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SYSTEMATIC REVISION OF THE CYNODONTINAE (TELEOSTEI: OSTARIOPHYSI: CHARACIFORMES)

by

Mônica Toledo-Piza

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, the City University of New York

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Abstract

SYSTEMATIC REVISION OF THE CYNODONTINAE (TELEOSTEI: OSTARIOPHYSI: CHARACIFORMES)

by

Mônica Toledo-Piza

Adviser: Dr. Melanie L. J. Stiassny

Osteological features of cynodontines and other characiforms were examined in an attempt to investigate monophyly of the Cynodontinae and relationships among their species. A number of derived characters corroborated the monophyly of the Cynodontinae. Two equally most parsimonious hypotheses account for relationships among cynodontines, differing in the placement of Rhaphiodon vulpinus. Under one hypothesis Rhaphiodon vulpinus is the sister group to the genus Cynodon, and together they are the sister group to Hydrolycus. Under the alternative hypothesis, Rhaphiodon vulpinus is the sister group to the clade formed by Hydrolycus n. sp. 2, H. armatus, and H. scomberoides. Hydrolycus n. sp. 1 is the sister group to the latter clade. Hydrolycus n. sp 1 is conservatively included within Hydrolycus.

There are two species in the genus Cynodon Agassiz, 1829. Cynodon gibbus Agassiz, 1829, occurs in the Rio Amazonas and Río Orinoco basins, the Rupununi River in Guyana, the Rio Tocantins drainage and the Rio Pindaré system, Maranhão, Brazil.

Cynodon n. sp. 1 occurs in the Rio Amazonas, and in the Essequibo and Demerara Rivers in Guyana.

There are four species in Hydrolycus Müller and Troschel, 1844. Hydrolycus scomberoides (Cuvier, 1819) occurs in the Rio Amazonas and its tributaries. Cynodon pectoralis Günther, 1866 is a synonym of Hydrolycus scomberoides. Hydrolycus armatus (Schomburgk, 1841) is a valid species and occurs in the central and eastern portions of the Rio Amazonas basin, the Rios Tocantins and Rio Capim, the Essequibo River in Guyana, and Río Orinoco basin. Hydrolycus n. sp. 2 occurs in sympatry with Hydrolycus armatus in most of the distributional range of the latter species in the Rios Amazonas, Tocantins, and Capim basins and Essequibo River in Guyana. It occurs also in the upper portions of the Río Orinoco basin. Hydrolycus n. sp. 1 is restricted to the Rio Negro and upper Río Orinoco basin.

Rhaphiodon Agassiz, 1829 is monotypic with R. vulpinus being the most widely distributed cynodontine. It occurs in the Rios Amazonas, Tocantins, Capim, and Río Orinoco basins; Rupununi River in Guyana, Río Paraná-Paraguay and Río Uruguay systems.

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INTRODUCTION

Fishes of the subfamily Cynodontinae Eigenmann, 1909 with their oblique mouth and a highly developed pair of dentary canines, are among the most distinctive Neotropical characiforms. Cynodontines are also among the largest Neotropical characiforms, with Hydrolycus armatus reaching at least 650 mm SL. They are important in the aquatic ecosystem as high-level predators (Smith, 1981:22), apparently using their large canines to stab prey which is then swallowed whole, head first (Goulding, 1980:185). Cynodontines are exploited commercially for food (Mendes dos Santos et al., 1984; Taphorn, 1992) although little valued as such (Begossi and Garavello, 1990; Begossi and Braga, 1992), a possible reason is their numerous intermuscular bones (Ringuelet et al., 1967; Novoa, 1982). Hydrolycus species are recognized as game fishes, having been recently added to the International Game Fish Association record list in the fly rod and line class (The International Game Fish Association, 1995).

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 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 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 in 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, MS) (fig. 1), both records lying outside the known range of recent cynodontines.

The cynodontine first named, Hydrolycus scomberoides, was described by Cuvier (1816:168). He proposed that species within his new genus Hydrocynus which included one species from Africa and four from South America (now assigned to a variety of different characiform families). These species were each placed in one of five different subdivisions, one of them consisting of Hydrocynus scomberoides. Cuvier characterized this subdivision as follows (my translation): "there is only one series of teeth in the upper and lower jaws; the teeth are alternatively very short and very long, especially the second two lower ones which pass through two holes in the upper jaw when the mouth is closed. The lateral line has large scales; the first dorsal is situated at the vertical through the interval between the ventrals and anal". Later, a more detailed description of the species was provided by Cuvier (1819:357), under the genus name Hydrocyon (for a discussion about the usage of the names Hydrocyon and Hydrocynus see Myers, 1950).

Agassiz (1829:59, 76) described the genus Rhaphiodon to include two new species, R. vulpinus and R. gibbus. The plates that accompany the descriptions are labeled Cynodon vulpinus (plate XXVI) and C. gibbus (plate XXVII) respectively, these names appearing in the text as junior synonyms attributed to Spix. Cuvier (1829:312) had already referred to these plates, mentioning the names C. vulpinus and C. gibbus in a footnote to the description of the genus Hydrocyon (Appendix). From this point forward, Rhaphiodon will be used in association with vulpinus, and Cynodon with gibbus and Cynodon n. sp. 1).

Schomburgk (1841:249) described a fourth cynodontine, Hydrocyon armatus, from British Guiana (=Guyana), and the name was subsequently placed by Eigenmann (1912:396) as a synonym of Hydrolycus scomberoides.

Müller and Troschel (1844:93) created the genus Hydrolycus to include the single species (Hydrocyon scomberoides) of Cuvier's (1816) second subdivision. Reinhardt (1849) created the genus Hydropardus to include his new species, H. rapax, from Uruguay (a name herein considered a junior synonym of Rhaphiodon vulpinus). Günther (1866:30), described Cynodon pectoralis from the upper Amazon River, according to him very similar to C. scomberoides. Gill (1870:93) described Hydrolycus copei without comment on its possible relationships with other cynodontines. This name was later shown to be synonymous with Charax tectifer Cope, 1870, not immediately related to cynodontines (Schultz, 1950, Géry, 1986). No cynodontine was described subsequent to Cope, 1870, and from that time until the late 19th century, cynodontines were mentioned only in lists of fishes collected by naturalists adding new records of their distribution.

