Fusion of the three ventral hypurals seems to occur in at least some *Acestrorhynchus* species. One cleared and stained specimen of *A. falcatus* (AMNH 43418, 140.0 mm SL) has the anterior portions of hypurals 1–3 fused. The posterior portions of these elements also seem fused, although the suture between the bony plates is still evident. In a smaller specimen of the same species (MZUSP 4572-91, 111.1 mm SL) the three ventral hypurals can still be distinguished as distinct elements, albeit in very close contact along their proximate margins. One dry skeleton of *A. heterolepis* (AMNH 93088) has the three ventral hypurals completely fused. One specimen of *A. microlepis* (AMNH 40106, 80 mm SL) has hypurals 1 and 2 fused into a single element. One specimen of *A. lacustris* has hypurals 1 and 2 fused anteriorly. Hypurals 1–3 of *A. nasutus* and *A. falcirostris* are separate. The condition for *Acestrorhychus* was coded as a missing entry.

Other characiforms that show fusion between hypurals are the Citharinidae-Distichodontidae assemblage, Hemiodontidae, Serrasalminae, *Crenuchus*, and *Poecilocharax*, discussed by Vari, 1979: 313). In all these taxa, the fusion is only of hypurals 1 and 2.

Roestes and *Gilbertolus* possess separate hypurals, however the presence of some degree of fusion in hypurals of *Acestrorhynchus*, a genus hypothesized as closely related to the Cynodontinae, renders the interpretation of this character ambiguous.

Intermuscular Bones

66. Epineurals

In all cynodontines the medial branch of one of the anterior epineural bones contacts the lateral surface of the neural complex of the Weberian apparatus.

An account of details of the intermuscular bones in teleosts was given by Patterson and Johnson (1995). Among ostariophysans, they recorded the intermusculars of the characiform *Alestes dentex* and three cypriniforms and pointed out the necessity of a fuller survey of the anterior intermusculars in otophysans. A complete survey of this character system is beyond the scope of the present study; however, examination of cynodontines and outgroups showed that there is a large degree of variation of intermuscular bones in characiforms. The condition present in cynodontines is, however, unique to this group within examined characiforms and hypothesized as synapomorphic.

67. Myorhabdoi

Rhaphiodon vulpinus possesses highly developed myorhabdoi (sensu Chapman, 1944) characterized by long, slender bones, branched dorsally, that project anteroventrally along the sides of the body dorsal to its longitudinal midline. Myorhabdoi are also present along the dorsal-fin pteryogiophores. The myorhabdoi are especially developed in the anterodorsal portion of the body, where they are almost horizontally aligned. In this region, some of the myorhabdoi bundle into a single, thick bone that attaches to the posterior surface of the neurocranium. Howes (1976: 224) and Lesiuk and Lindsey (1978) described this bundle of intermuscular bones as being attached to the pterotic. Examination of this feature shows, however, that this tendon attaches to the region of the supraoccipital just posterior to the posterior margin of the parietal, and dorsal to the epioccipital.

Patterson and Johnson (1995) mentioned the presence of myorhabdoi in various teleost groups as autapomorphic for those taxa in which they occur. Within characiforms, myorhabdoi are present in the gasteropelecids (Weitzman, 1954: 224), and in *Citharinus*. In none of these taxa are the myorhabdoi as developed as in *Rhaphiodon*. In gastero-

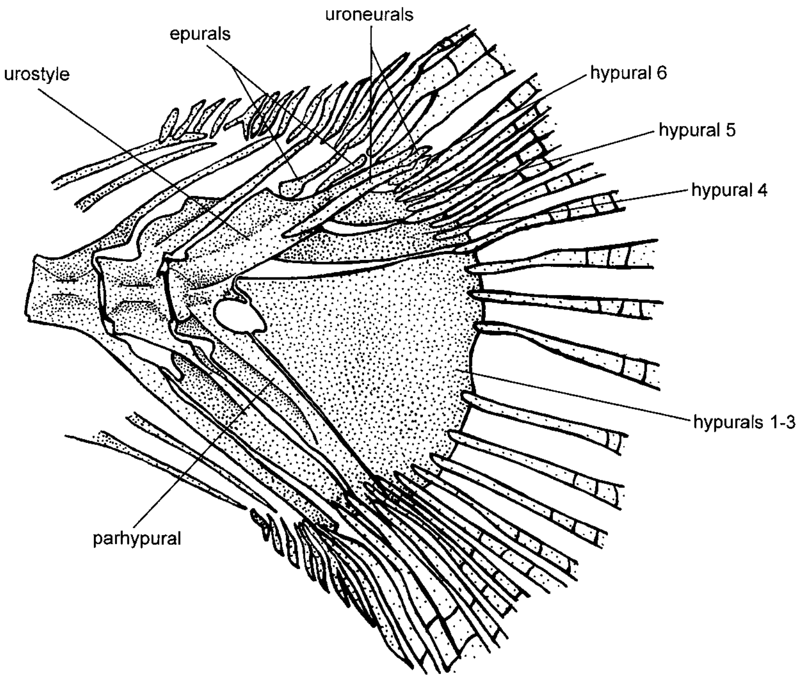

Fig. 19. Caudal skeleton of *Cynodon gibbus*, MZUSP 32587; left side, lateral view, anterior to left.

pelecids some of the intermuscular bones also attach to the neurocranium, at the region of the supraoccipital crest (Weitzman, 1954: 218). These are apparently epipleurals (labeled as epl in figure 2 in Weitzman, 1954: 244). There is also an intermuscular bone attached to the posttemporal + supracleithrum (figured but not labeled in figure 2 in Weitzman, 1954: 244). I was unable to determine whether it consists of a myorhabdoi. In *Citharinus* the myorhabdoi do not attach to the neurocranium.

Although closest relatives remain to be elucidated, gasteropelecids do not seem to be closely related to the Cynodontinae, a hypothesis also supported by Weitzman (1954: 230), who, in addition to and Castro and Vari (1990), suggested that gasteropelecid relationships may lie within some tetragonopterine lineage. *Citharinus* is related to the Citharinidae-Distichodontidae lineage, the other members of which do not possess myorhabdoi. Therefore, in agreement with Patterson and Johnson (1995), the myorhabdoi should be hypothesized as independent acquisitions in the characiform taxa in which they are present.

The presence of myorhabdoi is unique to *Rhaphiodon* within cynodontines and hypothesized as autapomorphic. Lesiuk and Lindsey (1978) considered that the epaxial musculature pulling on this bundle of intermuscular bones (described by them as forming a cable-like tendon, and labeled as T in their fig. 2), provided the force to rotate the head upward.

MISCELLANEOUS

68. Scales

The scales of *Hydrolycus scomberoides* are characterized by serrations on their exposed portion (as opposed to cycloid scales in the remaining cynodontine species). This kind of scale was termed spinoid by Roberts (1993: 62). He restricted the term ‘‘ctenoid scales,’’ usually employed for any kind of serrated scales, to scales in which the spines along the margin are formed as separate ossifications. The presence of spinoid scales is not unique to *H. scomberoides*, among characiforms and the distribution of such scales were discussed by Vari (1995: 28). According to Vari, the various characiforms that possess spinoid scales are more closely related to diverse taxa with cycloid scales. In addition, serrations on the scales of most of the taxa in which they are present differ in form and distribution. The spinoid scales of *H. scomberoides* most resemble those of *Galeocharax gulo* illustrated in Roberts (1993: 69, fig. 6). Therefore, spinoid scales are hypothesized as having independent origins in taxa in which they occur and are autapomorphic for *H. scomberoides*.

69. Gasbladder

The gasbladder of *Rhaphiodon vulpinus* was described in detail and figured by Nelson (1949) and Lesiuk and Lindsey (1978). The most distinctive feature of the gasbladder in this species is the presence of a series of fringelike appendices along the length of the lateral surface of the posterior chamber. These appendices extend laterally, penetrating into the body wall. Nelson (1949) suggested that the appendices form a refinement for the reception of vibrations and/or pressure changes in the overall functioning of the gasbladder and Weberian apparatus in hearing and hydrostatic perception. Lesiuk and Lindsey (1978) noted the proximity between the appendices in the swim bladder to the pored scales on the lateral-line.

Cynodon and *Hydrolycus* species lack appendices in the gasbladder. The condition in *Rhaphiodon vulpinus* is unique among characiforms and is considered autapomorphic.

PHYLOGENETIC RECONSTRUCTION

The preceding section detailed the series of derived characters congruent with a hypothesis of the monophyly of the Cynodontinae, subunits within the subfamily, and diagnostic for cynodontine species. Characters pertaining to a hypothesis of cynodontine relationships with other characiforms are also discussed. The analysis of cynodontine relationships resulted in a single most parsimonious cladogram, 66 steps; CI: 0.86; RI: 0.92.

Synapomorphies and autapomorphies are plotted on cladogram of figure 20 according to the character numbers in the previous section. Although they were included in the various analyses performed, characters 7, 11, 12, 15, 23, 29, 34, 38, 46, 47, 55–57, 60, 61, and 65 are not plotted on the cladogram. These characters either pertain to the question of phylogenetic relationships of cynodontines with other characiforms or hypotheses about their evolution were problematic. These problems are discussed for each of these characters in the previous section. Various analyses that included, excluded, or tested different codings for these characters did not affect the resulting scheme of cynodontine intrarelationships. In figure 20 characters with one asterisk represent features that are homoplastic within cynodontines but have a single most-parsimonious optimization on the final cladogram. Characters with two asterisks are ambiguous, having two equally parsimonious explanations for their distribution within the final most-parsimonious hypothesis of relationships proposed herein.

MONOPHYLY OF CYNODONTINAE

The hypothesis of the monophyly of the Cynodontinae is supported by a series of 24 synapomorphies listed below and discussed in the previous section. Nineteen of these represent characters unique, unreversed, and not further modified within the Cynodontinae. Characters 51 and 62 are proposed as additional synapomorphies for the Cynodontinae with a further modification in *Rhaphiodon vulpinus* (see monophyly of the latter genus); character 45 is further modified in *Rhaphiodon vulpinus* and *Hydrolycus scomberoides*; character 20 is partially reversed in *Hydrolycus armatus* and *H. tatauaia*; character 41 is further modified in *Cynodon*. Characters 26, 28, and 54 are ambiguous.

Synapomorphies:

1. Contact between antorbital and lateral margin of lateral ethmoid (character 2).
2. Presence of two processes on ventral portion of mesethmoid (character 5).
3. Articulation between anterior portion of palatine and posterior portion of vomer (character 13).
4. Shallow depression on lateral surface of vomer for articulation of maxilla (character 14).
5. Great expansion of dilatator fossa to cover most of the dorsal surface of frontal (character 19).

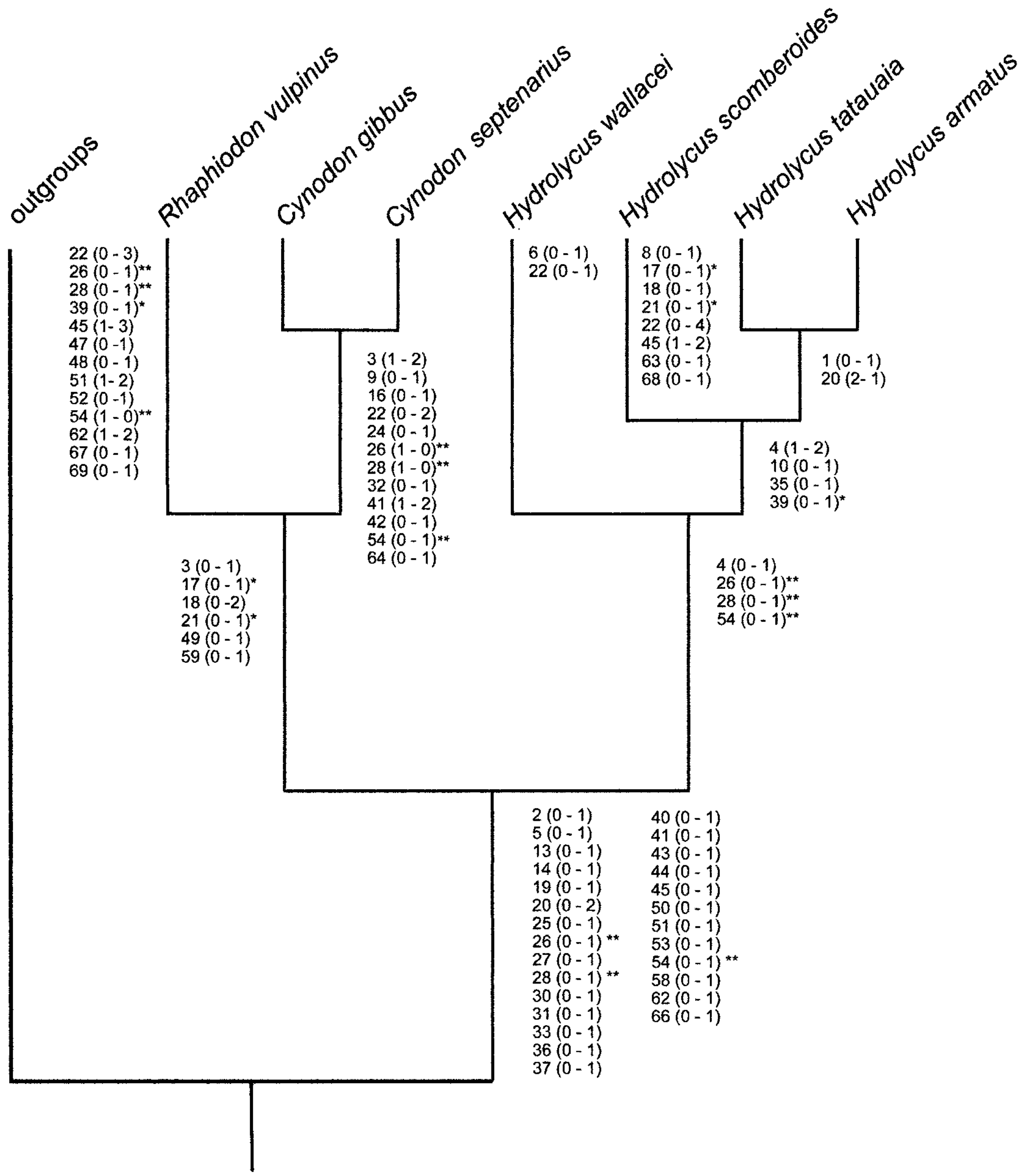

Fig. 20. Cladogram of the most parsimonious hypothesis of relationships of cynodontine species. Numbers followed by one asterisk indicate homoplastic characters within the Cynodontinae, and numbers followed by two asterisks indicate ambiguous characters.

6. Lack of a shelf on frontal at posterodorsal edge of orbit, partially reversed in *Hydrolycus armatus* and *H. tatauaia* (character 20).
7. Portion of basioccipital that articulates with vertebral column flared posteriorly and forming a receptacle for first centrum (character 25).
8. Dorsal elongation of posterior portion of symplectic to fit into a groove in medial face of lower arm of the hyomadibula (character 27).

9. Ectopterygoid teeth arranged in a patch covering most or entire surface of ectopterygoid (character 30).
10. Attachment between posterior portion of ectopterygoid and anteroventral portion of metapterygoid (character 31).
11. Five branchiostegal rays on ceratohyal (character 33).
12. Foramen for dentary canine in anterior portion of snout, with ascending process of maxilla shifted posteriorly, not contacting the premaxilla, and forming the posterior and lateromedial portion of foramen (character 36).
13. Teeth horizontally aligned in mandibular replacement trench, with tips of replacement teeth projecting posteriorly (character 37).
14. Anterior portion of first hypobranchial anteroventrally prolonged into a prong-shaped process extending from the ventrolateral margin of its main body (character 40).
15. Anterior portion of first ceratobranchial curved dorsally, forming an angle relative to the longitudinal axis of the remaining portion of that ossification, further enlarged in *Cynodon* (character 41).
16. Lack of a direct contact between neural complex of Weberian apparatus and posterior margin of neurocranium (character 43).
17. Transverse process of second vertebra bifurcated distally into two short processes that clasp the transverse process of third centrum (character 44).
18. Highly modified lateral process of second vertebra, further modified in *Rhaphiodon vulpinus* and *Hydrolycus scomberoides* (character 45).
19. Process on fourth centrum attached by ligaments to a process on anterior portion of fifth centrum (character 50).
20. Second process on ventral portion of fifth vertebra extending ventral to process of fourth vertebra, further modified in *Rhaphiodon vulpinus* (character 51).
21. Elongate parapophyses of precaudal vertebrae, with parapophysis of one vertebra extending anteriorly and articulating with vertebra anterior to it (character 53).
22. Enlarged coracoids (character 58).
23. Anterior portion of cleithrum ending in a vertically elongate process that articulates with anterior portion of enlarged coracoids, further modified in *Rhaphiodon vulpinus* (character 62).
24. Medial branch of one of the anterior epineurals contacting neural complex of Weberian apparatus (character 67).

Ambiguous features for this clade are:
A_1. Process on shaft of hyomandibula, absent in *Cynodon* (character 26)
A_2. Metapterygoid teeth, absent in *Cynodon* (character 28).
A_3. Attachment of Baudelot's ligament to ventral portion of enlarged lateral process of second vertebra, absent in *Rhaphiodon* (character 54).