The subfamily name Cynodontinae first appeared in Eigenmann's list of fishes collected in the Río Paraguay (1907:154). A complete list of genera of the subfamily

Cynodontinae (Hydrolycus, Cynodon, and Rhaphiodon) was presented by Eigenmann (1910:444). From that time until the present no major change in systematics of the group has been made. In summary, there are three genera (Hydrolycus, Rhaphiodon, and Cynodon) with six nominal species, four of which are recognized as valid: H. scomberoides, with H. armatus as a synonym; H. pectoralis; R. vulpinus, with Hydropardus rapax as a synonym; and C. gibbus. Other generic names were subsequently proposed (Rhaphiodontichthys Campos, 1945 and Camposichthys Travassos, 1946); however, these were attempts to deal with nomenclatural problems created by the work of Agassiz (1829) (problems related to nomenclature of Rhaphiodon and Cynodon were discussed by Toledo-Piza and Lazara (MS) which is included in Appendix).

In recent years there has been a considerable increase in population samples of cynodontines available for study. In particular collections made by Michael Goulding in the Brazilian Amazon and now part of the holdings of the Museu the Zoologia da Universidade de São Paulo (MZUSP), showed that the group is more heterogeneous than previously recognized. Géry (1986) examined part of this material, recognized undescribed forms, and made comments on nomenclatural problems concerning species of Hydrolycus. He did not formally describe new forms or attempt to delimit their distributional ranges.

Recognition of Cynodontinae as a natural group has never been debated, probably as a consequence of similarities in body shape and general external features shared by all species, combined with their very distinctive appearance relative to other characiforms. However, there have been only two attempts to diagnose the group as a monophyletic unit in the sense of Hennig (1966). Howes (1976) and Lucena (1993), both of whom addressed the question of cynodontine relationships within characiforms (discussed below), reported a few characters proposed as synapomorphies for the Cynodontinae. Studies focused on the question of monophyly of the group are likely to provide additional characters to corroborate this hypothesis. Recently, for instance, 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). Larval extra-oral teeth were proposed by Buckup and Pertry (1994) as an additional synapomorphy for the group.

Authors prior to Howes (1976) and Lucena (1993), made no definitive comments about relationships of the group. Their ideas about relationships can be inferred only from the classifications they proposed. 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, 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 Cynodontidae. However, no further information was given concerning their relationships with other characiforms. The extent to which these classifications were intended to reflect close relationships among these groups is unclear, but even if the taxonomy was intended to convey concepts of relationships, no distinction was made, among features used to diagnose the groups, between derived and primitive features. As a consequence many groupings proposed by these authors do not constitute monophyletic units. These previous studies also focused on the proposal of more inclusive groups without any explicit hypothesis as to which group might be most closely related to the Cynodontinae.

The study of Howes (1976) was the first attempt to establish phylogenetic relationships of the Cynodontinae, by focusing on shared derived features, and it was also the first to hypothesize a sister-group relationship for the group. Based mainly on myological features, that author concluded that the genus Roestes (= Gilbertolus) is the sister-group of the group formed by Hydrolycus, Rhaphiodon, and Cynodon. He included these four genera in the tribe Cynodontini. Members of the Characini

(Characinae, sensu Eigenmann, 1910) constitute the sister group to the Cynodontini, and these two tribes together form the subfamily Characinae (Howes, 1976).

The next study to address the relationships of the Cynodontinae was that of Lucena (1993) who proposed Acestrorhynchus as its sister-group. Cynodontinae plus Acestrorhynchus were hypothesized as the sister-group of all members of the Characidae as defined by Lucena (1993). In this scheme of relationships Roestes is more closely related to the group formed by the Heterocharacini (sensu Géry, 1966) plus Gnathocharax. Lucena (1993) had different interpretations of some characters used by Howes to relate Roestes to the Cynodontinae. The question of cynodontine relationships with other characiforms is discussed below in "Relationships of the Cynodontinae with other characiforms."

The question of the relationships of genera within the Cynodontinae has been only addressed by Howes (1976), who hypothesized that Rhaphiodon and Cynodon are sister genera and together form the sister-group of Hydrolycus. The latter genus was not included in the analysis of Lucena (1993). In face of the increase in number of cynodontines that can be recognized (as proposed by Géry, 1986 and mentioned above) an analysis that includes all forms is the best approach to establish supraspecific groups within the Cynodontinae. This study, thus, has four primary aims: 1) to determine the recognizable species of Hydrolycus, Cynodon, and Rhaphiodon and estimate their geographic distributions; 2) to determine whether Hydrolycus, Cynodon, and Rhaphiodon are monophyletic; 3) to resolve cynodontine intrarelationships; and 4) to examine the hypothesis of monophyly of the Cynodontinae and discuss hypotheses of their relationships with other characiforms.

MATERIAL AND METHODS

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 specimen, except when the structure being measured or counted was recognizably abnormal or damaged, in which case corresponding data were taken from the right side if possible. 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 in radiographs. Counts and measurements follow Fink and Weitzman (1974) except as noted, and with some additions given below, and are presented in tables and/or in the text.

Measurements:

- Body depth at dorsal-fin origin: measured immediately anterior to the origin of the dorsal fin.

- Body depth at pelvic-fin origin: measured immediately anterior to the insertion of the unbranched pelvic-fin ray.

- Body depth at pectoral-fin origin: measured immediately anterior to the insertion of the unbranched pectoral-fin ray. This additional measurement of body depth was taken in Rhaphiodon vulpinus in order to give an estimate of the overall elongation of the body in this species.

- Dorsal-fin origin to caudal-fin origin: measured to the 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: measured between anterior and posterior termination of the fin base.

- Anal-fin base: measured between anterior and posterior termination of the fin base.

- Inter-orbital width: measured between the borders of the frontal bones at the anterior termination of the supraorbitals.

- Post-orbital length: from posterior bony orbital margin to the posteriormost termination of the opercular bone (without including the fleshy opercular flap).

- Upper jaw length: from tip of snout to the distal termination of the maxillary bone.

- Dentary canine length: from base to tip of largest canine tooth in the dentary.

Measurements of anal-fin length were not included because tips of the anterior fin rays were damaged in the majority of specimens.

Counts:

- Scales along lateral-line series: counted as a longitudinal scale row along the perforated lateral-line scales, including those on the base of the caudal-fin.

- Scale rows below lateral-line: number of longitudinal rows of scales counted from the 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. More replicable ways of taking this count were attempted in the beginning phase of the study (e.g., counts also taken at the level of the pelvic-fin origin, in addition to the ways already mentioned). Those counts, however, 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 of the anal-fin origin, rendered more replicable counts, although there was still some associated inaccuracy especially in species with smaller scales (e.g. Hydrolycus armatus), accounting for at least some of the observed intraspecific variation .

- Gill rakers on first ceratobranchial: 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 way 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 more 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.

In tables and the text, subunits of the head are presented as proportions of head length (HL). Head length and measurements of body parts are given as proportions of standard length (SL). 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.

Phylogenetic procedures

Study of phylogenetic relationships of the Cynodontinae was based on examination of osteological features. A total of 70 characters were defined and they are described in detail in "Character description and analysis" and summarized in Table 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 included 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 used also as the basis of illustrations or specific observations noted in the text. Justification for choice of these taxa is provided below in this section. The remaining species listed provided additional observations on characiform osteological characters. In the text, whenever a character is mentioned for outgroup genus without a species name provided, it refers to species listed below in this section, and does not imply that the character is present in all species of the genus.

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

- Anostomidae:

Anostomus anostomus: AMNH 43354, 3, 41.4-48.9 mm SL.

Laemolyta taeniata: AMNH 39992, 1, 155.4 mm SL.

- 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 n. sp. 1 (*): 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 n. sp. 1 (*): MZUSP 32638, 2, 152.0-163.0 mm SL.

Hydrolycus n. sp. 2 (*): 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 n. sp. 2): 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 unregistered, 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.

- 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 mm SL.

Acestrorhynchus falcatus: (*) MZUSP 4572-91, 1, 111.1 mm SL; AMNH 43418, 1, 140 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 microlepis (*): 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 ogilvei (*): 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 mm SL.

Ichthyborus quadrilineatus: AMNH 57408, 1, 106.7 mm SL.

Xenocharax spilurus (*): MRAC 80-51-P-610-614, 1, 93 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 Platinick, 1981; Wiley, 1981; Swofford et al., 1996; Wiley et al., 1991).

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). The small number of taxa involved in the analysis made possible the use of the exhaustive search option, which evaluates every possible combination of the taxa in the search for the most parsimonious tree. Autapomorphies and characters pertinent to the question of the relationships of

Cynodontinae with other characiforms were not included in computation of tree statistics.

Nine of seventy characters defined in the present study are multistate. Such characters were first analyzed as unordered. Three multistate characters (3, 42, and 52) have states that could be ordered sequentially according to their divergence from that putatively primitive condition. An analysis with these characters as ordered was also performed and the results compared with those of the unordered analysis.

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).

Missing entries in the data matrix (represented by "?") were employed in the present study for two distinct situations: 1) character state not checked in the terminal concerned due to lack of study material (only one instance represented by character 16 in Rhaphiodon vulpinus); and 2) character state inapplicable (e.g. character 7, orientation of the ventral processess of the mesethmoid in taxa that lack such ventral processes; coded for characters 7, 8, 13, and 40).

Character polarity was determined by outgroup comparison and in one instance (character 40) by using ontogenetic information. Outgroup comparisons were made to a diversity of characiform taxa. Thirty-three outgroup taxa indicated by stars following the species name in the list of material examined, above, 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 (discussed in "Phylogenetic relationships of the Cynodontinae with other characiforms"). These taxa, in addition to the seven cynodontines, were all checked for character examined and observations were summarized in a preliminary data matrix. In addition to these taxa, a number of other characiform taxa not directly related to cynodontines (listed below, without asterisk preceding species names) was examined in order to access the distribution of the character in question within characiforms. Occurrence of charater states hypothesized as derived for cynodontines in these more distantly related outgroups is discussed under the appropriate characters. The matrix presented in this study (Table 1) was restricted to those taxa used as actual outgroups (referred to as proximate outgroups) in the parsimony analysis.

Four different analyses using different combinations of outgroups were undertaken in order to access their impact in the outcoming cladogram. The first one used Roestes and Gilbertolus, hypothesized to form a monophyletic assemblage that is the sister group to the Cynodontinae (Howes, 1976; Lucena and Menezes, in prep.). In the second analysis Acestrorhynchus, hypothesized as the sister group to the Cynodontinae by Lucena (1993), was used as outgroup. In the third analysis the clade formed by Roestes and Gilbertolus, and Acestorhychus was used. The fourth analysis used the clade formed by Roestes and Gilbertolus, and the Heterocharacini plus Gnathocharax as outgroups. The latter two taxa have been hypothesized as closely related to Roestes and Gilbertolus (Lucena, 1993) and also share some characters with cynodontines.

The "Character description and analysis" section includes a description of each character, its variation within the cynodontines and its occurrence in characiform outgroups. Optimization of each character in the resulting most parsimonious cladograms follows the osteological descriptions of each character. In order to simplify discussion, characters in the "Phylogenetic results" section, are referred to only by their numbers. The reader is referred to the "Character description and analysis" section for detailed description of the character of interest.

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.

Abbreviations

Institutional abbreviations. - Abbreviations for institutions follow Levinton et al. (1985) and Levinton and Gibbs (1988).