The Cynodontinae consists of two primary monophyletic lineages, one formed by the genus *Hydrolycus* and the other by a *Cynodon* and *Rhaphiodon* clade.

MONOPHYLY OF *HYDROLYCUS*

Only one uniquely derived feature supports the monophyly of *Hydrolycus* (character 4). In addition three derived features shared between *Hydrolycus* species and *Rhaphiodon vulpinus* (characters 26, 28, and 54) are ambiguous, having two equally parsimonious explanations for their distribution on the most-parsimonious cladogram.

1. Dorsoventral enlargement of mesethmoid spine being almost round in shape from a lateral view, further enlarged in *Hydrolycus scomberoides*, *H. armatus* and *H. tatauaia* (character 4)

Ambiguous features for this clade are:
A_1. Process on shaft of hyomandibula, also present in *Rhaphiodon* (character 26).
A_2. Metapterygoid teeth, also present in *Rhaphiodon* (character 28).
A_3. Attachment of Baudelot's ligament to ventral portion of enlarged lateral process of second vertebra, also present in *Cynodon* (character 54).

INTRAGENERIC RELATIONSHIPS IN *HYDROLYCUS*

Within *Hydrolycus*, *H. wallacei* is hypothesized as the sister group to a clade formed by *H. scomberoides*, *H. armatus*, and *H. ta-*

tauaia, which is diagnosed by the following synapomorphies:

1. Further dorsoventral enlargement of mesethmoid spine (character 4–state 2).
2. Posterior orientation of portion of lateral wing of mesethmoid where part of ligamentous tissues from maxilla attach (character 10).
3. Highly enlarged dentary canines with their tips extending through nasal opening when mouth is closed (character 35).
4. Spines on dorsal margin of gill-rakers on first ceratobranchial not conspicuously larger than spines on lateral surface of gill-rakers (independently acquired in *Rhaphiodon vulpinus* (character 39).

Hydrolycus armatus and *H. tatauaia* share the following synapomorphy:

1. Reduced fifth infraorbital, with contact between fourth and sixth infraorbitals (character 1).
2. Reduced shelf on frontal at posterodorsal edge of orbit (character 20–state1).

No unique autapomorphies were discovered for either *Hydrolycus armatus* or *H. tatauaia*.

Hydrolycus scomberoides is characterized by the following autapomorphies:

1. Reduction of ventral lamella of mesethmoid (character 8).
2. Lateral-ethmoid-orbitosphenoid contact, independently acquired in clade formed by *Rhaphiodon* and *Cynodon* (character 17).
3. Intermediate distance between orbitosphenoid and parasphenoid (character 18).
4. Reduced dorsal portion of sphenotic spine, no longer contacting ventrolateral margin of frontal, independently acquired in clade formed by *Rhaphiodon* and *Cynodon* (character 21).
5. Anterior portion of frontal shelf truncated at midline of orbit (character 22–state 4).
6. Dorsoventrally flat and laterally directed lateral process of second vertebra (character 45–state 2).
7. Insertion of pelvic fins far from ventral profile of body (character 63).
8. Serrations on exposed portion of scales (character 68).

Hydrolycus wallacei is characterized by the following autapomorphies:

1. Ventral processes of mesethmoid anteriorly directed (character 7).
2. Lack of an anterior shelf of frontal (character 22–state 1).

MONOPHYLY OF *CYNODON* and *RHAPHIODON* clade

Monophyly of the clade formed by *Cynodon* and *Rhaphiodon* is supported by six synapomorphies:

1. Medial process on posterior margin of antorbital, further enlarged in *Cynodon* (character 3).
2. Lateral ethmoid-orbitosphenoid contact, independently acquired in *Hydrolycus scomberoides* (character 17).
3. Reduced distance between orbitosphenoid and parasphenoid (character 18–state 2).
4. Reduced dorsal portion of sphenotic spine no longer contacting ventrolateral margin of frontal, independently acquired in *Hydrolycus scomberoides* (character 21).
5. Enlargement of fourth pleural rib + parapophysis (character 49).
6. Fusion and corrugated pattern of contralateral coracoids (character 59).

MONOPHYLY OF *CYNODON*

The two species of *Cynodon* share nine synapomorphies plus three characters whose distribution can be explained by two equally parsimonious hypotheses:

1. Further enlargement of posterior margin of antorbital (character 3–state 2).
2. Posterior extension of triangular portion of ventral diverging lamella of mesethmoid reaching posteroventral margin of vomer (character 9).
3. Lack of a rhinosphenoid (character 16).
4. Anterior shelf of frontal having a curved edge (character 22–state 2).
5. Lack of a dorsal posttemporal fossa, bordered by supraoccipital, parietal, and epioccipital (character 24).
6. Contact between anterior tip of ectopterygoid and posterior portion of mesethmoid (character 32).
7. Further dorsal elongation of anterior portion of first ceratobranchial (character 41–state 2).

8. Processes on ventral surface of first centrum (character 42).
9. Anal fin with 61 or more branched rays (character 64).

Ambiguous features for this clade are:

A_1. Lack of a process on shaft of hyomandibula (character 26).

A_2. Lack of metapterygoid teeth (character 28).

A_3. Attachment of Baudelot's ligament to ventral portion of enlarged lateral process of second vertebra, (character 54).

No unique autapomorphies were discovered for either *Cynodon gibbus* or *C. septenarius*.

MONOPHYLY OF *RHAPHIODON*

Rhaphiodon is monotypic, represented by a highly specialized species *R. vulpinus*. The autapomorphies characterizing *Rhaphiodon vulpinus* are as follows:

1. Anterior shelf of frontal having a straight edge (character 22–state 3).
2. Spines on dorsal margin of gill-rakers on first ceratobranchial not conspicuously larger than spines on lateral surface of gill-raker, independently acquired in the formed by *Hydrolycus tatauaia*, *H. armatus*, and *H. scomberoides*) (character 39).
3. Highly modified lateral process of second vertebra (character 45 -state 3).
4. Anterior elongation of bladelike portion of tripus (character 47).
5. Posterior portion of transformator process of tripus forming a 90° angle relative to its anterior portion, and ending in an enlarged rectangular bony plate (character 48).
6. Further enlargement of ventral process of fifth vertebra (character 51–state 2).
7. Highly modified fifth pleural rib (character 52).
8. Lack of an anterodorsal projection at anterior portion of cleithrum (character 62–state 2).
9. Presence of myorhabdoi (character 67).
10. Presence of fringelike appendices along lateral surface of posterior chamber of gasbladder (character 69).

Ambiguous features for this species:

A_1. Process on a shaft of hyomandibula, also present in *Hydrolycus* (character 26).

A_2. Metapterygoid teeth present, also present in *Hydrolycus* (character 28).

A_3. Lack of attachment of Baudelot's ligament to lateral process of second vertebra (character 54).

TAXONOMIC ACCOUNT

SUBFAMILY CYNODONTINAE EIGENMANN, 1907

Rhaphiodontinae: Travassos, 1946: 136.
Cynodoninae: Fowler, 1958: 10.
Cynodontidae: Greenwood et al. 1966: 395.
Cynodontini: Howes, 1976: 206.

DIAGNOSIS: The subfamily Cynodontinae is diagnosed within characiforms by a series of derived features listed in Monophyly of the Cynodontinae under Phylogenetic Reconstruction above. Externally, cynodontines are most readily distinguished from all other characiforms by their oblique mouth and a pair of highly developed dentary canines.

REMARKS: Howes's (1976) concept of the Cynodontini included *Roestes*. Herein, the Cynodontinae includes only the genera *Cynodon*, *Rhaphiodon*, and *Hydrolycus*. Lucena and Menezes (1998) placed the Cynodontinae (as herein defined) together with the Roestinae (which included *Roestes* and *Gilbertolus*) in the family Cynodontidae.

Key to genera of Cynodontinae

1. Dorsal-fin origin located distinctly anterior to vertical through anal-fin origin (Rios Amazonas, Tocantins, Capim, and Río Orinoco basins and Essequibo River drainage in Guyana) . . . . *Hydrolycus*

– Dorsal-fin origin located at, or slightly posterior to, vertical through anal-fin origin . . 2

2. Branched anal-fin rays 60 or more; dorsal-fin origin located slightly posterior to middle of body length (snout to dorsal-fin origin 52.6–59.0 of SL); body depth at dorsal-fin origin 19.8–26.4 of SL; 51–54 vertebrae (Rios Amazonas, Tocantins, Capim, and Río Orinoco basins; Demerara River and Essequibo River drainage in Guyana; Rio Pindaré drainage, Maranhão state, Brazil) . . . . *Cynodon*

– Branched anal-fin rays 50 or less; dorsal-fin origin located on posterior third of body length (snout to dorsal-fin origin 69.3–74.4 of SL); body depth at dorsal-fin origin 12.7–19.6 of SL; 62–68 vertebrae (Rios Amazonas, Tocantins, Capim, and Río Orinoco basins; Rupununi River in Guyana; Rio Paraná-Paraguay and Río Uruguay systems) . . . . *Rhaphiodon*

Genus *Hydrolycus* Müller and Troschel, 1844

Hydrolycus Müller and Troschel, 1844: 93 (type species *Hydrocyon scomberoides* Cuvier, 1819 by original designation; confirmed under opinion 1581 of ICZN 1990: 76).

DIAGNOSIS: *Hydrolycus* is characterized by derived features listed above in Monophyly of *Hydrolycus* under Phylogenetic Reconstruction. Externally *Hydrolycus* species can be distinguished from remaining cynodontines by the relative position of the dorsal fin which is located distinctly anterior to the vertical through the anal-fin origin (a key to *Hydrolycus* species is presented in Toledo-Piza et al., 1999). In *Cynodon* and *Rhaphiodon* the dorsal-fin origin is located at, or slightly posterior to, the vertical through the anal-fin origin.

DISTRIBUTION: Rios Amazonas, Tocantins, Capim, and Río Orinoco basins and Essequibo River drainage in Guyana.

Genus *Cynodon* Agassiz, 1829

Cynodon Agassiz, 1829: 77 (type species *Cynodon gibbus*).
Cynodon Cuvier, 1829: 312.
Camposichthys Travassos, 1946: 132 (type species *Cynodon gibbus* by original designation).

DIAGNOSIS: *Cynodon* is diagnosed by the synapomorphies listed in Monophyly of *Cynodon* under Phylogenetic Reconstruction. Externally, *Cynodon* can be easily distinguished from other cynodontines by its relatively long anal fin with 60 or more branched rays in comparison to less than 50 in *Rhaphiodon* and *Hydrolycus*. The anal-fin origin in *Cynodon* is located approximately at the vertical through the middle of the body length, almost reaching the tips of the pelvic-fin rays; in *Hydrolycus* and *Rhaphiodon* the anal-fin origin is located far posterior to the vertical through the middle of the body.

DISTRIBUTION: Rios Amazonas, Tocantins, Capim, and Río Orinoco basins; Demerara River and Essequibo River drainage in Guyana; Rio Pindaré drainage, Maranhão State, Brazil.

REMARKS: The nomenclature of *Cynodon* and *Rhaphiodon* has been the subject of debate by many authors including Campos (1945), Travassos (1946), Kottelat (1988), Eschmeyer and Bailey (1990), Eschmeyer (1990), and Whitehead and Myers (1971), as a consequence of problems arising from differences in the interpretation of the works of Agassiz (1829) and Cuvier (1829). A petition was submitted to the International Commission on Zoological Nomenclature proposing the conservation of the usage of these genus names (acknowledgment of receipt appeared in Bull. Zool. Nomen (54): 77 under Case 3041 by M. Toledo-Piza and K. J. Lazara) and publication and ruling of the case are awaited.

Key to species of *Cynodon* Agassiz, 1829

1. Branched pelvic-fin rays 8; band of dark pigmentation covering caudal-fin base (fig. 21) 2
– Branched pelvic-fin rays 7; no band of dark pigmentation covering base of caudal fin (fig. 24); orbital diameter 30.1–34.4 of HL (Rio Amazonas and its tributaries between mouths of Rios Içá and Tapajós; Essequibo River drainage and Demerara River in Guyana; upper portions of Río Orinoco basin in Venezuela) . . . . *C. septenarius*, new species
2. Orbital diameter 24.9–33.8 of HL (mean 29.2), branched anal-fin rays 68–80 (2 specimens with 65 rays) (Rio Amazonas and Río Orinoco basins, Rupununi River in Guyana, Rio Tocantins drainage and Rio Pindaré system, state of Maranhão, Brazil) . . . . *C. gibbus*
– Orbital diameter 29.8–34.4 of HL (mean 31.8), branched anal-fin rays 63–67 (upper Maroni River, French Guiana) . . . . *C. meionactis* (see below)

COMMENTS ON *CYNODON MEIONACTIS*

I examined one paratype (MNHN 1998-400) and one nontype specimen of *C. meionactis* (MNHN 1998-1769). Dr. M. Jégu checked characters of the holotype (MNHN 1998-0397). I concluded that *C. meionactis*

Géry et al., 1999, is different from *C. septenarius*.

Cynodon septenarius and *C. meionactis* have a relatively large orbital diameter compared to *C. gibbus*. *Cynodon septenarius* can be distinguished from *C. meionactis* by the lack of the band of dark pigmentation on the base of the caudal-fin rays (fig. 24), present in *C. meionactis* (Géry et al. 1999: 71, figs. 1 and 3); and in having i,7 pelvic-fin rays compared to i,8 in *C. meionactis*. The number of anal-fin rays showed a large degree of variation in *C. septenarius* (61–77) overlapping with that of *C. meionactis* (which has 63–67, Géry et al., 1999: 70). However, the variation observed in *C. septenarius* does not demonstrate any geographical pattern.

Géry et al. (1999: 71, 77) also suggested the existence of an undescribed *Cynodon* species in the upper Rio Negro, however, they did not formally describe it, although the diagnostic features provided by those authors for that form conform to those of *C. septenarius*. In addition, according to the present study, *C. septenarius* is the only *Cynodon* species that occurs in the upper Rio Negro, the area from which the specimens examined by Géry et al. (1999) originated.

Géry et al. (1999) hypothesized that *C. meionactis*, was endemic to the upper Maroni River basin pending examination of specimens that might originate from Suriname. No *Cynodon* specimens from Suriname were examined in the present study and the closest known occurrence of the genus in the Guianas is in Guyana where *C. gibbus* occurs in the Rupununi area and *C. septenarius* occurs in the lower portions of the Essequibo River drainage and in the Demerara River. Studies of other characiform taxa have revealed species restricted to the Maroni River system of Suriname and French Guiana with some of them also occurring in the Mana River drainage (e.g., *Cyphocharax punctatus*, Vari, 1992a; *Hemiodus huraulti*, Langeani, 1996; *Semaprochilodus varii*, Castro, 1988, also see Planquette et al., 1996).

In the present study, complete descriptions are provided for *C. gibbus* and *C. septenarius*. Detailed information on *C. meionactis* is provided by Géry et al. (1999).

Cynodon gibbus Agassiz, 1829

Rhaphiodon gibbus Agassiz, 1829: 77, pl. XXVII (plate labeled *Cynodon gibbus*) (original description, type locality: Brazil). ● Lasso, 1988: 132 (Venezuela, lower Río Orinoco, identification based on location).

Cynodon gibbus: Cuvier, 1829: 312 (named in a footnote to the description of the genus *Hydrocyon*; nomen nudum). ● Valenciennes, 1849: 333 (Brazilian Amazon; description). ● Kner, 1859: 46 (Brazil, Rio Branco). ● Günther, 1864: 359 (based on Valenciennes, 1849). ● Cope, 1878: 688 (Peru; identification based on location). ● Steindachner, 1883: 15 (Peru, Río Huallaga). ● Ulrey, 1895: 296 (Brazil, Rio Tocantins specimen in poor condition; identification based on location). ● Eigenmann and Eigenmann, 1891: 59 (Peru, list of species). ● Fowler, 1906: 467 (Peru; description; identification based on location); 1945: 158, fig.50 (Peru; list of species); 1950: 330 (literature compilation, references in part); 1975: 277 (literature compilation). ● Eigenmann, 1910: 444 (literature compilation). ● Eigenmann and Allen, 1942: 271 (Peru, Yurimaguas; common name). ● Campos, 1945: 473 (Brazil, Rio Amazonas; description). ● Schultz, 1950: 48 (references, in part). ● Lowe-McConnel, 1964: 110 (Guyana, Essequibo River, Dadanawa ponds). ● Ovchynnyk, 1967:Appendix A (list of freshwater fishes of Ecuador). ● Howes, 1976: 204 (specimens at the BMNH). ● Mendes dos Santos et al., 1984: 40 (Brazil, Rio Tocantins). ● Taphorn and Lilyestrom, 1984:70 (Venezuela, Río Apure drainage). ● Lauzanne and Loubens, 1985: 56 (Bolivia, Río Mamoré, Trinidad). ● Géry, 1986: 66 (key to cynodontine species). ● Ortega and Vari, 1986: 10 (list of freshwater fishes of Peru). ● Barriga, 1991: 30 (list of freshwater fishes of Ecuador, common name). ● Taphorn, 1992: 436 (Venezuela, Río Apure drainage). (Not Eigenmann, 1912; ● Pellegrin, 1909; Di Caporiacco, 1935; Boeseman, 1952).

Raphiodon gibbus: (genus name misspelled): Müller and Troschel, 1844: 94 (Brazil); 1845: 19 (identical with Müller and Troschel, 1844).

Cynodus gibbus: (genus name misspelled) Machado-Allison, 1987: 134 (Venezuela, Llanos, identification based on location).

DIAGNOSIS: *Cynodon gibbus* can be distinguished from *Cynodon septenarius* by the presence of a band of dark pigmentation that covers the base of the caudal-fin rays (fig. 21), the presence of 8 (versus 7) branched pelvic-fin rays, and by a relatively smaller orbital diameter (24.9–33.8 versus 30.1–34.4

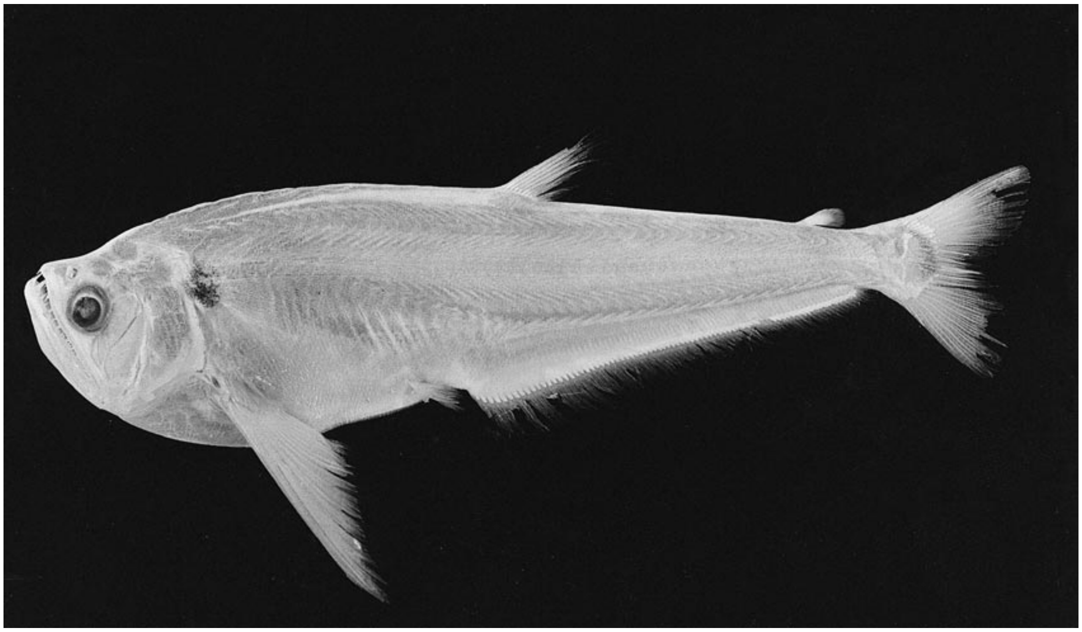

Fig. 21. *Cynodon gibbus*, neotype, MZUSP 6539, 146.4 mm SL, Brazil, Amazonas, Lago Manacapuru.

of HL) (fig. 22). *Cynodon gibbus* differs from *C. meionactis* by the relative smaller orbital diameter (24.9–33.8, mean 29.2 versus 29.8–34.4, mean 31.8, respectively) and higher number of branched anal-fin rays (68–80, 2 specimens with 65 rays, versus 63–67, respectively). See also comments under Remarks, previous comments on *C. meionactis*, and Géry et al. (1999).

DESCRIPTION: (table 1) Body compressed laterally, deep anteriorly, greatest body depth approximately at vertical through pectoral-fin base, depth decreasing posteriorly. Dorsal profile of head concave at interorbital region. Predorsal body profile strongly convex, forming pronounced hump at vertical through middle of orbit; straight and slightly posteroventrally slanted at dorsal-fin base, proportionally less slanted and almost straight in region of body extending from that point to vertical through last anal-fin ray; concave between latter point and origin of dorsalmost procurrent caudal-fin ray. In a small specimen 35 mm SL, dorsal profile of head straight, dorsal profile of body convex anterior to dorsal-fin origin, straight posteriorly. Ventral profile of body convex to posterior tip of coracoids; straight and posterodorsally slanted (sometimes slightly convex) to pelvic-fin base; straight from that point to anal-fin origin; straight and posterodorsally slanted along anal-fin base, concave from rear of anal fin to caudal-fin origin. Ventral surface of body with keel from isthmus to pelvic fin-base; keel anteriorly supported by expanded coracoids.

Infraorbitals and opercular bones with laterosensory canal system highly branched; canals more developed in larger individuals. Mouth obliquely aligned relative to horizontal axis of body, with upper jaw very long relative to head length; posterior tip of maxilla extending to vertical through posterior tip of second infraorbital; relatively more elongate in smaller individuals. Third infraorbital not in contact with preopercle ventrally. Adipose eyelid with notch in region of orbital margin where second and third infraorbitals meet.

Teeth in both jaws conical, in single row, varying in size. Premaxilla with 3 small canines, similar in size, one at the anterior and one at the posteriormost portion; third canine sometimes slightly smaller, located anterior to posteriormost canine and separated from it usually by 2 or 3 small conical teeth; sev-

TABLE 1
Morphometric and Mertistic Data of *Cynodon gibbus* and *Cynodon septenarius*

	Cynodon gibbus				*Cynodon septenarius*			
Character	neotype	n	range	mean	holotype	n	range	mean
MORPHOMETRICS								
Standard length	146.4	72	77.0–280.0		247.0	51	94.5–312.0	
Body depth at pelvic-fin origin	25.3	67	21.5–31.0	25.9	27.7	47	22.4–28.9	25.5
Body depth at dorsal-fin origin	23.4	71	19.8–25.9	22.7	25.1	51	20.5–26.4	23.0
Snout to dorsal-fin origin	53.4	70	52.9–59.0	54.9	55.5	51	52.6–57.1	54.9
Snout to pectoral-fin origin	25.5	72	24.8–28.9	26.3	26.8	51	24.4–27.9	26.0
Snout to pelvic-fin origin	43.9	70	43.3–49.3	45.4	45.9	48	43.2–47.9	45.4
Snout to anal-fin origin	51.1	72	50.2–58.0	53.0	53.6	51	49.7–55.9	53.2
Eye to dorsal-fin origin	45.9	72	45.1–52.3	48.1	48.2	51	45.5–51.0	48.1
Dorsal-fin origin to caudal-fin origin	47.4	72	43.8–48.5	46.7	47.1	51	44.7–48.4	46.7
Dorsal-fin origin to adipose fin origin	35.1	72	31.3–36.5	33.9	34.5	51	32.4–35.8	34.4
Pectoral-fin origin to anal-fin origin	28.6	72	26.3–33.1	29.3	28.3	51	26.3–33.1	29.6
Caudal-peduncle length	6.5	71	5.5–7.6	6.5	6.0	51	5.1–8.3	6.4
Caudal-peduncle depth	7.0	71	5.6–7.5	6.6	7.4	51	6.1–7.8	6.8
Head-length	19.8	72	19.0–22.1	20.3	20.4	51	18.8–21.8	20.0
Snout length	26.2	72	23.5–29.4	26.5	25.2	51	23.4–27.8	25.3
Orbital diameter	28.3	72	24.9–33.8	29.2	30.0	51	30.1–34.4	32.0
Interorbital width	31.4	72	26.1–36.6	30.3	30.2	51	23.5–30.9	27.8
Postorbital length	48.6	72	43.3–54.7	48.2	48.6	51	42.7–49.6	46.5
Dorsal-fin base	5.7	72	4.5–6.5	5.7	6.2	51	5.0–6.6	6.0
Dorsal-fin length	14.3	46	13.1–17.0	15.1	13.2	36	13.3–15.9	14.7
Anal-fin base	45.8	71	41.5–49.0	45.2	44.6	51	42.0–48.1	44.7
Pectoral-fin length	31.1	57	28.9–34.0	31.7	30.7	45	27.4–33.0	30.4
Pelvic-fin length	7.3	55	6.9–10.5	8.3	7.8	43	7.3–9.1	8.2
Upper jaw length	82.4	72	75.5–84.6	80.8	77.2	51	75.7–84.6	79.4
Dentary canine length	13.1	71	11.6–16.9	14.4	12.1	49	9.6–16.1	12.7
MERISTICS								
Scales along lateral-line series	105	70	96–109	102.8	103	50	100–109	103.7
Scale rows above lateral line	19	70	17–23	20.1	16	51	15–21	17.3
Scale rows below lateral line	21	70	18–23	20.1	18	51	13–20	16.6
Scale rows around caudal peduncle	29	68	25–35	29.7	30	51	24–30	27.0
Branched anal-fin rays	78	69	65–80	73.7	76	50	61–77	70.0
Branched pectoral-fin rays	14	72	14–17	15.7	15	50	15–17	15.8
Gill-rakers on first ceratobranchial	17	69	16–20	18.1	15	50	15–21	18.2

eral small conical teeth between anteriormost and middle canines. Maxilla with slightly enlarged conical teeth separated by smaller teeth of similar size; teeth gradually becoming smaller posteriorly. Dentary with well-developed canine, extending up into snout when mouth is closed, tip of canine reaching nostrils anteriorly. Dentary with one smaller canine anterior to largest canine; smaller canine about half the size of the largest dentary canine and preceded by another smaller conical tooth anteriorly; dentary canines posterior to largest canine separated by conical teeth of varying size; teeth gradually decreasing in size posteriorly. Teeth on ectopterygoid and mesopterygoid very small and conical. No teeth on metapterygoid.

Scales without distinct serration, scales small on dorsal portions of body, scale size increasing toward lateral line; largest scales along lateral line; scales on region dorsal to anal fin small. Scales along predorsal midline very small, arranged in somewhat irregular rows. Row of scales forming keel from posterior portion of coracoid to pelvic-fin base less rounded in shape than those covering rest of body. Scales below lateral line obliquely arranged. Lateral-line scales with

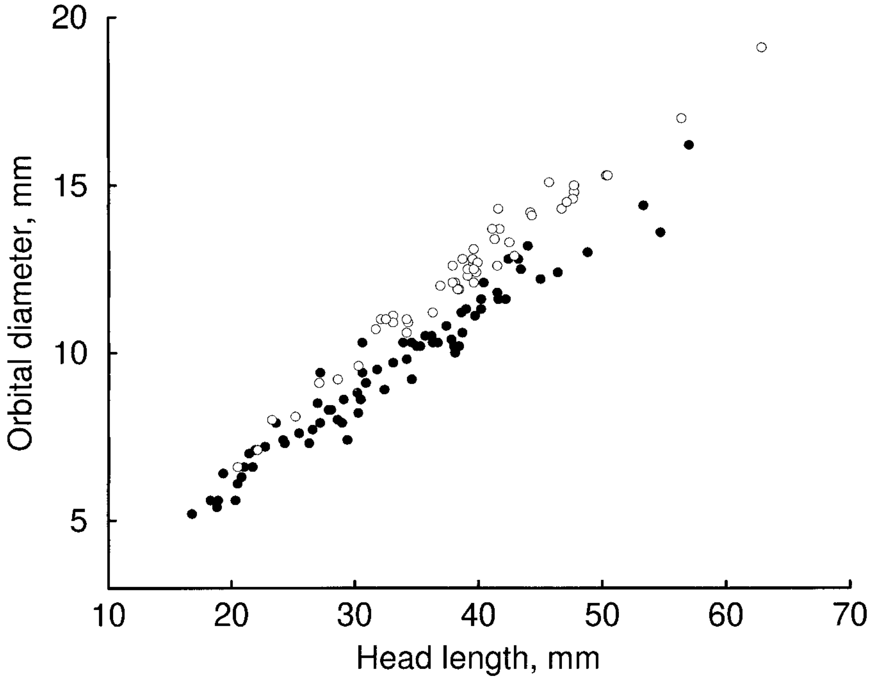

Fig. 22. Plot of orbital diameter against head length, both in millimeters, for *Cynodon gibbus* (filled in circles) and *Cynodon septenarius* (open circles).

many divergent side branches from main lateral-line canal. Divergent branches more developed in larger individuals; no side branches of lateral-line canal present in specimens under 80 mm SL. Lateral-line canal extending to posterior tip of middle caudal-fin ray.

Dorsal-fin rays ii,10. Dorsal-fin origin slightly posterior to vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 19th or 20th vertebra. Distal margin of dorsal fin straight to somewhat concave. First anal-fin pterygiophore inserting behind hemal spine of 22nd to 24th vertebrae. Distal margin of anal fin straight. Scales covering one-third to one-half length of anal-fin rays, less so in specimens smaller than 80 mm SL. Pectoral-fin rays pointed distally. Posterior tip of longest pectoral-fin ray extends beyond vertical through anal-fin origin, and reaches vertical through dorsal-fin origin. Pelvic fin short, rays i,8 (7 in three specimens, see comments under Remarks). Pelvic-fin base inserted at level of ventral profile of abdomen. Caudal fin forked, middle caudal-fin ray elongate, slightly longer than rays immediately dorsal and ventral to it, but its tip not extending to, or beyond, vertical through tip of dorsalmost principal ray; distal margin of upper lobe somewhat concave, and of lower lobe rounded; scales covering only basal portion of fin rays, not extending onto their branched portions.

VERTEBRAE: 51 (2); 52 (9); 53 (13); 54 (1); 55(1).

COLOR IN ALCOHOL: Specimens retaining guanine on scales with silver coloration on sides of body and head (including lower jaw, except for tip) to horizontal through dorsal margin of orbit, darker dorsally, including tip of lower jaw. In many specimens dark pigmentation of head extends to dorsal half of opercle and around infraorbitals. Specimens lacking guanine with yellowish-tan ground coloration (dark tan in some specimens) on sides of body and head, slightly darker dorsally. Specimens show varying degrees of guanine retention. Spot of dark pigmentation on posteriormost portion of supracleithrum. Specimens retaining pigmentation on fins with dorsal fin dusky; distal half of pelvic fins and dorsal portion of pectoral fins (es-

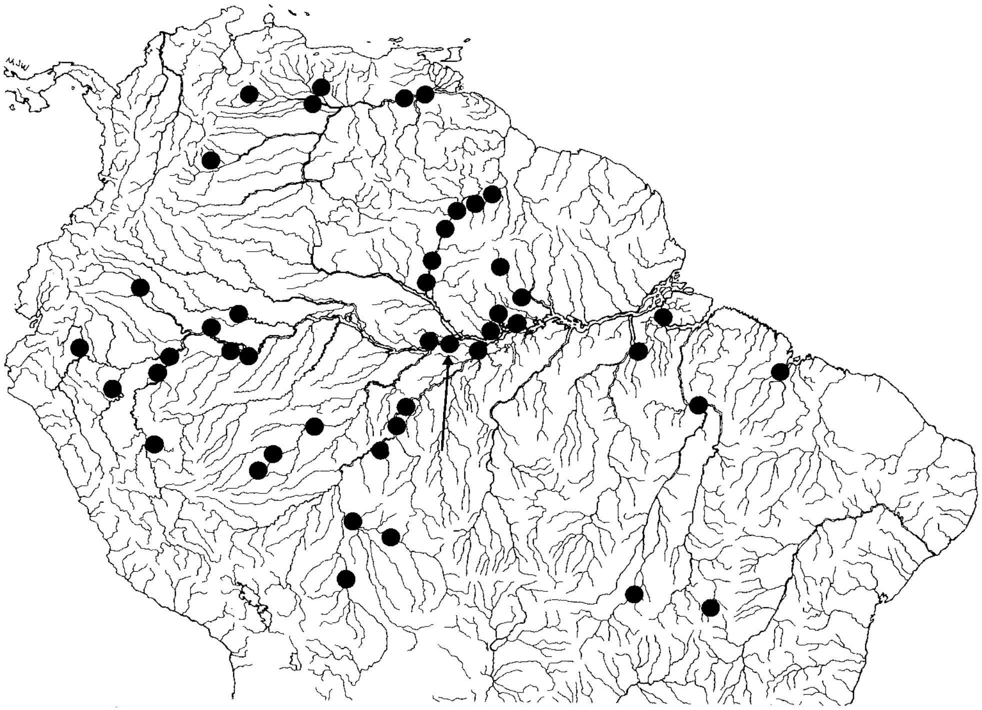

Fig. 23. Map of central and northern portions of South America showing geographic distribution of *Cynodon gibbus*. (Arrow indicates locality of neotype). Some symbols represent more than one lot of specimens or locality.

pecially unbranched pectoral-fin ray) covered with dark chromatophores. Distal half of anal fin with band of dark chromatophores. Base of caudal-fin rays with dark pigmentation forming vertically elongate blotch, less conspicuous on ventral portion of caudal-fin base. Adipose fin hyaline.

GEOGRAPHIC DISTRIBUTION: *Cynodon gibbus* is widely distributed throughout the rivers of the Amazon basin ranging from the westernmost portions of the basin in the Ríos Marañon and Ucayali east to the drainages of the rios Purus, Madeira, Branco, Amazonas, Trombetas, Xingu, and Tocantins basins (fig. 23). Three specimens (MZUSP 43613) were collected in Rio Pindaré, Maranhão state, Brazil representing the only record of a Cynodontinae in a drainage of northeastern Brazil. *Cynodon gibbus* also occurs in the middle and lower portions of the Río Orinoco basin, and in the Rupununi River, in the upper portions of the Essequibo River, Guyana.