Text and figure abbreviations. - The following abbreviations are used in the figures and text:

ANT	antorbital
AS-METH	articular surface on lateral wing of mesethmoid
BBR_n	basibranchial n
BHY	basihyal
BL	Baudelot's ligament
CBR	ceratobranchial
CL	cleithrum
CLU	claustrum
C_n	centrum n
COR	coracoid
CORF	coracoid foramen
DL-METH	diverging lamella of the mesethmoid
ECT	ectopterygoid
EPU	epural
EXT	extrascapular
FR	frontal
GR	gillraker
HL	head length
$HYBR_n$	hypobranchial n
HYP_n	hypural n
INT	intercalarium

IO	infraorbital n
LE	lateral ethmoid
LEP	lateral ethmoid process
LP-C_n	lateral process of centrum n
MAX	maxilla
MEC	mesocoracoid
MES	mesopterygoid
MEST	mesopterygoid teeth
METH	mesethmoid
METHS	mesethmoid spine
NAP_3	neural arch and pedicle of third vertebra
NAS_n	neural arch and spine of n vertebra
NC	neural complex
OP	opercle
ORB	orbitosphenoid
OS	os suspensorium
PA	parietal
PARA	parasphenoid
PCL	postcleithrum
PH	parhypural
PMAX	premaxilla
POP	preopercle

PR	pleural rib
PRP_4	pleural rib+parapophysis of fourth vertebra
PTM	posttemporal
PTO	pterotic
PTS	pterosphenoid
RAD	radials
RS	rhinosphenoid
SC	scaphium
SCA	scapula
SCL	supracleithrum
SL	standard length
SN	supraneural
SPH	sphenotic
SPHS	sphenotic spine
SUO	supraorbital
TP-TR	transverse process of tripus
TP_n	transverse process of n vertebra
TR	tripus
URO	uroneural
UST	urostyle
V	vomer
VC	vomer crest

VR	vomer ridge
VP-METH	ventral process of the mesethmoid
VP_n	vertebral parapohysis n

RELATIONSHIPS OF THE CYNODONTINAE TO OTHER CHARACIFORMS

A historical overview of the hypotheses of cynodontine relationships was presented in the introductory section of the present study. In the following section a more detailed account of the problem will be provided and the evidence supporting these different hypotheses will be discussed.

Howe's (1976) and Lucena's (1993) studies constitute the only previous attempts to establish phylogenetic affinities of the Cynodontinae, focusing on shared derived features. According to Howes (1976) Roestes is the sister group to the assemblage formed by Cynodon, Rhaphiodon, and Hydrolycus. In Lucena's analysis (1993) Acestrorhynchus is hypothesized as closely related to the Cynodontinae, with Roestes being more closely related to the Heterocharacini and Gnathocharax.

That Roestes is the sister group to the Cynodontinae was proposed by Géry and Vu-Tân-Tuê (1963:244) in their brief discussion of relationships of that genus to other characiforms (my translation): "It is not impossible that Roestes would be the link between the Characinae and the Rhaphiodontinae." Howes (1976) provided support for this hypotheses from characters of the cranial musculature.

A brief comment on the status of the genus Roestes is appropriate at this point. In a recent review of Roestes Günther, 1864, Lucena and Menezes (in prep.) 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. ogilvei, R. molossus, and one undescribed species. The two genera were diagnosed as a monophyletic unit referred to as the Roestini. Howes (1976) followed Menezes (1974) including the species he examined (alatus) in the genus Roestes. Herein, following Lucena and Menezes (in prep.), the genus name Gilbertolus will be employed for the species occurring west of the Andes. The specimens examined by Howes (1976) were reexamined in the present study and assigned to G. atratoensis.

In the present study three characters were found to be unique to cynodontines and Gilbertolus among characiforms and are listed below (for a detail description of these characters see "Character description and analysis" section):

1) Enlarged posterodorsal coracoid foramen (character 58).

2) Enlarged mesocoracoid (character 61).

3) Posteriorly shifted articulation of the scapula relative to the medial portion of cleithrum (character 62).

The characters listed above are absent from Roestes. These characters (among others) were used as evidence of a close relationship between the Roestini and cynodontines (Lucena and Menezes, in prep.). Under such a hypothesis these characters have to be interpreted either as synapomorphic for the assemblage formed by Roestes, Gilbertolus, and the Cynodontinae with a reversal to the primitive condition in Roestes, or as having independent origins in Gilbertolus and the Cynodontinae.

In the hypothesis proposed by Lucena (1993) the genus Roestes (based on the examination of R. ogilvei) was hypothesized as the sister group to the group formed by the Heterocharacini (sensu Géry, 1966) and Gnathocharax based on the following synapomorphies:

1) Orbitosphenoid with an elongate, spinous process on posteroventral region.

2) Posteroventral margin of preopercle forming an acute angle.

3) Pair of ventral processes on centrum 2.

These characters are present also in the specimen of Gilbertolus examined in the present study. In the present analysis the few following characters were examined that are shared among Roestes, Gilbertolus, members of the Heterocharacini, Gnathocharax, and the Cynodontinae.

1) Third posttemporal fossa bordered by the epioccipital and exoccipital (Cynodontinae, Roestes, Gilbertolus, and the Heterocharacini (except Hoplocharax) and Gnathocharax) (character 24).

2) Absence of postcleithrum 2 (Cynodontinae, Gilbertolus, and Gnathocharax)(character 56).

3) Absence of postcleithrum 3 (Cynodontinae, Gilbertolus, Roestes, and Gnathocharax). (character 57).

Howes (1976) listed 7 myological characters that according to him are unique to Gilbertolus and cynodontines, and he expanded the definition of his Cynodontini (consisting of Hydrolycus, Cynodon, and Rhaphiodon) to include Gilbertolus. Although a myological study was not conducted in the present study, a mention of those characters is pertinent to the present discussion on cynodontine relationships.

1) *Adductor mandibulae* A1 reduced to small slip of muscle (i.e. it does not extend along

the ventral border of A2).

2) *Adductor mandibulae* A2 divided by *levator arcus palatini*.

3) *Levator operculi* arising in part from the tendon of *lateralis superficialis* and in part from supracleithrum.

4) *Levator arcus palatini* confined to the dorsal part of hyomandibula.

5) *Sternohyoideus* dorsally divided.