Cynodon gibbus is found in sympatry with *C. septenarius* in Rio Uatumã, a tributary of the Rio Amazonas, Brazil. In the Rio Branco, a tributary of Rio Negro, the two species are found in proximate localities: *Cynodon gibbus* (MZUSP 32595) at Mararú, and *C. septenarius* (MZUSP 32596) at the confluence of Rio Branco and Rio Xeriuni. In the Rio Trombetas drainage samples of *Cynodon gibbus* were examined only from localities below the cataracts of Cachoeira da Porteira, at the mouth of the Rio Mapuera, whereas specimens of *C. septenarius* examined were collected in the Rio Mapuera (above Cachoeira da Porteira).

REMARKS: The features that distinguish *Cynodon gibbus* from its congener, *C. septenarius*, seem consistent throughout the samples examined. However, in a few instances some incongruences were observed. Table 2 shows that three specimens (AMNH 12542, MZUSP 32595, and MCNG 19340) assigned to *Cynodon gibbus* have 7 branched pelvic-fin rays on the left side (they have 8 branched rays on the right side). In 11 specimens, pelvic-fin ray counts could not be taken because of fin damage.

In spite of the significant difference in orbital diameter (fig. 22) this feature show a slight overlap between the two species (table 1). Specimens of *Cynodon gibbus* with relative orbital diameters larger than 30.5 mm SL are found in the Río Orinoco drainage and in Rios Madeira, Xingu, Branco, and Ucayali in the Amazon basin, not conforming, however, to any geographic pattern. In a few instances the band of dark pigmentation at the base of the caudal fin was faint, in many cases evidently a preservation artifact.

The problems mentioned above made species determination difficult in a few instances. In most of the cases such specimens belonged to lots with a number of other specimens that consistently showed all the features diagnostic for *Cynodon gibbus*. In other cases (e.g., MCNG 19340) the specimens originated in a region where *C. septenarius* does not occur. Given these facts and because these specimens showed some of the distinguishing features of *Cynodon gibbus*, they were assigned to that species.

Cynodon gibbus was described on the basis of a single specimen collected by Spix and Martius and originating from the rivers of Brazil (‘‘Brasiliae fluviis’’ in Agassiz, 1829: 78). Many specimens on which Agassiz’s descriptions were based are housed at the MHNN, Neuchâtel (see, *Rhaphiodon vulpinus*, below). The rest of Spix and Martius’s specimens remained at the Zoologische Staatssammlung München but were destroyed during a bombing raid in 1944 (Terofal, 1983 and Kottelat, 1988). I was unable to locate any specimen of *Cynodon gibbus* potentially used by Agassiz as a basis for his description and it may have been destroyed. The number of nine pelvic-rays (‘‘pinnae pectoralis ventrales 9’’, Agassiz, 1829: 78) reported in the original description can be used to identify the specimen Agassiz examined as *Cynodon gibbus*. As discussed above, *Cynodon gibbus* has i,8 pelvic-fin rays (total of nine) and *C. septenarius* has i,7 (total of eight). A few specimens of *Cynodon septenarius* also have a total of nine pelvic-fin rays (see discussion under Remarks of that species). The areas in Brazil sampled by Spix and Martius (Papavero, 1971, map 7 following page 66), where *Cynodon* occurs, encompass the distribution of *Cynodon gibbus* and *C. septenarius*. Therefore, we cannot absolutely determine that the specimen examined by Agassiz was *Cynodon gibbus* or *C. septenarius* with an aberrant number of pelvic-fin rays. Agassiz did not mention any pigmentation associated with the caudal fin, so this feature cannot be used to resolve the problem. But since only three out of 45 specimens of *C. septenarius* had nine pelvic-fin rays, the nine pelvic-fin rays reported by Agassiz (in Agassiz, 1829: 78) can be argued as evidence that the specimen he was dealing with was indeed *Cynodon gibbus*.

In light of the discussion above and in order to stabilize the nomenclature of *Cynodon gibbus*, a specimen MZUSP 6539, 146.0 mm SL is herein designated as neotype of *Cynodon gibbus* Agassiz, 1829. Agassiz (1829) reported the specimen of *Cynodon gibbus* as originating from the rivers in Brazil (‘‘Brasiliae fluviis’’). Papavero (1971, map following page 66) described the itinerary of Spix and Martius’s collecting trip. The specimen herein designated as neotype of *Cynodon gibbus* originated from Lago Manacapuru, Amazonas State, located within the region from which the Spix and Martius collections were made.

MATERIAL EXAMINED: 226 specimens (72, 77.0-280):

TYPE MATERIAL: MZUSP 6539 (1, 146.0) Lago Manacapuru; NEOTYPE (present designation); see discussion above under Remarks.

NONTYPE MATERIAL: *BOLIVIA. El Beni*: AMNH 77340 (1, 85.7) mouth of Río Ibarre; USNM 305368 (2, 169.0–261.0) Ballivia, Río Cuiraba at 10 km NE El Porvenir Biological Station, at 40 air km E San Borja; MNHN 1989 1457 (4, 119.7–180.0), Trinidad, Santa Rosa. *BRAZIL. Amazonas*: BMNH 1913.7.7:5 (1, 225.0); BMNH 1970.4.2:2 (1, 159.0) Manaus; USNM 229138 (1, 86.8) embayment of Ilha da Marchantaria; USNM 229139 (1, 157.0) near Manaus, Lago Terra Preta, Janauari; MCZ 21389 (1, 171.0) Manaus and environs; MCZ 21331 (2, 217.0–220.0) Lago Janauari; INPA 5328 (3, 191.0–200.0) Rio Amazonas, Ilha do Caieiro, Lago do Rei; INPA 5348 (1, 221.0) Rio Uatumã; MCZ 21411 (1, 112.6)

SERPA, Rio Amazonas at Itacoatiara; MZUSP 13497 (1, 226.0) Rio Amazonas, Itacoatiara; MZUSP 21489 (1, 130.0) Pauini; MCZ 21392 (2, 82.6–189.0) Rio Javari; MCZ 21403 (4, 122.4–133.7) Río Putumayo near the Brazilian-Colombian border; MCZ 21380 (1, 98.4) Lago Coari; MZUSP 27340 (3, 144.0–157.0) Costa do Capacete, Rio Solimões, Município of Tabatinga; MZUSP 35550 (1, 124.0) Igarapé Joari, Humaitá; MZUSP 6972 (1, 100.0) Rio Madeira; *Pará*: CAS 53414 (1, 134.1) Lago Grande, into Rio Amazonas; CAS 69890 (1, 200.0) ''Santarém River''; CAS 79320 (2, 219.0–226.0) Santarém Market; INPA 5340 (1, 122.0) Rio Mapuera, Cachoeira São Francisco, Cachoeira Porteira; INPA 5341 (1) Rio Mapuera, Cachoeira da Égua; INPA 5326 (1, 167.0); INPA 5327 (1, 163.0), Rio Tocantins, Icangui; MZUSP 32588 (1, 176.0); MZUSP 32589 (1, 226.0) Rio Itacaiunas, Caldeirão; MZUSP 32587 (1, 149.9) Rio Xingu, Belo Monte; *Rondônia*: INPA 14528 (1, 128.0) Rio Mamoré, below Surpresa, and the mouth of Rio Guaporé; INPA 14529 (2, 230.0) Rio Guaporé, Pimenteiras; INPA 14530 (1, 280.0) Rio Jamari, below Samuel dam; MZUSP 32592 (5, 159.0–193.0); MZUSP 32593 (31, 170.0–258.0) Rio Madeira, Calama; *Roraima*: NMW 68729 (2, 183.0–198.0); NMW 57862 (1, 186.0) Rio Branco; MZUSP 32594 (1, 215.0) Rio Branco, Cachoeira do Bem-Querer; MZUSP 32595 (4, 132.0–160.0) Rio Branco, Mararã; NMW 57112 (1, 226.0) Conceição, Rio Branco; NMW 57113 (1, 238.0) Rio Branco, Boa Vista; *Goiás*: MZUSP 40401 (1, 185.0) Rio Macacos, tributary of Rio Paranã, Fazenda Fortaleza, Flores de Goiás; MZUSP 40737 (1, 157.0) Rio Paranã, above mouth of Rio Atalaia, Village of Porto Real, Monte Alegre de Goiás; MZUSP 4840 (1, 98.0) Rio Araguaia, Aruanã; *Acre*: AMNH 223194 (2, 127.9–134.7) vicinity of Rio Macaua, tributary of Rio Iaco, a tributary of Rio Purus, near Sena Madureira; MCZ 33512 (1, 131.6) vicinity of Rio Macaua, tributary of Rio Iaco (tributary of Rio Purus); *Maranhão*: MZUSP 43613 (3, 208.0–280.0) Lago do Viana, Rio Pindaré system; MNHN 1683 (1, 211.0) Brazil, ''Amazone''; MZUSP 3119 (1, 216.0) Pará and *Amazonas*; MNHN 1994 –0170 (2) Brazil, Rio Solimões; NMW 57110 (1, 140.4) Rio Purus. *COLOMBIA*. *Meta*. ANSP 128216 (1, 194.0) Laguna Mozambique at Mozambique Ranch; NE portion of lake; ANSP 128257 (1, 155.0) Laguna Mozambique, central pond, part of ox-bow N of and connecting with E current of laguna. *ECUADOR*. *Napo*: BMNH 1970.4.3.6 (1, 100.4) Jatuncocha; FMNH 103386 (2, 193.0–232.0) outflow of Laguna Jatuncocha; FMNH 103387 (2, 171.0–218.0) Río Yasuni, 1–2 km downstream from confluence with Río Jatuncocha; FMNH 103388 (1, 258.0) Río Yasuni, Laguna Jatuncocha; FMNH 103389 (3, 86.9–189.0) mouth of Quebrada to the Río Tiputini. *GUYANA*. CAS 16076 (1, 107.2) Menari Ranch, near Lathan (=Lethem?), border with Brazil; BMNH 1972.7.27:43–45 (3, 211.0 from one specimen), Rupununi, Dadanawa ponds. *PERU*. *Loreto*: ANSP 136849 (2, 134.2–134.6) vicinity of Iquitos, Moronacocha outlet, right bank of Río Nanay; CAS 134786 (2, 98.3–99.1) near Pebas, caño Tuye; CAS 134787 (1, 119.7) near Pebas, Río Ampiyacu; CAS 166549 (1, 85.3) near Pebas; USNM 167773 (2, 147.0–190.0) Lago Sanango, near Yurimaguas; CAS 69886 (3, 156.0–208.0) Lago Sanango, large cutoff lake of Río Huallaga, above Yurimaguas, connected to river by narrow channel; MZUSP 26107 (1, 151.0), Río Ucayali, Jenaro Herrera; *Ucayali*: MZUSP 26176 (3, 102.0–105.0) Río Ucayali, Bagazan, Coronel Portillo; MZUSP 26728 (1, 107.0) Río Ucayali, Pucallpa, Coronel Portillo, Departamento Ucayali; *Amazonas*: LACM 39857–10 (1, 35.0), LACM 39883–7 (1, 162.0); LACM 41724–12 (1, 94.9) Río Santiago at La Poza; LACM 36343–3 (1, 208.0) Ayambis; ANSP 21208 (2, 133.8–152.0) Peruvian Amazon; *VENEZUELA*. *Anzoátegui*: ANSP 149475 (1, 78.8) river shore, N bank of río Orinoco, just downstream from Ciudad Bolivar; *Delta Amacuro*: CAS 50771 (1, 96.5) Delta Amacuro, in cove on shore; LACM 43295–89 (65, 100.0–144.0) Río Orinoco, on N shore at Isla Portuguesa; LACM 43382–22 (11, 77.1–125.0) Río Orinoco, secondary caño about 500 m from its mouth in caño Guarguapo; LACM 43399–25 (2, 102.0–104.0) Río Orinoco, Caño Chivera, Isla Chivera, near Barrancas; UMMZ 211280 (1, 112.2) lagoon in Río Orinoco, 131 nautical miles

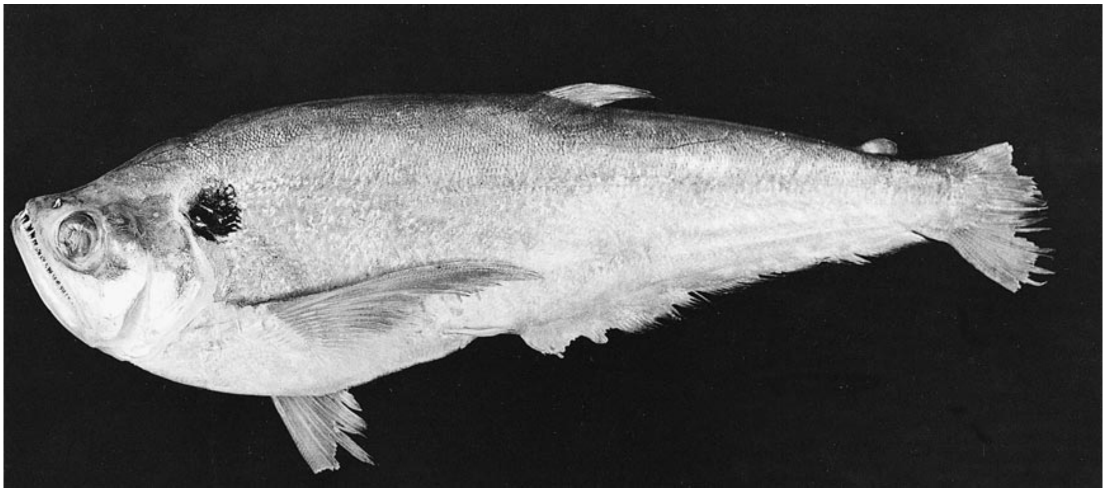

Fig. 24. *Cynodon septenarius*, new species, holotype, MZUSP 32590, mm SL, Brazil, Amazonas, Rio Tefé, Supiã-Pucu.

from Sea Buoy; USNM 222855 (2, 136.0), USNM 233932 (1, 147.0) Río Orinoco, small caño near mouth of Caño Socoroco, 11 nautical miles upstream from sea buoy; *Portuguesa*: MCNG 19340 (1, 138.0) caño Igues; *Apure*: USNM 258193 (1, 115.4) side channel of Río Apure ca. 5 km W of San Fernando de Apure; ANSP 160097 (1,122.0) Río Orinoco at El Burro; *Bolivar*: USNM 222848 (1, 212.0) Río Orinoco, cove at W end of Islote Fajardo, 182 nautical miles upstream from Sea Buoy; ANSP 166727 (6, 120.0–195.0) Caicara. *Guarico*: USNM 257564 (1, 208.0) Río Orituco where crossed by road from Calabozo.

Cynodon septenarius, new species

Cynodon gibbus: (misidentification): Eigenmann, 1912: 395 (British Guiana [= Guyana]; description); 3 of 7 cited specimens examined). ● Pellegrin, 1909: 148 (Brazil, Tonnantins [= Tonantins]).

DIAGNOSIS: *Cynodon septenarius* lacks the band of dark pigmentation covering the base of the caudal-fin rays that is characteristic of *C. gibbus* (compare figs. 24 and 21). Dark pigmentation is sometimes scattered in the region of the caudal peduncle and caudal-fin base, but in those cases the pigmentation is never very dense and does not form the conspicuous dark band present in *C. gibbus*. The presence of 7 (versus 8) branched pelvic-fin rays and the relatively larger orbital diameter (30.1-34.4 versus 24.9-33.8 of HL) also distinguish *Cynodon septenarius* from *C. gibbus* (see comments under Remarks of these two species accounts). *Cynodon septenarius* can be distinguished from *Cynodon meionactis* by the lack of the band of dark pigmentation covering the base of the caudal-fin rays present in the latter species, and the presence of 7 (versus 8) branched pelvic-fin rays. See also under Comments on *C. meionactis*, and see Géry et al. (1999).

DESCRIPTION: (Table 1) Body compressed laterally, deep anteriorly, greatest body depth approximately at vertical through pectoral-fin base, depth decreasing progressively posteriorly. Dorsal profile of head concave at interorbital region. Predorsal body profile strongly convex, forming pronounced hump at vertical through middle of orbit; straight and slightly posteroventrally slanted along dorsal-fin base, proportionally less slanted and almost straight in region of body extending from that point to vertical through last base of anal-fin ray; concave between latter point and origin of dorsalmost procurrent caudal-fin ray. Ventral profile of body convex to posterior tip of coracoids; straight and posterodorsally slanted (sometimes slightly convex) from that point to pelvic-fin base; straight from there to anal-fin origin; straight and posterodorsally slanted along anal-fin base, then concave to caudal-fin origin. Ventral surface of body with keel extending from isthmus to pelvic-fin base; keel anteriorly supported by expanded coracoids.

Laterosensory canal system in infraorbitals and opercular bones highly branched; canals more developed in larger individuals. Mouth obliquely aligned relative to horizontal axis of body. Upper jaw very long relative to head length; posterior tip of maxilla extending posteriorly to vertical through posterior tip of second infraorbital; relatively more elongate in smaller individuals. Third infraorbital not in contact with preopercle ventrally. Adipose eyelid with notch in region of orbital margin where second and third infraorbitals meet.

Teeth in both jaws conical, in single row, varying in size. Premaxilla with 3 small canines of similar size, one in anterior and one in posteriormost portion; third canine sometimes slightly smaller, intermediate in position to 2 others and usually separated from posteriormost canine by 2 or 3 small conical teeth. Several small conical teeth located between anterior and middle canines. Maxilla with slightly enlarged conical teeth separated by smaller teeth of similar size; teeth gradually becoming smaller posteriorly.

Dentary with well-developed canine, extending up into snout when mouth is closed, tip of canine reaching nostrils anteriorly. One smaller dentary canine, about half size of largest, followed by another smaller conical tooth anteriorly; canines posterior to largest canine progressively decreasing in size; dentary canines separated by conical teeth of various sizes. Teeth on ectopterygoid and mesopterygoid very small and conical. No teeth on metapterygoid.

Scales without distinct serration. Scales small on dorsal portions of body; scale size increasing towards lateral line with largest scales along lateral line; scales on region dorsal to anal fin small. Scales along pre dorsal midline very small and arranged in somewhat irregular rows. Row of scales forming keel from posterior portion of coracoid to pelvic-fin base less rounded in shape than those covering the rest of the body. Scales below lateral line obliquely arranged. Lateral-line scales with many divergent branches of lateral-line canal. Divergent branches more developed in larger individuals; dorsal and ventral branches of lateral-line canal starting to develop in specimens of 110 mm SL. Lateral-line canal extending to posterior tip of middle caudal-fin ray.

Dorsal-fin rays ii,10. Dorsal-fin origin slightly posterior to vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 19th to 21st vertebrae. Distal margin of dorsal fin straight to somewhat concave. First anal-fin pterygiophore inserting behind hemal spine of 22nd to 24th vertebrae. Distal margin of anal fin straight. Scales covering basal one-third to one-half length of anal-fin rays. Pectoral-fin rays i,15–17; fin pointed distally. Posterior tip of longest pectoral-fin ray extends beyond vertical through anal-fin origin, and reaches vertical through dorsal-fin origin. Pelvic fin short; pelvic-fin rays i,7. Base of pelvic fin inserted at level of ventral profile of abdomen. Caudal fin forked, middle caudal-fin ray elongate, slightly longer than rays immediately dorsal and ventral to it, but its tip not extending to vertical through tip of dorsalmost principal ray. Distal margin of upper caudal-fin lobe somewhat concave, with lower lobe rounded. Scales covering only basal portion of caudal-fin rays, not extending onto their branched portions.

VERTEBRAE: 51(2), 52(6), 53(19), 54(5).

COLOR IN ALCOHOL: Specimens retaining guanine on scales with silver coloration on sides of body and head (including lower jaw, except for tip) as far dorsally as horizontal through dorsal margin of orbit darker dorsally, including tip of lower jaw. In many specimens dark pigmentation of dorsal portion of head extends onto dorsal half of opercle and around infraorbitals. Specimens lacking guanine with yellowish-tan ground coloration (dark tan in some specimens) on sides of body and head, slightly darker dorsally. Specimens show varying degrees of guanine retention. A few specimens from the Rio Negro (MZUSP 32597) have an overall body coloration darker than the usual pattern exhibited by other specimens. Spot of dark pigmentation present on posteriormost portion of supracleithrum. Specimens retaining pigmentation on fins with dorsal fin dusky and distal half of pelvic fins and dorsal portion of pectoral fins (especially unbranched

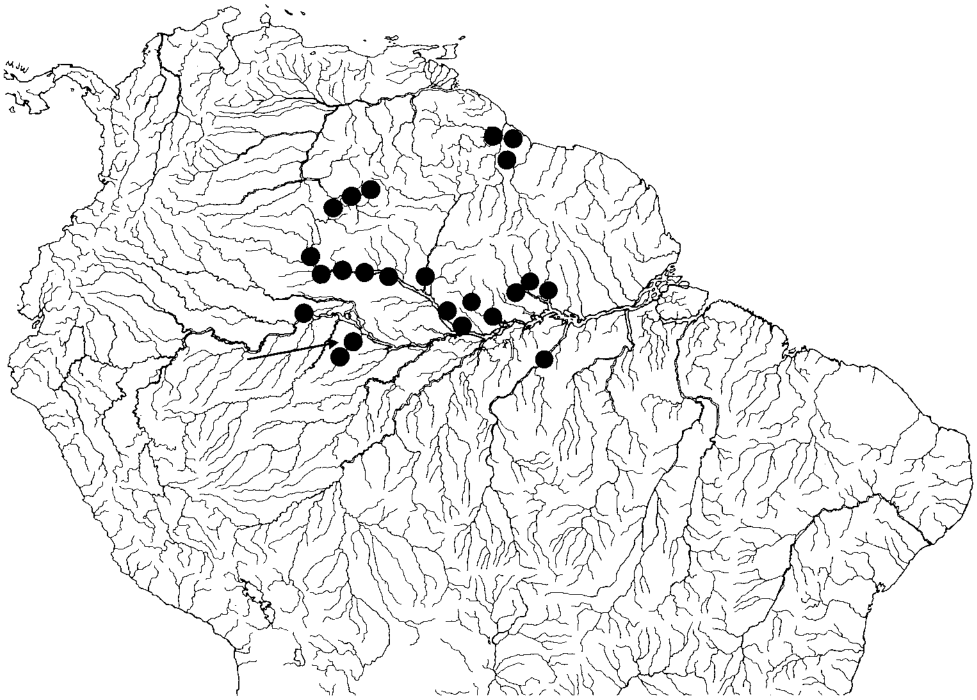

Fig. 25. Map of central and northern portions of South America showing geographic distribution of *Cynodon septenarius* (arrow indicates type locality). Some symbols represent more than one lot of specimens or locality.

pectoral-fin ray) covered with dark chromatophores. Distal half of anal fin with band of dark chromatophores. Adipose fin hyaline.

GEOGRAPHIC DISTRIBUTION: *Cynodon septenarius* occurs in the Rio Solimões/Amazonas drainage east of the mouth of Rio Içá (located close to the border of Brazil and Colombia), eastward into the Rios Negro, Branco, Trombetas, and Tapajós (fig. 25). *Cynodon septenarius* also occurs in the Essequibo and Demerara Rivers in Guyana, and in the upper portions of the Río Orinoco basin in Venezuela. *Cynodon septenarius* is found in sympatry with *C. gibbus* in a few localities within the Amazon basin (see geographic distribution of *C. gibbus*, for details).

ETYMOLOGY: The specific name, *septenarius*, is a Latin adjective which means ‘‘consisting of seven,’’ in reference to the seven branched pelvic-fin rays that distinguishes this species from its congeners, *C. gibbus* and *C. meionactis*.

REMARKS: Three specimens (MZUSP 32597, 2 specimens and MZUSP 32585) of *Cynodon septenarius* have 8 branched pelvic-fin rays, the former having 7 on the right side, and the latter 8 on both sides, and 1 specimen (MZUSP 32590) has 6 pelvic-fin rays (table 2). Since these atypical specimens belong to lots with other specimens with 7 branched pelvic-fin rays, and, in addition, lack the band of dark pigmentation at the caudal-fin base characteristic of *C. gibbus* and *C. meionactis*, and have relatively large orbital diameters, they were herein assigned to *C. septenarius*.

MATERIAL EXAMINED: 187 (51, 94.5-312):

TYPE MATERIAL: Holotype: BRAZIL. *Amazonas*: MZUSP 32590 (247.0 mm SL) Rio Tefé, Supiã-Pucu (between 3°40′ and 4°20′S; 65°50′ and 65°10′W), collector: Michael Goulding, 28 July 1979; paratypes: BRAZIL. *Amazonas*: MZUSP 53306 (9, 204–248.0), CAS 204164 (2, 223.0–230.0), INPA 14531 (2, 237.0–240.0), MCP 21735 (2, 232.0–235.0), MNRJ 18171 (2, 240.0–243.0), USNM 352434 (2, 240.0–245.0) all taken with holotype.

TABLE 2
Frequency Distribution of Pelvic-Fin Rays in *Cynodon* species

Species	Pelvic-fin rays 6	7	8
C. gibbus	—	3	58
C. septenarius	1	44	3

NONTYPE MATERIAL: *BRAZIL Amazonas*: INPA 5451 (1, 167.0) Rio Uatumã, at Balbina dam; INPA 5512 (1, 165.0) Rio Uatumã, Sumaúma (= Samaúma?); INPA 5347 (1, 212.0) Rio Uatumã, Igarapé Anauá; INPA 5509 (1, 159.0) Rio Uatumã, Santa Luzia; INPA 5821 (5, 175.0–187.0) Rio Negro; INPA 8493 (3, 106.1–138.2) Rio Negro, between Tarumã and Tarumã-Mirim; MZUSP 31129 (1, 200.0); MZUSP 32605 (2, 177.0–196.0) Rio Negro, Ilha de Tamaquaré; MZUSP 6145 (4, 174.0–182.0) Rio Negro, above Manaus; MZUSP 6196 (2, 164.0–189.0) Igarapé Jaraqui, left margin of Rio Negro, above Manaus; MCZ 21409 (1, 191.0) Rio Negro, Lago do Aleixo; MZUSP 32599 (2, 206.0–208.0) Rio Negro, São Pedro; MZUSP 32597 (7, 200.0–213.0), MZUSP 32598 (1, 168.0) São Gabriel da Cachoeira; MZUSP 32601 (1, 194.0) Rio Negro, Anavilhanas; MZUSP 32603 (2, 187.0–213.0) Rio Negro, Cachoeira do Bicho-Açu; NMW 57111 (1, 171.0), mouth of Rio Negro; MZUSP 21707 (4, 170.0–190.0) Lago Janauacá and surroundings, Rio Solimões; MZUSP 26933 (1, 212.0) Lago Janauacá and around Manaus; MCZ 150891 (1, 191.0), MZUSP 32602 (1, 168.0) Rio Marauiá, near mouth; MZUSP 32604 (3, 213.0–239.0) Rio Marié, Lago do Curuá-Muru; MZUSP 32590 (20, 204.0–247.0) Rio Tefé, Supiã-Pucu; MZUSP 32591 (24, 139.0–226.0) Rio Tefé, Mastro; MNHN 1909 0300 (1, 189.0) Rio Tonantins; MZUSP 32600 (1, 199.0) Rio Arirará, near mouth; *Pará*: INPA 5325 (1, 161.0) Rio Trombetas, below Cachoeira Porteira; MZUSP 32586 (3, 164.0–202.0) Rio Trombetas, Cuminá; MZUSP 5415 (11, 174.0–184.0) Rio Trombetas, Oriximiná; INPA 5367 (1, 203.0) Rio Trombetas, Lago Tapagem; MZUSP 15641–15647 (8, 164.0–202.0) mouth of Lago do Leonardo, Reserva Biológica de Trombetas; INPA 7116 (2, 225.0) Rio Cupari, tributary of Rio Tapajós, near mouth; MZUSP 21389 (1, 183.0) Rio Tapajós, São Luís; MZUSP 32585 (55, 164.0–236.0) Rio Tapajós, between Itaituba and São Luís; INPA 7115 (2, 208.0–209.0) Rio Cupari, tributary of Rio Tapajós, near mouth; INPA 5334 (1, 214.0) Rio Tocantins, Itupiranga; *Roraima*: MZUSP 32596 (2, 202.0–205.0) Rio Branco, Xeriuni. *GUYANA*. AMNH 223193 (2, 109.6–140.5), AMNH 223192 (1, 229.0), FMNH 53513 (1, 210.0), CAS 79232 (1, 312.0) Malali; FMNH 53514 (2, 94.5–200.0), CAS 79231 (2, 228.0–282.0) Wismar; AMNH 72950 (1, 253.0) confluence of Mazaruni and Cuyuni Rivers, about 100 m off Kartabo Point; AMNH 17634 (1, 147.0) Guyana; *VENEZUELA*. *Amazonas*: ANSP 159592 (10, 180.0–235.0) Río Sipapo, mouth of lagoon ca. 3 km above Pendare; ANSP 161553 (4, 181.0–215.0) Río Cunucunuma ca. 40 km from confluence with Río Orinoco; ANSP 161555 (3, 205.0–222.0) Río Cunucunuma ca. 40–50 km above confluence with Río Orinoco; ANSP 161554 (3, 193.0–215.0) Río Orinoco at sand playa just upstream from Quiratare; ANSP 161557 (1, 199.0) rocks on western shore of Río Casiquiare ca. 2 km downstream from mouth of Río Pamoni.

Genus *Rhaphiodon* Agassiz, 1829

Rhaphiodon Agassiz, 1829: 59 (type species: *Rhaphiodon vulpinus*).

Rhaphiodontichthys Campos, 1945: 473 (type species *Rhaphiodon vulpinus* by original designation).

See remarks under Genus *Cynodon* for question related to the nomenclature of *Rhaphiodon*.

DIAGNOSIS AND DISTRIBUTION: Same as *R. vulpinus*, below.

Rhaphiodon vulpinus Agassiz, 1829

Rhaphiodon vulpinus Agassiz, 1829: 76, pl. 26 (original description, type locality: Brazil). ● Evermann and Kendall, 1906: 85 (collection locality unknown, market at Buenos Aires, Argentina). ● Fowler, 1906: 467 (description, Peruvian Amazon, specimen not examined). ● Eigenmann and Bean, 1907: 667 (Brazil, lower Amazon). ● Eigenmann and Ogle, 1907: 31 (Paraguay). ● Eigenmann, 1910: 444 (literature compilation). ● Bertoni, 1939: 56 (upper Rio

Paraná, identification based on location). ● Fowler, 1945: 157, fig. 49 (literature compilation);
–1950: 332 (literature compilation). ● Nelson, 1949: 495–523 (morphology). ● Schultz, 1950: 49 (Argentina, Paraguay, Amazon). ● Lowe-McConnell, 1964: 110 (Guyana, Rupununi River system). ● Ringuelet et al., 1967: 167 (Rio Paraná and Río de la Plata systems, based on location). ● Britski, 1972: 82, fig. 4 (literature compilation, fishes from the state of São Paulo, Brazil). ● Nielsen, 1974: 45 (*Hydropardus rapax* Reinhardt, 1849 placed as a synonym). ● Saul, 1975: 112 (Ecuador, Río Aguarico, specimen not examined). ● Howes, 1976: 205–229 (myology, functional morphology). ● Lesiuk and Lindsey, 1978: 991–997 (Brazil: Rio Negro, functional morphology). ● Géry and Poivre, 1979: 1–4 figs.1–4 (description of juvenile teeth). Mendes dos Santos et al., 1984: 40 (Brazil, Rio Tocantins; photograph, description). Géry and Mahnert, 1984: 174 (Ecuador, Río Napo system, specimen not examined). Lauzanne and Loubens, 1985: 56, fig. 52 (Bolivia, Río Mamore: Trinidad). ● Di Persia and Neiff, 1986: 612 (list of species from Río Uruguay system). ● Géry, 1986: 66, pl.6a, b (key to cynodontine species). ● Ortega and Vari, 1986: 10 (in list of freshwater fishes of Peru). ● Ferreira et al., 1988: 344 (Brazil, Roraima, Rio Mucajaí, specimen not examined). Goulding et al., 1988: 127 (Brazil, Rio Negro). ● Galvis et al., 1989: 122 (Colombia, Río Meta system, specimen not examined). Arandas-Rego and Pavanelli 1990: 99 (parasitized by proteocephalids Cestoda, Brazil, at Salobra, Mato Grosso; identification based on location). Barriga, 1991: 30: (in list of freshwater fishes of Ecuador, common name). ● Taphorn, 1992: 439 (description, Venezuela, Apure).

Cynodon vulpinus: Cuvier, 1829: 312 (named in a footnote to the description of *Hydrocyon*). ● Valenciennes, 1849: 329 (Brazil; description). ● Günther, 1864: 359 (based on Valenciennes, 1849). ● Kner, 1859: 47 (Brazil; description, not able to associate with a specific specimen at NWM). ● Peters, 1877: 472 (Venezuela, Calabozo, specimen not examined). ● Steindachner, 1883: 15 (Peru, Río Huallaga; description). ● Perugia, 1891: 49 (Río Paraguay and Río de La Plata systems, identification based on location). ● Boulenger, 1898: 426 (Brazil, Rio Juruá). ● Goeldi, 1898: 463, 483 (common name, literature compilation). ● Pellegrin, 1899: 157 (Venezuela, Apure); 1909: 150 (Brazil: Santarém, Rio Negro, Tabatinga). Devincenzi, 1924: 172 (Río Uruguay, Concordia, identification based on location). ● Devincenzi and Barattini, 1926: pl.12 (Uruguay). ● Devincenzi and Teague, 1942: 82 (Río Uruguay; diagnosis, identification based on location). ● Eigenmann and Kennedy, 1903: 528 (Paraguay, Río Paraguay, Asunción).