6) Pectoral fin musculature highly developed. *Abductor superficialis* virtually continuous with *sternohyoideus* i.e. not separated by the cleithrum.

7) Accessory abductor muscle.

8) First *obliquus ventralis* divided.

In Lucena's (1993) phylogenetic study of the family Characidae, Howes's (1976) characters 1 and 4 were not confirmed. Character 1 was present only in Roestes and was absent from the Cynodontinae. Character 4 seems to be widespread among characids. Lucena and Menezes (in prep.) reevaluated a few other myological characters previously examined by Howes (1976). An accessory *abductor* (character 7 above) muscle is unique to the Cynodontinae and Gilbertolus among examined characiforms; *adductor mandibulae* A2 divided by *levator arcus palatini* (character 2 above) was confirmed (also present in other characiform outgroups and hypothesized as having an independent origin); *abductor superficialis* virtually continuous with the *sternohyoideus* i.e. not separated by the cleithrum (character 6 above) was not confirmed in their analysis (restricted to the Cynodontinae); a unique condition of *abductor superficialis* muscle in cynodontines, Roestes and Gilbertolus was observed.

Evidence presented by Howes (1976) and Lucena and Menezes (in prep.), together with some characters confirmed in the present analysis, provides support for a hypothesis of close relationship between Gilbertolus (and Roestes) and the Cynodontinae. Characters shared by the Cynodontinae with Roestes and Gilbertolus that occur also in Gnathocharax and/or members of the Heterocharacini (listed above), might be indicative of a close relationship between these taxa at a more inclusive level. Characters shared by Roestes, Gilbertolus, Gnathocharax and the Heterocharacini (Lucena, 1993 and confirmed in the present study, see above) also have to be analyzed in a broader context.

Future studies should focus on identification of synapomorphies at increasingly higher levels of universality. Evidence for monophyly of the Cynodontinae and subunits within (Cynodon, Rhaphiodon, and Hydrolycus) is herein presented. Lucena and Menezes (in prep.) present evidence on the monophyly of the assemblage formed by Roestes plus Gilbertolus (their Roestini) as well as for each of these genera.

Neither the genus Gnathocharax nor the Heterocharacini were the subject of a detailed study that establish their monophyly and phylogenetic relationships. Géry (1966) defined the Heterocharacini in which he included three monotypic genera, Heterocharax Eigenmann, 1912, Lonchogenys Myers, 1927, and Hoplocharax Géry, 1966 based mainly on the pointed preopercle and overall external similarity. Both Myers (1927) and Géry (1966) suggested a close relationship between members of the Heterocharacini and Roestes and Gilbertolus. Gnathocharax Fowler, 1913 was hypothesized to be more closely related to Gilbertolus (Böhlke, 1955). Howes (1976) suggested that relationships of Gnathocharax were with the Heterocharacini, a hypothesis subsequently supported by

Lucena (1993) (characters listed above). A phylogenetic study of the Heterocharacini and Gnathocharax will undoubtly provide a better understanding about the hypothesis of a close relationship between the Cynodontinae and Roestes and Gilbertolus.

Lucena's (1993) analysis of 69 characiform taxa and 122 characters resulted in a phylogenetic hypothesis in which Acestrorhynchus is the sister group to the Cynodontinae. These two taxa share two characters unique among characiforms: short gill rakers on first ceratobranchial, wide at the base and with many conspicuous spines on the dorsal surface; direct contact between rhinosphenoid and parasphenoid previously hypothesized as unique for Acestrorhynchus (Menezes and Géry, 1983). These two taxa also share presence of two branchiostegal rays on the posterior ceratohyal, a feature that only occurs in Ctenolucius (Vari, 1995) elsewhere among characiforms, and most parsimoniously interpreted as an independent acquisition in Ctenolucius and cynodontines (see character 35 in "Character description list and analysis.").

Three additional characters most parsimoniously interpreted as synapomorphic for Acestrorhynchus and the Cynodontinae in Lucena's analysis occur also in other characiforms:

1) Teeth on the mesopterygoid.

2) Orbital ring delimited dorsally by the sixth infraorbital and supraorbital or by the latter only (independent origin in Hepsetus, and the Ctenoluciidae).

3) Premaxillary main tooth row having a large conical tooth in the anterior portion, larger than the remaining teeth, and another one similar in size in the posterior region, with many smaller conical teeth in between (independent origin in Acanthocharax,

Cynopotaminae (sensu Menezes, 1976), and Charax.

The question of the phylogenetic relationships of Acestrorhynchus is controversial. The genus was previously hypothesized as closely related to Oligosarcus (Menezes, 1964) and both were included in the subfamily Acestrorhynchinae (Menezes, 1976) based mainly on the possession of teeth on the ectopterygoid. Menezes and Géry (1983) suggested that Acestrorhynchinae might not constitute a monophyletic unit. This proposition was confirmed in Buckup's (1991) phylogenetic analysis of 78 characters in 27 characiform taxa, in which Acestrorhynchus is hypothesized as more closely related to the clade formed by erythrinids, lebiasinids, ctenoluciids and Hepsetus. According to Vari (1995:25) a hypothesis of a close relationship of Acestrorhynchus with the Lebiasinidae, Erythrinidae and Ctenoluciidae is not supported by the data he (Vari, 1995) analyzed. He mentioned that the phylogenetic placement of that genus has not yet been critically examined.

Buckup's (1991) and Lucena's (1993) studies constitute the first attempts to establish hypotheses of phylogenetic relationships among major characiform lineages. They have provided a framework for studies focusing on specific portions of the cladograms generated by them. The phylogenetic relationships of Acestrorhynchus need to be reevaluated focusing on features that corroborate the monophyly of the genus and a critical examination of the features used to hypothesize their relationships with the various taxa mentioned above.

Evidence currently available and discussed above provides better support, in terms of number of shared derived features, for a close relationship between

Cynodontinae and Gilbertolus plus Roestes rather than between Acestrorhynchus and cynodontines. However, a well corroborated hypothesis will be possible only with study of all taxa involved, including the Heterocharacini and Acestrorhynchus.