Raphiodon vulpinus (genus name misspelled): Müller and Troschel, 1844: (Brazil); 1845: 19 (identical to Müller and Troschel, 1844). ● Cope, 1878: 688 (upper Amazon, specimen not examined). ● Eigenmann, 1906: 524, pl.11 (photograph of head); 1907: 154 (Paraguay, identification based on location). Starks, 1913: 20 (Brazil, Pará; description). ● López et al., 1984: 76 (Uruguay, Río Ururguay, Salto Grande dam, identification based on location). ● Godoy, 1987: 192–193 (Brazil: Santa Catarina, figured).

Hydropardus rapax Reinhardt, 1849: 46–57 (original description; type locality: Uruguay, Montevideo).

Cynodon vupinus: (species name misspelled) Eigenmann and Eigenmann, 1891: 59 (literature compilation).

Rhaphiodon vulpinum: (species name misspelled) Eigenmann and Allen, 1942: 271 (Peru, Río Pacaya; common name). ● Schultz, 1944: 273 (literature compilation);

Rhaphiodontichthys vulpinus: Campos, 1945: 473 (Brazil: Rio Amazonas; description). ● Mago Leccia, 1970: 74 (in list of species from Venezuela). ● Cala, 1977: 9 (Colombia, Río Orinoco system, specimen not examined).

Raphiodontichthys vulpinus (generic name misspelled): Machado-Allison, 1987: 134 (Venezuela, Llanos, specimen not examined).

DIAGNOSIS: *Rhaphiodon vulpinus* can be distinguished from all other cynodontines by the placement of the dorsal fin on the posterior third of the body length (figs. 26, 28) (predorsal distance being 69.3–74.4 versus 52.2–61.1 of SL in all other cynodontines), by its very elongate body relative to its depth (body depth at dorsal-fin origin 12.7–19.6 versus 19.1–33.7 of SL in all other cynodontines), and by a higher number of vertebrae (62–68 versus 44–54 in all other cynodontines). It can be further distinguished from all *Hydrolycus* species by the insertion of the dorsal fin slightly posterior to the vertical through the anal-fin origin (anterior to that point in *Hydrolycus*) and from *Cynodon* by the lower number of anal-fin rays (38–50 versus 61–80 in *Cynodon*).

DESCRIPTION: (table 3) Body very elongate, compressed laterally, greatest body depth at

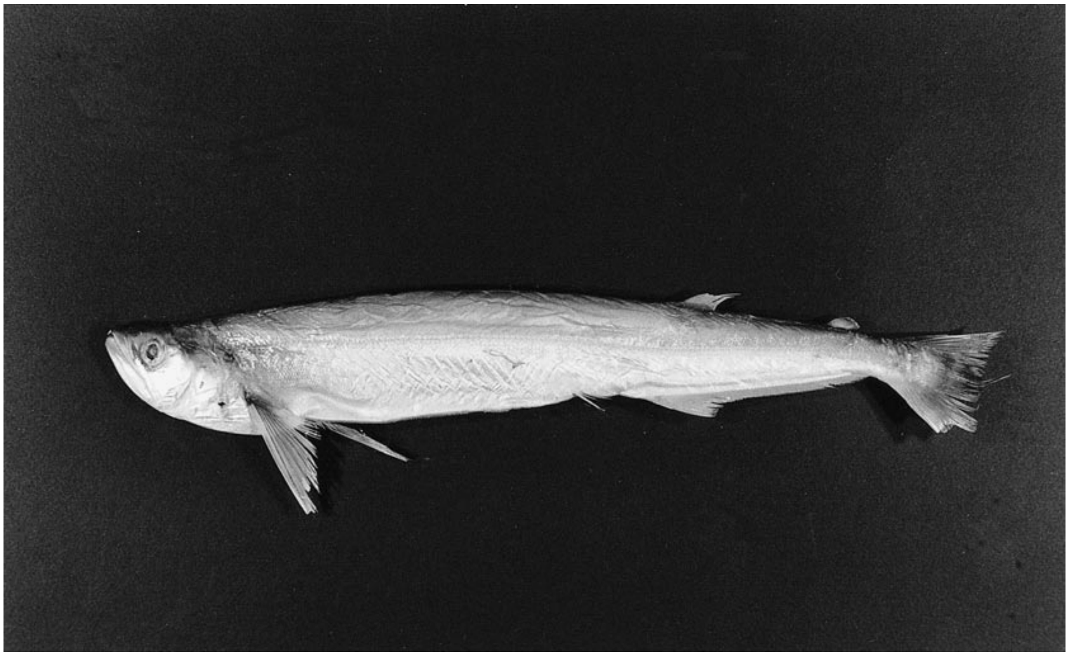

Fig. 26. *Rhaphiodon vulpinus*, MZUSP 32809, 305 mm SL, Brazil, Pará, Rio Xingu, Belo Monte.

vertical through pectoral-fin origin, depth decreasing posteriorly. Dorsal profile of head slightly concave, ranging from barely concave to straight in specimens smaller than 50 mm SL; degree of concavity varies depending on degree of bending in region posterior to head at time specimen was preserved. Predorsal profile of body straight to slightly concave; slightly posteroventrally slanted at dorsal-fin base, proportionally less slanted from that point to vertical through last anal-fin ray; concave between latter point and origin of dorsalmost procurrent caudal-fin ray. Ventral profile of body convex to pelvic-fin origin, convexity more pronounced anteriorly, less so between vertical through innermost pectoral-fin ray and pelvic-fin origin; straight to anal-fin origin, posterodorsally slanted along anal-fin base, straight to origin of ventralmost procurrent caudal-fin ray. Ventral surface of body with keel from isthmus to anus, interrupted at vertical through pelvic-fin base; keel anteriorly supported by expanded coracoids.

No serrations at margin of opercular bones. Laterosensory canal system in infraorbitals and opercular bones highly branched; canals progressively more pronounced in larger individuals, canals absent in specimens under 50 mm SL.

Mouth obliquely aligned relatively to horizontal axis of body, angle of mouth relative to horizontal plane varying depending on degree of flexure posterior to head at time of specimen preservation. Upper jaw very long relative to head length; posterior tip of maxilla extending slightly beyond vertical through posterior tip of second infraorbital in specimens under 40 mm SL, progressively shorter in larger individuals, not reaching that point in the largest specimens examined.

Second and third infraorbitals not in contact with preopercle posteriorly. Snout shorter than orbital diameter. Adipose eyelid with notch in region of orbital margin at vertical through middle of second infraorbital.

Teeth in both jaws conical, in single row, varying in size. Teeth in upper jaw partially covered by skin laterally, smaller teeth only with tips apparent. Premaxilla delimited by one canine anteriorly and one canine, slightly smaller, posteriorly; one large conical tooth located between two canines, placed closer to posteriormost canine; several small conical teeth between anterior and posteriormost canines; maxilla with conical teeth of vari-

TABLE 3

Morphometric and meristic data of holotype of *Rhaphiodon vulpinus*, MHNN 822; holotype of *Hydropardus rapax*, ZMC 183; and all other specimens of *Rhaphiodon vulpinus* from which measurements were taken. Specimens from upper Rio Xingu, Brazil, MZUSP 32808, included. See text for details on counts indicated below by an asterisk. Dashes indicate proportions that could not be determined because of the condition of the specimen.

			Rhaphiodon vulpinus		
Character	MHNN 822	ZMC 183	n	range	mean
MORPHOMETRICS					
Standard length	303.0	623.0	62	68.9–604.0	
Body depth at pelvic-fin origin	12.9	—	58	13.3–19.9	16.3
Body depth at dorsal-fin origin	13.3	14.8	62	12.7–19.6	15.0
Body depth at pectoral-fin origin	15.1	18.1	62	16.0–21.2	18.4
Snout to dorsal-fin origin	72.9	69.8	61	69.3–74.4	71.9
Snout to pectoral-fin origin	23.1	22.0	62	20.9–25.4	23.1
Snout to pelvic-fin origin	60.4	—	59	57.4–63.3	60.0
Snout to anal-fin origin	70.0	68.4	62	67.4–73.2	69.6
Eye to dorsal-fin origin	65.3	62.4	62	61.0–68.0	64.5
Dorsal-fin origin to caudal-fin origin	28.2	28.9	62	26.5–32.8	28.8
Dorsal-fin origin to adipose fin origin	17.0	18.6	61	15.3–19.8	17.5
Pectoral-fin origin to anal-fin origin	48.2	48.8	61	42.2–54.7	48.6
Caudal-peduncle length	6.7	7.1	61	6.2–8.3	7.2
Caudal-peduncle depth	5.5	5.8	62	5.3–7.3	6.2
Head-length	19.3	18.5	62	17.2–22.5	19.3
Snout length	26.4	28.4	62	25.2–29.3	26.9
Orbital diameter	20.0	17.8	61	17.5–26.6	21.6
Interorbital width	16.8	20.7	61	14.7–19.4	17.2
Postorbital length	55.0	55.9	62	46.5–58.9	52.6
Dorsal-fin base	5.3	5.5	62	4.4–6.5	5.3
Dorsal-fin length	—	9.4	54	8.6–12.2	10.0
Anal-fin base	25.9	24.1	62	23.6–28.4	26.3
Pectoral-fin length	—	—	47	20.9–29.2	24.3
Pelvic-fin length	—	—	52	4.4–6.6	5.6
Upper jaw length	69.3	69.7	62	67.1–76.1	
Dentary canine length	17.6	19.3	60	12.1–18.3	16.1
MERISTICS					
Scales along lateral-line series	135	121	61	122–152*	131.2
Scale rows above lateral line	29	—	52	22–33	26.1
Scale rows below lateral line	16	—	53	15–22	19.0
Scale rows around caudal peduncle	37	27	52	30–39	34.2
Branched anal-fin rays	45	37	57	38–50*	43.2
Branched pectoral-fin rays	16	15	60	12–17	15.3
Gill–rakers on first ceratobranchial	17	18	56	15–21	17.6

able size anteriorly, teeth gradually becoming smaller and of more similar size posteriorly. Dentary with one very well developed canine extending through snout when mouth closed, tip of canine reaching nostrils anteriorly; canine larger relative to head length in larger specimens; two conical teeth anterior to largest dentary canine, anteriormost smallest; canine teeth posterior to largest dentary canine varying in size, separated by small conical teeth; teeth gradually decrease in size posteriorly. Specimens under 60 mm SL with row of very small conical teeth internal to main series posteriorly. Teeth on ectopterygoid, mesopterygoid, and metapterygoid small and conical.

Scales without distinct serration. Scales small, larger laterally at level of lateral line. Scales along predorsal midline arranged in somewhat irregular rows. Scales below lateral line obliquely arranged. Lateral-line scales with many divergent branches of the lateral-line canal. Divergent branches more pronounced in larger individuals; lateral-line canal without branches in specimens under 60 mm SL; specimens of 180 mm SL with one ventrally and one dorsally directed branch of lateral-line canal. Lateral-line canal extending to posterior tip of middle caudal-fin rays.

Dorsal-fin rays ii,10. Dorsal-fin origin located on posterior third of body length, slightly posterior to vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 35th (rarely 34th) to 38th vertebrae. Distal margin of dorsal fin slightly convex; diminutive scales on dorsal-fin base, extending one-fifth of distance of fin ray on membrane between fin rays, to lesser extent on remaining rays, scales not as extensive in individuals under 170 mm SL, absent in individuals under 60 mm SL. First basal anal-fin pterygiophore inserting behind hemal spine of 36th (rarely 35th) to 38th vertebrae. Distal margin of anal fin straight. Anal fin covered with scales over half of length of fin rays, more so in larger specimens. No scales covering anal-fin rays in specimens under 60 mm SL. Pectoral-fin rays pointed distally. Posterior tip of longest pectoral-fin ray extending to a point far anterior to vertical through dorsal-fin pelvic-fin origins. Pelvic fin very short. Pelvic-fin rays i,6–7. Pelvic fin pointed distally with first and second branched rays longest. Tips of fin reaching anus. Pelvic-fin base inserted at level of ventral profile of abdomen. Caudal fin almost straight, dorsal lobe slightly convex; caudal fin covered with scales for approximately two-thirds of length of middle rays; degree of coverage decreasing toward dorsal and ventral procurrent rays. Middle caudal-fin ray longest, its tip extending posteriorly to vertical through tip of dorsalmost principal ray, more pronounced in larger individuals, those under 60 mm SL without prominent middle caudal-fin ray.

VERTEBRAE: 62(1); 64(4); 65(7); 66(10); 67(8); 68(1).

COLOR IN ALCOHOL: Specimens retaining guanine on scales with silver coloration on sides of body and head (including lower jaw, except for tip) as far dorsally as horizontal through dorsal margin of orbit. Head and body tan to brownish dorsally, including tip of lower jaw. Specimens under 60 mm SL with silver coloration on abdominal region, remaining portions of body yellowish-tan ground coloration.

Specimens lacking guanine with tan ground coloration on sides of body and head, slightly darker dorsally. Specimens from the Rio Negro have a much darker ground coloration of body and head, with region of head around orbit and opercular region with more conspicuous dark pigmentation. Specimens retaining pigmentation on fins with dorsal fin slightly dusky; dorsal portion of pectoral fin covered with dark chromatophores at its base and outermost fin rays. Caudal fin dusky posteriorly, sometimes with tips of fin-rays dark. Adipose fin hyaline.

GEOGRAPHIC DISTRIBUTION: Main rivers and their tributaries in the Amazon basin from the Río Ucayali system in Peru, eastward to Rio Xingu in Brazil; Rio Tocantins and Rio Capim basins; lower to upper portions of Río Orinoco basin; Rupununi River in the upper Essequibo River system in Guyana; Rio Paraná/ Paraguay, and Uruguay basin, south to Río de la Plata in Argentina (fig. 27).

GEOGRAPHIC VARIATION: The population samples herein identified as *Rhaphiodon vulpinus* from the Río Orinoco, Rio Amazonas, Río Paraguay-Paraná, and Río Uruguay systems, except for a few specimens detailed below, either agree, or show a very large degree of overlap in all meristic and morphometric characters studied.

Three large specimens (MZUSP 32808, 578–604 mm SL) from the upper portions of the Rio Xingu in Brazil, have a considerably higher number of lateral-line scales (142 in one specimen, 150 in two specimens) and branched anal-fin rays (50 in all three specimens) compared to specimens from the remaining portions of the species range (122–138 and 38–47 for lateral line scales and branched anal-fin rays respectively), including specimens from the lower portions of the Rio Xingu. Until more specimens from the region become available for study, the cited specimens are tentatively assigned to *Rhaphiodon vulpinus*.

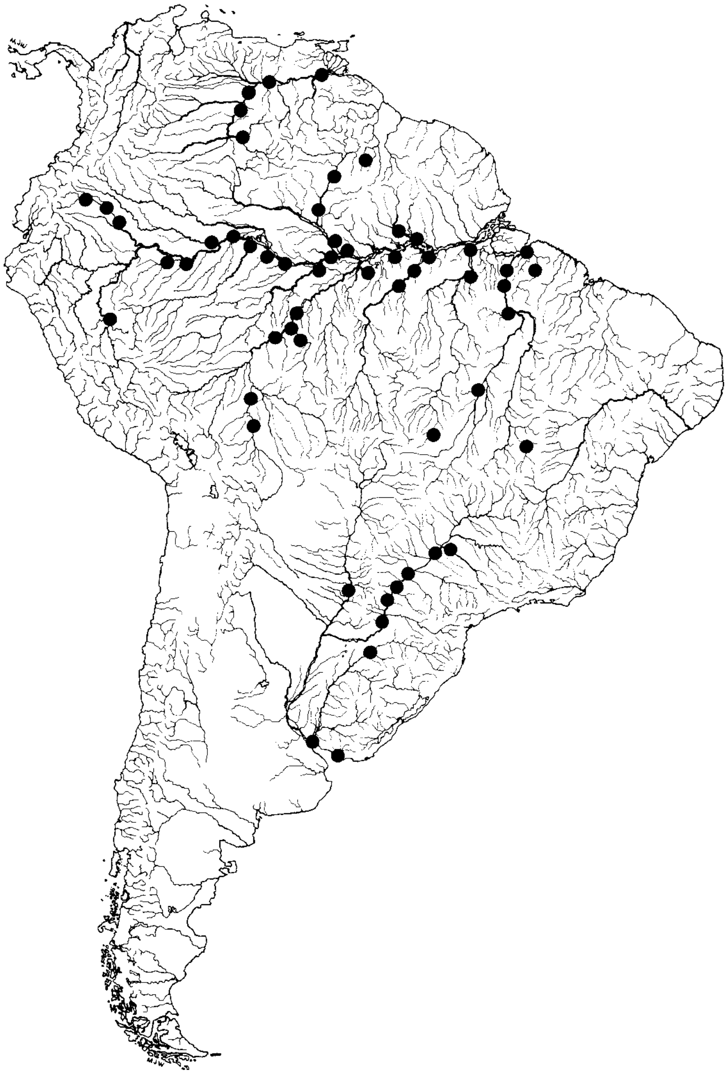

Fig. 27. Map of South America showing geographic distribution of *Rhaphiodon vulpinus* (type locality inexact = ''Brasiliae fluviis'' [= rivers of Brazil]. Some symbols represent more than one lot of specimens or locality.

See above under Color in Alcohol for geographical variation in color patterns.