Phylogenetic relationships of the genus Agoniates Müller and Troschel, 1845 are also controversial. Eigenmann (1912:317) noted similarity 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 5 branchiostegal rays, and length of pectoral fins might constitute derived specializations shared by Agoniates and the Cynodontinae. In Lucena's (1993) analysis, Agoniates is hypothesized as the sister group to all other Characidae except 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). A ridge on the lateral surface of the vomer (character 16) is a derived feature shared by Agoniates and Hydrolycus. An analysis focusing on the question of the relationships of this genus definitely needs to be pursued; however, due to the larger number of derived features shared by the Cynodontinae and characiform outgroups discussed above, the features shared by cynodontines and Agoniates are hypothesized herein as having originated independently.

CHARACTER DESCRIPTION LIST 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 Table 1. Synapomorphy numbers provided after the description of each character below correspond to that in "Synapomorphy List", and on cladograms 1 and 2 of figures 23 and 24, respectively. Ambiguous characters at various levels of the analysis are indicated by letters followed by numbered subscripts.

Orbital region

1. Fifth infraorbital (IO_5).

Cynodontines have six canal-bearing bones forming the orbital ring with bony plates which 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 Hydrolycus n. sp. 1, IO_5 typically reaches the posterior margin of the infraorbital series and IO_4 and IO_6 are not in contact (fig. 2B). In Hydrolycus armatus and Hydrolycus n. sp. 2, IO_5 is greatly reduced, with the posteroventral margin of the IO_6 in contact with the posterodorsal margin of IO_4 (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 Hydrolycus n. sp. 2 is, however, unique among characiforms, and considered synapomorphic for the clade formed by these two species in both cladograms 1 and 2 (synapomorphy 49).

2. Antorbital (ANT).

All cynodontines have the antorbital bone contacting the lateral margin of the ventral wing of the lateral ethmoid. The antorbital in characiform outgroups with 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 a 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 antero-posteriorly 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 "Relationships of the Cynodontinae with other characiforms," and the features shared by these two 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 in both cladograms 1 and 2 (synapomorphy 1).

3. Antorbital.

The antorbital bone in all Hydrolycus species is a flat, plate like ossification, without a process extending from the main body of the bone.

The antorbital in Rhaphiodon and Cynodon 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 larger degree medially, especially in the middle portion of the process.

Flat antorbitals are observed in the majority of characiform outgroups. In some characiforms, however, 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, therefore, the elaboration found in their antorbitals does not seem to be directly comparable to that of cynodontines.

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

Rhaphiodon is hypothesized as derived, as opposed to the condition of a flat, plate-like ossification found in Hydrolycus and widespread among characiforms outgroups. In cladogram 1 the medial process on the posterior margin of the antorbital constitutes a synapomorphy for Cynodon and Rhaphiodon (synapomorphy 30), with its further enlargement in Cynodon representing a synapomorphy for the genus (synapomorphy 37). In cladogram 2 it is most parsimoniously hypothesized as an independent acquisition in each of the two genera (synapomorphy 78, and autapomorphy 84).

Neurocranium

A series of features of the anterior portion of the neurocranium (mesethmoid - vomer region) provide considerable morphological information pertinent to the elucidation of the phylogenetic relationships of the Cynodontinae. The modifications associated with this region provide diagnostic features for the Cynodontinae and subunits within. Such modifications are detailed below.

4. Mesethmoid (METH).

Hydrolycus species have the anterior portion of the mesethmoid, which forms an articular surface for the premaxillae, dorso-ventrally expanded, and almost round in shape when examined from a lateral view (METHS in figs. 3-5). This feature was previously noted by Starks (1926:165) for Hydrolycus scomberoides (H. pectoralis in that author's publication).

In Cynodon and Rhaphiodon the mesethmoid ends in a conical, spine-like process (METHS in figs. 6 and 7), the condition observed in the majority of examined characiform outgroups and considered plesiomorphic (Weitzman, 1962:19; Roberts, 1969:405; Vari, 1979:277). A vertically enlarged anterior portion of the mesethmoid was observed in Mylossoma, and Roeboexodon guyanensis among examined outgroups. In the latter species the enlargement of the anterior portion of the mesethmoid is accomplished by the vertical expansion of the spine and is continuous with an expansion of median portion of the ventral surface of the mesethmoid, a condition different from that in cynodontines. This vertical expansion of the anterior portion of the mesethmoid 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 on these modifications). The condition observed in Hydrolycus is unique among examined outgroups and in cladogram 1 is most parsimoniously interpreted as a synapomorphy for that clade (synapomorphy 46). In cladogram 2 the elaboration of the anterior portion of the mesethmoid is hypothesized as synapomorphic for the clade formed by Hydrolycus and Rhaphiodon vulpinus with a reversal to the primitive condition in the latter species (synapomorphy 75).

5. Mesethmoid.

Hydrolycus n. sp. 2, H. scomberoides, and H. armatus in addition to having the anterior tip of the mesethmoid vertically enlarged (character 4), also have this portion of the mesethmoid upturned (figs. 3 and 5). As a consequence, the anterodorsal surface of the mesethmoid is not wedge-shaped as in the majority of characiforms. Rather, its convexity is interrupted by a notch at the posterior region of the mesethmoid spine. This feature was also noted by Starks (1926:165) for Hydrolycus scomberoides (H. pectoralis in that author's publication).

In Cynodon, Rhaphiodon and Hydrolycus n. sp. 1 the dorsal surface of the anterior portion of the mesethmoid is gently convex and not interrupted by a notch as noted above. In the latter species (fig. 4) the condition seems intermediate between that of Cynodon and Rhaphiodon, and the remaining Hydrolycus species. Although Hydrolycus n. sp. 1 also has a vertically enlarged mesethmoid spine, when observed from a lateral view the anterior portion of the mesethmoid is somewhat convex, with the convexity not conspicuously interrupted by a notch as in other Hydrolycus species.

The modification of the anterior portion of the mesethmoid as described for Hydrolycus species (with the exception of H. n. sp. 1) is not found in examined characiform outgroups and is, therefore, hypothesized as synapomorphic for the clade formed by Hydrolycus n. sp. 2, H. scomberoides, and H. armatus in both cladograms 1 and 2 (synapomorphy 47).

In Roeboexodon guyanensis the anterodorsal portion of the mesethmoid is highly modified with two processes extending laterally. Two longitudinal ridges extend posteriorly from these lateral projections as far as the anterior margins of the frontals. This condition is very different from the primitive condition described above for characiform outgroups and it comprises a different, more complex set of modifications than that described for cynodontines.

6. Ventral process of the mesethmoid (VP-METH) (sensu Starks, 1926:163).

All cynodontines have a pair of processes projecting ventrally from the ventral surface of the mesethmoid (figs. 3-7). 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 the 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 processess 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 outgroups, ventral processes of the mesethmoid, similar to those 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 ventrolaterally 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 some Hydrolycus species, detailed below). The sheet of connective tissue noted for cynodontines was not found in these outgroups. Rather in 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) describes the mesethmoid of Hoplias and Erythrinus as being similar to that of Brycon. The latter genus does not have 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 are in contact with the upper portions of the vomer by a synchondral joint surface (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 was 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 is connected. In cynodontines it is possible to recognize a distinct structure extending laterally from the mesethmoid on to 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 with 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 portion 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 was observed in this study in Carnegiella strigata and 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*) the same author (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 groups in which relatively similar processes were observed (listed above) are hypothesized as being more closely related to groups that lack well-developed processes. *Prochilodus rubrotaeniatus*, *Caenotropus maculosus*, *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, the Heterocharacini, Acestrorhynchus, see discussion on section about cynodontine interrelationships) lack any processes on the ventral portion of the mesethmoid that bear any resemblance to those described for the Cynodontinae. As a consequence, the ventral processes on the mesethmoid as described for the Cynodontinae is hypothesized as synapomorphic (synapomorphy 11).

7. Ventral processes of the mesethmoid

In all cynodontines, except Hydrolycus n. sp. 1, the ventral processes of the mesethmoid are ventrally directed at an approximately 90 degree angle relative to the mesethmoid spine (figs 4, 6-8). In Hydrolycus n. sp. 1 (fig. 4), 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 on the mesethmoid as described for cynodontines. According to each of the two most parsimonious hypotheses of cynodontine intrarelationships generated in the present study this character is interpreted as an autapomorphy for Hydrolycus n. sp. 1 (E_2).

8. Vomer - mesethmoid contact.

In Hydrolycus n. sp. 2, H. armatus, H. scomberoides, and Rhaphiodon vulpinus, the anterior surface of the vomer contacts the ventral process of the mesethmoid along the posterior surface of the latter bone (figs. 3,5, and 7). In Hydrolycus n. sp. 1 and

Cynodon (figs. 4 and 6) the vomer does not directly contact the ventral processes of the mesethmoid. In these taxa the contact between the vomer and the mesethmoid occurs dorsal to the posterior surface of the ventral processes, leaving the processes free of contact with any other ossification.

This character was coded as a missing entry in all outgroups used to root the cladogram in the various analysis undertaken since they lack the ventral processes on the mesethmoid and, therefore, the variation associated with this element in cynodontines is inapplicable for outgroups. 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. erythrinids), a condition similar to that in Hydrolycus n. sp. 2, H. armatus, H. scomberoides, and Rhaphiodon vulpinus. However, as noted under character 6 above, homology propositions for the ventral processes of the mesethmoid in cynodontines relative to the condition found in characiform outgroups are not clear, and moreover, all taxa that possess similar processes are more closely related to taxa that do not possess 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 sp. due to the poor condition of the specimen available (AMNH 32485, 35 mm SL).

The distribution of this character in cladogram 1 renders any kind of optimization for the character states arbitrary. As a consequence it is impossible unambiguously to propose this character as an additional synapomorphy for any clade under the phylogenetic reconstruction summarized in cladogram 1. In cladogram 2, the lack of a direct contact between the vomer and the mesethmoid is hypothesized as a synapomorphy for Hydrolycus n. sp. 2, H. armatus, H. scomberoides, and Rhaphiodon vulpinus (all of which possess state 0) (I_1), with the outgroup node optimized as having state 1 (see also discussion of this character in "Phylogenetic results").

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, in the ventral processess of the mesethmoid. In cynodontines those elements delimit a groove or fossa that provide 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 below.

9. Ventral diverging lamellae of the mesethmoid.

All cynodontines with the exception of Hydrolycus scomberoides have well developed ventral diverging lamellae of the mesethmoid (sensu Weitzman, 1962:19). Posteriorly, the lamella of each side is in contact with the upper central portion of each lateral ethmoid. At its anterior region 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 bony plate, triangular in shape, with one corner of the triangle pointing toward the posterior edge of the vomer (DL-METH in figs. 3-7) (from this point forward the entire element will be referred to as the ventral 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 different condition from the one described above. In this species the portion of the ventral lamellae that extends along the ventral portion of the mesethmoid, between the lateral ethmoid and anterior portion of the mesethmoid, is highly reduced compared to that of remaining cynodontines. As a consequence there is no continuity of the lamella at the ventral surface of the mesethmoid with the portion of the lamella extending from the lateral wing of the mesethmoid (fig 4). This latter portion is well-developed and similar to what occurs in other Hydrolycus species (see discussion below).

The ventral diverging lamellae of the mesethmoid are reduced or absent in many characiform outgroups, e.g. erythrinids, lebiasinids, ctenoluciids, 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 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 mesethmoid 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 do not correspond to the ventral diverging lamella of the mesethmoid as described by Weitzman (1962:19). Characiforms with well developed ventral diverging lamella of the mesethmoid include Roestes, Gilbertolus, Charax, Roeboexodon, the Cynopotaminae (Menezes, 1976), Acanthocharax, and Agoniates.

A reduced ventral lamella of the mesethmoid is restricted to Hydrolycus scomberoides within cynodontines, a condition most parsimoniously interpreted as autapomorphic for this species (autapomorphy 59).