REMARKS: *Rhaphiodon vulpinus* was described on the basis of a single specimen collected by Spix and Martius in the rivers from Brazil (''Brasiliae fluviis''). The type locality of *Rhaphiodon vulpinus* was not located precisely. Papavero (1971; map following page 66) described the itinerary of the Spix and Martius collecting trip. *Rhaphiodon vulpinus* occurs in all portions of the Amazon basin where they collected. Within the Rio Paraná system they collected in a few tributaries of the upper Rio Paraná. Some specimens examined in the present study come from the Rio Paraná itself, and lower portions of a few of its tributaries. Therefore, its is possible that the holotype of *Rhaphiodon vulpinus* originated in the Rio Paraná basin. Kottelat (1988) commented on the status of the Spix and Martius specimens that Agassiz used as the basis for his descriptions and cited the

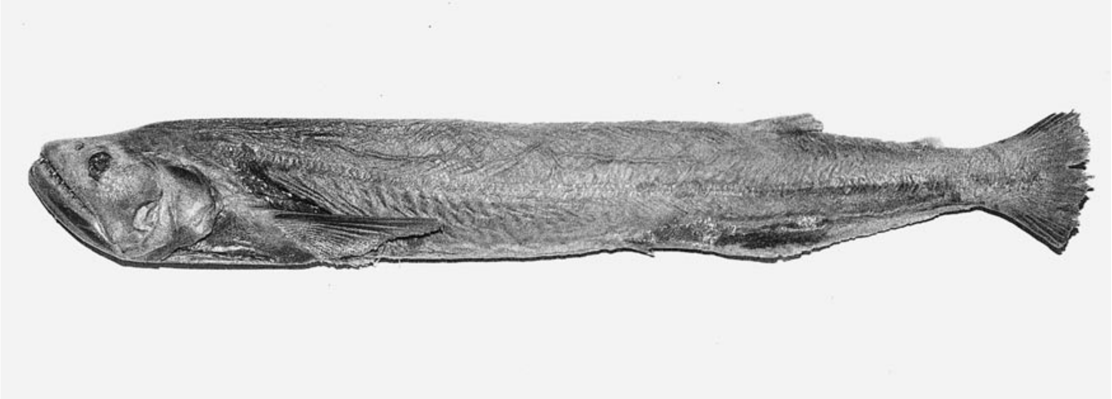

Fig. 28. *Rhaphiodon vulpinus*, holotype, MHNN 822, 303 mm SL, Brazil.

specimen in the collection of the Musée d'Histoire Naturelle, Neuchâtel (MHNN 822) as the potential holotype. That specimen was examined in the present study (fig. 28) and it is herein regarded as the holotype of *Rhaphiodon vulpinus* Agassiz, 1829. The proportional depths at the pelvic- and pectoral-fin origins in this specimen lie slightly outside the range observed for all other specimens used as the basis for the morphometric characterization of this species (table 3). The differences may be preservation artifacts in this very old specimen.

The holotype of *Hydropardus rapax* Reinhardt, 1849 (ZMC 183), herein placed in the synonymy of *Rhaphiodon vulpinus*, was also examined (fig. 29). The length of the dentary canine is relatively higher than the maximum value found in the remaining specimens of *R. vulpinus* in which this feature was measured (19.3 versus 12.1–17.9 of HL for *R. vulpinus*). As mentioned in the description above, the dentary canine is larger relative to head length in larger specimens. Since the holotype of *Hydropardus rapax* is the largest examined specimen herein assigned to *Rhaphiodon vulpinus*, the higher value for the relative size of the dentary canine observed in the specimen may be a function of its larger size. A few meristic features of *Hydropardus rapax* also lie outside the range presented by the remaining *Rhaphiodon vulpinus* specimens (table 3). The holotype of *Hydropardus rapax* has 121 lateral line scales, 27 scales around the caudal peduncle, and 37 branched anal-fin rays (versus 122–125; 30–39, and 38—50, respectively, for *Rhaphiodon vulpinus*). The holotype of *Hydropardus rapax* comes from Montevideo, Uruguay. Whether the specimen was actually collected in Montevideo or was shipped from there to Europe may be resolved after translation of the original description published in Danish. As already mentioned above under Geographic Variation, no meristic or morphometric differences were found among the samples examined that conform to any geographical pattern. Specifically, specimens from the Río Paraná/Paraguay, and Uruguay basins do not show a tendency toward lower values for the meristic features mentioned above for *Hydropardus rapax* that could suggest that the latter would be distinct from *Rhaphiodon vulpinus*.

Rhaphiodon is the most widely distributed cynodontine genus in South America and also the least speciose. *Hydrolycus* and *Cynodon* do not occur south of the Amazon basin in the Río Paraná/Paraguay and Río Uruguay basins. Four *Hydrolycus* species were recognized two of which were previously undescribed. Three *Cynodon* species were recognized two of which was previously undescribed. Only one species was recognized within *Rhaphiodon*. Widely distributed characiform species, that occur throughout the major river drainages in South America (i.e., Río Orinoco, Rio Amazonas, Río Paraná/Paraguay and Río Uruguay basins) are not limited to cynodontines. Other examples include *Curimatella dorsalis* (Eigenmann and Eigenmann, 1889), recently revised by Vari

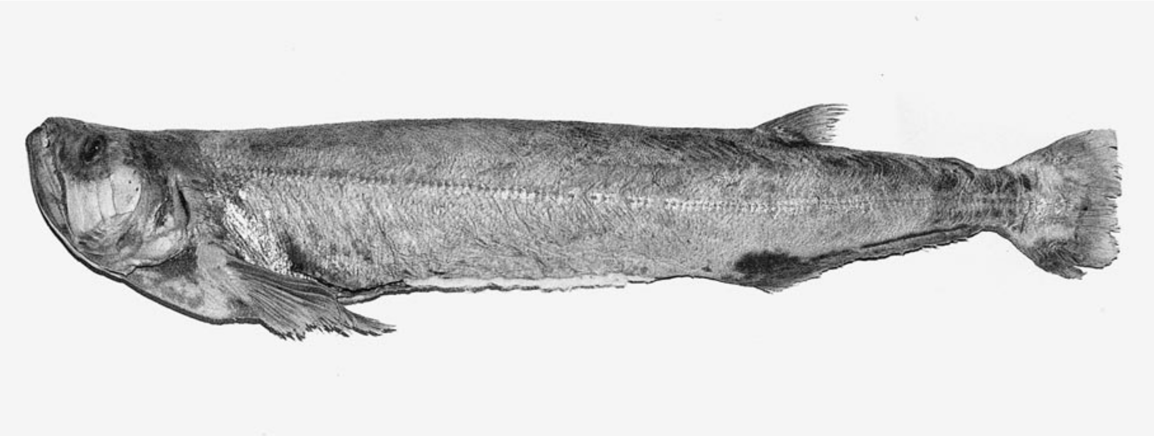

Fig. 29. *Rhaphiodon vulpinus*, holotype of *Hydropardus rapax*, ZMC 183, 623 mm SL, Uruguay, Montevideo.

(1992b), and *Thoracocharax stellatus* (Kner, 1859), see Weitzman (1960: 220).

MATERIAL EXAMINED: 420 specimens (63, 68.9–623.0):

TYPE MATERIAL: MHNN 822 (1, 303.0) Brazil; holotype of *Rhaphiodon vulpinus* Agassiz, 1829. ZMUC 183 (1, 623.0) Montevideo, Uruguay; holotype of *Hydropardus rapax* Reinhardt, 1851.

NONTYPE MATERIAL: *ARGENTINA*. *Buenos Aires*: AMNH 12251 (3, 163.0–215.0) Buenos Aires, Darsena Norte; BMNH 1881.7.2:17 (1, 604.0) R. Plate (= Río de la Plata); CAS 113493 (1, 455.0); USNM 55574 (2, 128.7–184.0) Buenos Aires; NMW 68551 (2) La Plata; *Santa Fé*: MCZ 828 (1, 252.0); NMW 57116 (2) Rosario; USNM 126662 (3, 170.0–181.0) Argentina; *BOLIVIA*. *El Beni*: AMNH 77450 (1, 56.8) Río Mamoré, Puerto Siles; AMNH 77507 (1, 168.0) Río Mamoré, ca. 15 km S Limoquije; MNHN 1989 1466 (1, 293.0) Trinidad, Laguna Capital; *BRAZIL*. *Amazonas*: MCZ 21379 (2, 319.0–366.0) Villa Bella, Rio Amazonas at Parintins and environs; BMNH 1893.4.24:30–31 (2, 317.0–350.0); MNHN 1909 0122 (1, 265.0) Manaus; USNM 307310 (2, 182.0–197.0); USNM 308672 (1, 188.0) ressaca at Ilha da Marchantaria; USNM 308643 (1, 81.6) near Manaus, Camaleão, Ilha da Marchantaria; MCZ 79141 (1, 73.3) Lago Jacaretinga, near Manaus; MCZ 21383 2 (365.0–387.0) Paraná do Janauari; MCZ 21373 (1, 321.0) Lago do Iranduba; BMNH 1897.12.1:181 (1, 147.4) Rio Juruá; BMNH 1925.10.28:121–124 (4, 350.0–379.0) Manacapuru; MZUSP 6537 (14, 215.0–264.0), MCZ 21402 (4, 35.6–99.0) Lago Manacapuru; BMNH 1976.11.12:201–203 (3, 30.6–47.9); USNM 310941 (2, 202.0–266.0) muddy igarapé connecting Rio Solimões and a blackwater lake ca. 15 km W of Coari; MZUSP 36093 (2, 291.0–327.0) Lago Pantaleão, mouth of Rio Japurá; MZUSP 36092 (1, 406.0) ressaca do Lago Urini, mouth of Rio Japurá; MZUSP 36101 (1, 470.0) Paraná do Castanho, Lago Amanã, mouth of Rio Japurá; MZUSP 27339 (1, 296.0) mouth of Rio Japurá, Rio Solimões; MCZ 21404 (1, 158.0) Rio Içá, near the Brazilian-Colombian border; MZUSP 23338 (1, 296.0) Rio Solimões, Fonte Boa; MZUSP 23453 (1, 276.0) Rio Solimões, near Ilha Baruruá, above mouth of Jutaí; MZUSP 23476 (1, 173.0) Rio Solimões, near Ilha Xibeco, above mouth of Jutaí; MZUSP 24936 (2, 228.0–295.0) Rio Solimões, Lago Janauacá and surroundings; MZUSP 24957 (6, 296.0–342.0) Lago Janauacá, right margin of Rio Solimões; MZUSP 26934 (1, 309.0) Lago Janauacá, Manaus, and surroundings; MNHN 1994 0169 (3, 160.0–189.0) Rio Solimões; MZUSP 13498 and 13499 (2, 312.0–354.0) Rio Amazonas, Itacoatiara; MZUSP 32813 (1, 330.0) Rio Negro, Anavilhanas, Lago do Prato; MZUSP 6143 (3, 274.0–463.0) Rio Negro, above Manaus; MZUSP 43317 (1, 394.0) Cantagalo, Rio Negro; NMW 57092 (2), NMW 57093 (5); NMW 57094 (1) mouth of Rio Negro; MCZ 21410 (3, 47.6–61.2) Rio Negro, Lago do Aleixo; MZUSP 37873 (1, 182.0) Igarapé Beem, Humaitá; MZUSP 6970 (1, 216.0) Rio Madeira, 25 km below Nova Olinda; MNHN 1909 0194 (1, 173.0) Tabatinga; MZUSP 23484 (2, 228.0–266.0), Lago do Prego, in front of Santo Antônio do Içá; MZUSP 23518 (1, 280.0) Santo Antônio do Içá, mouth of Rio Içá; MCZ 21390 (3, 259.9–310.0) Rio Javari at the Peruvian-Brazilian border; MZUSP 24606 (1, 209.0) mouth of Rio Paciá; MZUSP 6319 (1, 215.0) Lago Castro, mouth of Rio Purus; MZUSP 6380 (2, 328.0–356.0) Rio Purus, Lago Beruri; NMW 57115 (1) Rio Purus; MCZ 21376 (1, 310.0) Rio Solimões at Tefé and environs; MZUSP 6097 (5, 300.0–389.0) Lago Puraquequara, Rio Puraquequara system; MZUSP 7527 (1, 265.0) Paraná de Urucará; *Pará*: CAS 71050 (2, 182.0–232.0), CAS 79265 (1, 391.0) Rio Santarém; MZUSP 23897 (1, 279.0) Rio Capim, near Badajós; MZUSP 23932 (6, 285.0–346.0) Rio Capim, Vila Santana; CAS 71051 (1, 221.0 mm SL) Rio Tapajós (into Rio Amazonas) at Santarém; CAS 79268 (1, 371.0) market at Santarém; MNHN 1909 0075 (1, 176.0) Santarém; MZUSP 24237 (3, 324.0–363.0) Rio Tapajós, Ilha Tapiúna; MZUSP 24247 (1, 363.0) Rio Tapajós, Aveiro; MZUSP 24314 (1, 384.0) Rio Tapajós, lake at Ilha do Campinho; MZUSP 24330 (3, 319.0–410.0) Rio Tapajós, Barreirinha; MZUSP 32819 (12, 306.0–393.0) Rio Tapajós, between Itaituba and São Luís; MZUSP 25299 (1, 444.0 right margin of Rio Tapajós, in front of National Park headquarters; MZUSP 25560 (1, 418.0) São Raimundo, left margin of Rio Tapajós, ca. km 51 of highway BR 230; MZUSP 25567 (1, 370.0) left margin of Rio Tapajós, between National Park headquarters (km 67) and Ramal Santa (km 64); MZUSP 5628 (4, 308.0–351.0) Lago Paru, Oriximiná; MZUSP 5677 (1, 321.0) Rio Trombetas, mouth of Lago Paru; MZUSP 5414 (2, 252.0–256.0); MZUSP 8258 (1, 247.0) Rio Trombetas, Oriximiná; MZUSP 9429 (1, 332.0) mouth of Cuminá–Miri, near Oriximiná; MZUSP 32810 (8, 258.0–354.0) Rio Trombetas, Cuminá; MZUSP 32811 (17, 267.0–393.0) Rio Trombetas, 20 km above mouth; MZUSP 15769 (1, 442.0) Rio Trombetas, igapó at Lago do Farias, Reserva Biológica de Trombetas; MCZ 21384 (1, 300.0), MCZ 21385 (1, 300.0) Rio Tocantins, Cametá; MZUSP 24077 (6, 169.0–203.0) Rio Tocantins, lake at the margins of Igarapé Espírito Santo between Baião and Tucuruí; MZUSP 24175 (2, 229.0–231.0) Rio Tocantins, Laguinho, near Tucuruí; MCZ 821 (1, 358.0), MCZ 21399–21400 (3, 269.0–293.0) Belém and environs; MZUSP 24014 (2, 255.0–336.0) Paraná Samaúma, mouth of Rio Tocantins; MZUSP 32820 (1, 327.0) Rio Itacaiúnas, Serra dos Carajás, Igarapé guas Claras; MZUSP 32821 (14, 281.0–396.0) Rio Itacaiúnas, Caldeirão; AMNH 3937 (2, 274.0–282.0), CAS 122083 (4, 266.0–285.0), NMW 57103 (1), NMW 57104 (3, 259.0–294.0 mm SL), NMW 57105 (5) Pará; MZUSP 3550 (3, 313.0–328.0), CAS 79267 (1, 320.0) Belém; UMMZ 203388 (2, 240.0–263.0) market in Belém; CAS 158801 (1, 46.6) Lago Grande, into Rio Amazonas; MZUSP 23987 (5, 238.0–280.0) Igarapé Sororoca, Furo de Panaquera; MZUSP 24005 (1, 282.0) Igarapé Coelho; MZUSP 31501 (1, 299.0), MZUSP 32809 (40, 285.0–437.0) Rio Xingu, Belo Monte; MCZ 21397 (2, 432.0–435.0) Rio Xingu, cascade region; *Roraima*: MZUSP 32816 (1, 415.0) Rio Branco, Marará; MZUSP 32817 (1, 363.0) Rio Branco, between its mouth and Rio Xeriuni; MZUSP 32818 (2, 361.0–366.0) Rio Branco, Cachoeira do Bem-Querer; *Maranhão*: CAS 149264 (1) Lagem Marsal Brook, into Rio Tocantins at Carolina; CAS 71047 (1, 73.7), MA, represa (= dammed up) Lagem Marsal brook into Rio Tocantins; *Goiá*s: MZUSP 40672 (4, 347.0–425.0); MZUSP 40864 (6, 342.0–405.0 mm SL) Rio Paranã, above mouth of Rio Bezerra, Monte Alegre de Goiás; MZUSP 40775 (1, 370.0) Rio Paranã, below mouth of Rio São Domingos, Nova Roma; MZUSP 40898 (2, 332.0–375.0) Rio Paranã, above mouth of Rio São Domingos, Fazenda Barra, São Domingos; *Rondônia*: MZUSP 32806 (4, 329.0–378.0); MZUSP 32807 (9, 196.0–403.0) Rio Madeira, Calama; MZUSP 32812 (2, 194.0–363.0) Rio Madeira, Cachoeira do Teotônio; MZUSP 13897 and 13898 (2, 302.0–358.0) Rio Machado, Lago do Paraíso; *Mato Grosso do Sul*:

MZUSP 43923 (1, 341.0) Rio Paraná, Rio Samambaia, municipality of Taquarucu; MZUSP 22622 (7, 295.0–332.0); MZUSP 22515 (13, 284.0–350.0) Rio Paraná, in front of Jupiá; *Mato Grosso*: MZUSP 22812 (1, 171.0) Rio Araguaia, Santa Terezinha; MZUSP 32808 (3, 597.0–600.0) Rio Xingu, confluence Rios Culuene and Sete de Setembro; *São Paulo*: MZUSP 23201 (2, 152.0–225.0) left margin of Rio Paraná, Jupiá dam; MZUSP 24386 (1, 446.0) Rio Tietê, Penápolis; *Paraná*: MZUSP 13225–13226 (2) Rio Paraná, Porto Mendes; MZUSP 13227–13231 (5); MZUSP 14699–14703 (5) PR, Rio Paraná, Porto Verde; MZUSP 21631 (1, 417.0) Rio Paraná, Guaíra, above Sete Quedas; MZUSP 43389 (1, 351.0) Rio Paraná, Itaipu Dam, Município of Foz do Iguaçu; MZUSP 43917 (1, 342.0), MZUSP 43918 (3, 382.0–401.0) Rio Paraná, Município of Porto Rico; MZUSP 3121 (3, 242.0–326.0) Amazonas and Pará; MNHN 4493 (1) Brazil; MNHN 1909 0318 (1, 252.0) Brazil; CAS 71052 (1, 248.0) South America; CAS 78305 (1, 148.0) aquarium specimen (died at the Steinhart Aquarium, San Francisco). *ECUADOR*. *Napo*: FMNH 103392 (1, 299.0) outflow of Laguna Jatuncocha; FMNH 104997 (2, 420.0) Río Payamino, 14.1 km upstream from mouth in Rio Napo; FMNH 104998 (1, 332.0) Rio Tiputini, near mouth in Rio Napo; MCZ 52354 (1, 318.0) Río Payamino and small tributary ca. 5–6 km upriver from the mouth, into Río Coca; *GUYANA*. BMNH 1972.7.27:51 (1, 401.0) Rupununi River; CAS 16071* (mixed lot) (6), Guyana, Menari Ranch, near Lathan (Lethem?), border with Brazil. *PARAGUAY*. BMNH 1935-6.4: 34–39 (6, 80.0–264.0) W Asunción; BMNH 1935-6.4:40 (1, 68.9) Asunción bay; CAS 18238 (1, 183.0 mm SL), Río Paraguay, Asunción; USNM 181596 (1, 134.3) Río Paraguay, Asunción Bay, near Asunción; UMMZ 208059 (1, 460.0), Pettirossi fish market (= Mercado Quatro) in Asunción (from ‘‘San Antonio’’); UMMZ 216640 (1, 196.0) Río Paraguay, Villeta between ‘‘el muelle y la barreria’’; NMW 57117 (1); USNM 55667 (1) Paraguay. *URUGUAY*. NMW 57114 (2) Uruguay. *VENEZUELA*. *Delta Amacuro*: CAS 50806 (1, 175.0) Río Orinoco, between Puerto Ordez and Ciudad Bolivar; USNM 222870 (1) Río Orinoco, first small caño on W side of Caño Paloma, 100 m above its mouth, 92 nautical miles upstream sea buoy; USNM 222871 (10, 246.0–279.0), USNM 233619 (1, 253.0), USNM 233930 (1, 340.0) Río Orinoco, inlet near Punta Cabrian, 150 nautical miles upstream from sea buoy; USNM 222880 (1, 265.0) Río Orinoco, N shore near San Felix, 176 nautical miles upstream from sea buoy; UMMZ 211306 (2, 145.0–249.0) lagoon of Río Orinoco, 201 nautical miles from sea buoy *Amazonas*: FMNH 103650 (1, 434.0) pool behind beach of Río Ventuari on S side of river ca. 5 hr. (ca. 12 km) above mouth in Río Orinoco Laguna Pavon; FMNH 103651 (1, 384.0) Rio Ventuari at beach and small backwater ca. 5 hr. above mouth; ANSP 161180 (1, 345.0) caño crossing Puerto Ayacucho-El Burro hwy. *Apure*: ANSP 165773 (1, 380.0) Río Capanaparo, backwater lagoon (mouth of Caño Las Varitas) near San Fernado de Apure-Puerto Haez hwy; *Monagas*: AMNH 47956 (1, 176.0) shore of Río Orinoco, Buoy 142 nautical miles downstream from Barrancas, north side Isla Varader inlet; USNM 222863 (1, 227.0) Río Orinoco, small caño near mouth of Caño Guarguapo, 146 nautical miles upstream from sea buoy; MNHN 1898 0024 (1, 256.0) Venezuela; *PERU*. *Loreto*: CAS 134788 (1, 76.5) Río Ampiyacu; CAS 134789 (1, 130.0) Río Ampiyacu, near Pebas; CAS 15726 (2, 207.0–282.0); CAS 15727 (1, 264.0) Río Pacaya, at the mouth, Bretana; CAS 79270 (2, 263.0–273.0) Río Pacaya (upstream) small, sluggish, brown lowland river, arising in lomas of Eastern Cordillera; into Río Ucayali at Bretana, MZUSP 15219 (3, 101.0–125.0) Caño Moema, Río Amazonas; MZUSP 26447 (1, 32.0) Supaycocha, Jenaro Herrera; CAS 79266 (1, 410.0) Lago Cashiboya, a cutoff of Río Ucayali (connected to river by a channel), above Contamana; MZUSP 26729 (1, 210.0) Río Ucayali, Pucallpa; USNM 280454 (1, 297.0) main channel and side pools of Río Ucayali, approximately 10 km upstream of Pucallpa; *Amazonas*: UMMZ 216909 (1, 287.0) Amazonas.

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APPENDIX 1

Character Matrix for Species of Cynodontinae and Genera of Proximate Outgroups

Taxon	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–69
Hydrolycus armatus	11021	00001	11111	00011	00101	11111	10111	11111	10111	10001	10111	11101	11001	1000
Hydrolycus tatauaia	11021	00001	11111	00011	00101	11111	10111	11111	10111	10001	10111	11101	11001	1000
Hydrolycus wallacei	01011	1?000	11111	00012	01101	11111	10110	11101	10111	00001	10111	11101	11001	1000
Hydrolycus scomberoides	01021	00101	11111	01112	14101	11111	10111	11111	10112	20001	10111	11101	11101	1010
Rhaphiodon vulpinus	01101	00000	1111?	01212	13101	11111	10110	11111	10113	11111	21101	11111	12002	1101
Cynodon gibbus	01201	01010	00110	11212	12111	01011	11110	11101	21111	20011	10111	11111	11011	1000
Cynodon septenarius	01201	01010	00110	11212	12111	01011	11110	11101	21111	20011	10111	11111	11011	1000
Roestes	00000	??000	0?000	00000	00100	00000	00000	000?0	00000	00000	00000	01000	00000	0000
Gilbertolus	00000	??000	0?000	00000	00100	00000	00000	000?0	00000	00000	00001	11001	10000	0000
Acestrorhynchus	00000	??100	0?000	0000?	?1000	000?0	00010	00100	00000	00000	00000	00000	0000?	0000
outgroup	00000	??000	0?000	00000	00000	00000	00000	000?0	00000	00000	00000	00000	00000	0000

APPENDIX 1. CHARACTER SUMMARY

1. Fifth infraorbital. 0, well developed, without contact between fourth and sixth infraorbitals; 1, greatly reduced, with posteroventral margin of sixth infraorbital in contact with posterodorsal margin of fourth infraorbital.
2. Antorbital-lateral ethmoid contact. 0, no contact; 1, antorbital contacting ventral wing of lateral ethmoid along its entire lateral edge.
3. Antorbital. 0, flat, platelike, without medial process; 1, with a short medial, vertically aligned process at its posterior edge that extends along posterior surface of ventral wing of lateral ethmoid; 2, with enlarged medial, vertically aligned process at its posterior edge that extends along posterior surface of ventral wing of lateral ethmoid.
4. Mesethmoid spine. 0, conical, or with a different type of elaboration of its anterior portion (Vari, 1979: 278–279); 1, dorsoventrally developed, almost round in shape; 2, further expanded.
5. Ventral process of mesethmoid (sensu Starks, 1926: 163). 0, absent; 1, present.
6. Orientation of ventral processes of mesethmoid. 0, ventrally oriented; 1, anteriorly oriented.
7. Vomer-mesethmoid contact. 0, anterior surface of vomer without contact with posterior surface of ventral processes of mesethmoid; 1, anterior surface of vomer contacting posterior surface of ventral processes of mesethmoid.
8. Diverging lamellae of the mesethmoid. 0, well developed; 1, reduced.
9. Portion of diverging lamellae of mesethmoid that contacts lateral surface of vomer. 0, covering only upper anterior corner of the lateral surface of vomer; 1, covering most of lateral surface of vomer.
10. Articular surface on lateral wing of mesethmoid. 0, absent; 1, present.
11. Ventral crest of vomer. 0, absent; 1, present.
12. Lateral arms of vomer. 0, continuous all the way to its anterior portion, almost proximate to articulation with mesethmoid (vomer is an inverted Y in cross section along its entire extension); 1, gradually reducing anteriorly extending just until posterior half of its extension (only posterior portion of vomer is an inverted Y in cross section).
13. Vomer-palatine contact. 0, articulation between vomer and palatine made through cartilaginous surface at other portions of these ossifications; 1, anterior portion of palatine with a cartilaginous surface contacting a cartilaginous surface at posterior portion of main body of vomer.
14. Portion on vomer for articulation of maxilla. 0, not modified in 1; 1, Presence of a shallow depression on its anterolateral surface where anterior tip of maxilla abuts.
15. Ridge on lateral surface of vomer. 0, absent; 1, present.
16. Rhinosphenoid. 0, present; 1, absent.
17. Lateral ethmoid-orbitosphenoid contact. 0, absent; 1, present.
18. Parasphenoid and main portion of orbitosphenoid. 0, well separated; 1, close to each other.
19. Dilatator fossa. 0, not extending anteriorly on dorsal surface of frontal or if so, only to dorsoposterior edge of orbit; 1, highly developed, extending anteriorly on dorsal surface of frontal beyond dorsoposterior edge of orbit.
20. Frontal shelf at posterodorsal edge of orbit. 0, well developed; 1, reduced; 2, absent.
21. Dorsal portion of sphenotic spine. 0, contacting ventrolateral margin of frontal; 1, not in contact with ventrolateral margin of frontal.
22. Anterior shelf of frontal. 0, laterally expanded; 1, lacking; 2, ventrally expanded with curved margin; 3, ventrally expanded with straight margin 4; ventrally expanded and truncated posteriorly.
23. Third posttemporal fossa bordered by epioccipital and exoccipital. 0, absent; 1, present.
24. Dorsal posttemporal fossa. 0, present; 1, absent.
25. Neurocranium-first vertebra joint. 0, portion of basioccipital at neurocranium-vertebral joint not flared posteriorly; 1, portion of basioccipital at neurocranium-vertebral joint flared posteriorly and forming a receptacle for first vertebra.
26. Hyomandibula. 0, shaft of bone contacting preopercle without a process; 1, with a process, separate from main body of hyomandibula.
27. Symplectic. 0, without posterior process contacting hyomandibula or if such a process contacts hyomandibula, it does not fit into a roofed over groove; 1, posterior portion extending dorsally to distinctly fit into a roofed over groove in medial face of lower arm of hyomandibula.
28. Metapterygoid teeth. 0, absent; 1, present.
29. Mesopterygoid teeth. 0, absent; 1, present.
30. Ectopterygoid teeth. 0, absent or not as in 1; 1, very small, arranged in a patch covering most or all surface of ectopterygoid.
31. Ectopterygoid-metapterygoid contact. 0, absent; 1, present.

32. Ectopterygoid-mesethmoid contact. 0, absent; 1, present.
33. Branchiostegal rays. 0, three or four rays; 1, five rays.
34. Posterior ceratohyal. 0, with one attached branchiostegal ray; 1, with two attached branchiostegal rays.
35. Lower jaw. 0, dentary with no developed canines or if canines developed not with one canine conspicuously more developed than others; 1, dentary with one canine of moderate to large size relatively more developed than remaining teeth; 2, dentary with a highly developed canine.
36. Foramen in anterior portion of snout for dentary canine. 0, not as in 1; 1, delimited anteriorly and laterally by the premaxilla, posteriorly and posteromedially by ascending process of maxilla and anteromedially by vomer-mesethmoid, with ascending process of maxilla passing posterior to dentary canine.
37. Replacement tooth trenches. 0, not as in 1; 1, shallow, open replacement trenches with teeth in mandibular replacement trench horizontally aligned, tip of replacement teeth projecting posteriorly.
38. Gill-rakers along leading portion of first ceratobranchial. 0, all elongate (teeth present or absent), or only the most anterior ones as in state 1; 1, all short, flattened, tooth-bearing bony plates.
39. Spines on free upper edge of gill-rakers of first ceratobranchial. 0, only slightly larger than remaining spines on gill-raker, but never prominent as in state 1; 1, considerably larger than those on surface.
40. Anterior portion of first hypobranchial. 0, unelaborated; 1, anteroventrally prolonged, into a prong-shaped process extending from ventrolateral margin of its main body.
41. Anterior portion of first ceratobranchial. 0, straight, not forming an angle relative to longitudinal axis of remaining portion of that ossification; 1, slightly dorsally directed, forming an angle relative to its longitudinal axis; 2, Dorsally directed portion of first ceratobranchial relatively longer and angle more pronounced than in 1.
42. Ventral processes on first centrum. 0, absent; 1, present.
43. Contact between neural complex of Weberian apparatus and posterior margin of neurocranium. 0, absent; 1, present.
44. Transverse process of second vertebra. 0, absent; 1, very developed, with distal bifurcation.
45. Lateral process of second centrum. 0, single structure extending laterally; 1, dorsoventrally expanded with two short processes at articular surface at its distal end; 2, dorsoventrally flat and with no processes as in 1; 3, triangular-shaped flat sheet of bone, from a dorsal view, extending laterally and posteriorly under tripus.
46. Lateral process of third centrum. 0, absent; 1, originating ventral to transverse process of second vertebra that is in contact with transverse process of third neural arch; 2, originating posterior to transverse process of second vertebra that is in contact with transverse process of third neural arch.
47. Bladelike portion of tripus. 0, not elongate; 1, anteriorly elongate.
48. Transformator process of tripus. 0, thin curved process with no modifications at its median end; 1, distal portion of process forming a 90° angle with anterior portion, and ending in enlarged rectangular bony plate.
49. Fourth pleural rib + parapophysis. 0, platelike lateral process; 1, with enlarged distal end forming a basal plate.
50. Process on posteroventral portion of fourth centrum attached by ligament to process on anterior portion of fifth centrum. 0, absent; 1, present.
51. Process on anteroventral portion of fifth vertebra. 0, absent; 1, present; 2, greatly developed.
52. Fifth pleural rib. 0, not as in 1; 1, relatively very short, with two processes on flattened proximal portion, one medially and other posteriorly directed, distal portion very slender.
53. Parapophysis of precaudal vertebrae. 0, not articulating with anterior vertebra; 1, articulating with anterior vertebra.
54. Baudelot’s ligament. 0, not connected to lateral process of second vertebra; 1, connected to lateral process of second vertebra.
55. Second postcleithrum. 0, present; 1, absent.
56. Third postcleithrum. 0, present; 1, absent.
57. Posterodorsal foramen in coracoid. 0, absent or if present not enlarged as in 1; 1, very enlarged.
58. Coracoids. 0, not expanded; 1, expanded.
59. Coracoids. 0, not fused or corrugated; 1, fused and having a corrugated pattern.
60. Mesocoracoid. 0, small, its dorsal tip reaching midlength of vertical portion of cleithrum; 1, enlarged, with broad articular surfaces with cleithrum and coracoid, its dorsal tip reaching midlength of vertical portion of cleithrum.
61. Articulation of scapula with medial surface of cleithrum. 0, not shifted posteriorly with scapular foramen covered by cleithrum; 1, shifted posteriorly with scapular foramen exposed in lateral view.

62. Anterior portion of cleithrum articulating with anterior margin of coracoid. 0, not ending in a distinct process; 1, forming a vertically elongate process with its anterodorsal tip pointed; 2, forming a vertically elongate process with its anterodorsal portion forming a continuous curve.
63. Pelvic-fin insertion. 0, at ventral profile of abdomen; 1, dorsally, far from theventral profile of abdomen.
64. Branched anal-fin rays. 0, 60 or less; 1, more than 60.
65. Hypurals. 0, hypural fan consisting of six separate hypural elements; 1, hypurals 1–3 fused into a single unit; 2, hypurals 2–3 fused into a single unit.
66. Anteromedial branch of anterior epineural. 0, not contacting neural complex of Weberian apparatus; 1, contacting neural complex of Weberian apparatus.
67. Myorhabdoi. 0, absent; 1, present.
68. Scales. 0, cycloid; 1, with serrations on exposed portion.
69. Fringelike appendices along lateral surface of posterior chamber of gasbladder. 0, absent; 1, present.

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