10. Ventral diverging lamellae of the mesethmoid.

The extent to which the triangular portion (described under character 9) of the ventral diverging lamella of the mesethmoid extends along the lateral surface of the vomer varies within cynodontines. In all Hydrolycus species and Rhaphiodon the triangular 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. 3-5, and 7). In Cynodon this lamella is further elongate, extending beyond the midline, and in many specimens reaching the posteroventral edge of the vomer (fig. 6). 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 of them the portion of the lamella at the ventral surface of the mesethmoid extends ventrally to contact the anterior portion of the vomer continuous with a 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, a condition in which the triangular portion of the ventral diverging lamella of the mesethmoid covers most of the lateral surface of the vomer is hypothesized as synapomorphic for Cynodon in cladogram 1 and 2 (synapomorphy 41).

11. 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 shows some differences among cynodontines. In Hydrolycus n. sp. 2, H. scomberoides, and H. armatus this portion of the lateral wing of the mesethmoid has a distinct articular surface that is oriented in a posterior direction (AS-METH in figs. 3 and 5). Ligamentous tissue from the maxilla converges anteriorly to attach to this articular surface. This articular surface forms an anterior boundary for the depression present on the lateral surface of the vomer where the maxilla abuts (see character 15 below), at the level of the synchondral joint between the vomer and ventral processes of the mesethmoid. In Cynodon, Rhaphiodon, and Hydrolycus n. sp. 1, 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 Rhaphiodon and Hydrolycus n. sp. 1 (figs. 4 and 7, respectively) than in Cynodon (fig. 6) 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. Comparison between the area in the mesethmoid where the maxilla attaches in characiform outgroups to that of cynodontines is complicated due to the highly modified mesethmoid region of cynodontines. The lateral wings of the mesethmoid in many characiforms outgroups have a cartilaginous cap that is continuous with the cartilaginous surface from the lateral portion of the vomer, being laterally oriented (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 which has a ventral to slightly lateral articular surface.

A posterior orientation of the articular surface of the lateral wing of the mesethmoid where part of the ligamentous tissue of the maxilla attaches is unique to Hydrolycus n. sp. 2, H. scomberoides, and H. armatus among examined characiforms, and seems to be the result of a 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 reorientation of the lateral wing of the mesethmoid is also expressed in the orientation of its articular surface with the premaxilla which is more closely associated with the lateral portion of the ventral processes of the mesethmoid in Hydrolycus n. sp. 2, H. scomberoides, and H. armatus when compared to the condition in Cynodon, and Hydrolycus n. sp. 1 (in Rhaphiodon the articular surface of the lateral wing of the mesethmoid where the premaxilla articulates with is less pronounced laterally). The condition observed in Hydrolycus n. sp. 2, H. scomberoides, and H. armatus is hypothesized as a synapomorphy for that assemblage in cladograms 1 and 2 (synapomorphy 48).

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 in cross-section through its posterior portion (see character 13 below) with the angle between the two arms of the "Y" very acute, and the standard, that forms a sagittal bony plate, elongate and contacting anteriorly a similar bony plate of the mesethmoid.

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 almost a 90 degree angle, whereas in cynodontines this angle is much greater. A vomer as described for the cynodontines was observed only in Distichodus fasciolatus, among examined characiforms, with the overall shape of this ossification being more similar to that of Cynodon.

12. Vomer (V)

In Hydrolycus species and Rhaphiodon the ectopterygoid is in close contact with the ventral surface of the vomer (character 32 below) and not with the mesethmoid as in Cynodon. A close contact between these two elements occurs in Acestrorhynchus and Hepsetus but represent a different set of modifications (discussed under character 32 below).

The ventral surface of the vomer in Hydrolycus species and Rhaphiodon bears two longitudinal crests situated side by side and separated by a longitudinal groove (can be seen from a lateral view, VC, in figs. 3-5, and 7). 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. Such a crest is developed to varying degrees among the cynodontines where it is present. It is relatively small in Rhaphiodon and Hydrolycus n. sp. 1 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 32) 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 possess two small projections of bone on the ventral surface of the vomer with ligamentous tissues from the mesopterygoid and ectopterygoid attaching to them. The ectopterygoid does not directly contact these processes in Gilbertolus atratoensis as it does in Hydrolycus and Rhaphiodon. The processess, although present, are not as developed in Gilbertolus atratoensis as they are in Hydrolycus and Rhaphiodon. In the specimen of Roestes ogilvei examined the processes are hardly noticed, and they are absent in the examined specimen of R. molossus. Additional specimens of Roestes and Gilbertolus need to be examined in order to check the variation of this feature in these genera. The possibility of a close relationship between Gilbertolus plus Roestes to the Cynodontinae was discussed in the previous section. If further studies substantiate this hypothesis the presence of the processes in the ventral surface of the vomer in these taxa might be hypothesized as different states of the same character (i.e. presence of small ventral processes on the surface of the vomer in Roestes and Gilbertolus; processes in the vomer highly developed in Hydrolycus and Rhaphiodon) and further analysis might lead to a hypothesis that this feature is synapomorphic for these taxa with a reversal to the primitive condition in Cynodon or with independent origins in Gilbertolus, Roestes, Hydrolycus, and Rhaphiodon. As a consequence, just the presence of processes on the ventral surface of the vomer is not proposed as a potential synapomorphy for the latter taxa at this time with the condition in Gilbertolus coded as "0". Rather, the possession of developed processes on the ventral surface of the vomer with their direct contact with the ectopterygoid is unique to Hydrolycus and Rhaphiodon among cynodontines, and two equally most parsimonious hypotheses explain the distribution of this character in cladogram 1. The first is the acquisition of the processes in the ancestor of the Cynodontinae clade with its subsequent loss in Cynodon (A_3). Alternatively, the process may have originated independently in Hydrolycus and Rhaphiodon vulpinus (C_3 and F_3). In cladogram 2 the highly developed ventral processes of the ventral surface of the vomer is hypothesized as a synapomorphy for Hydrolycus and Rhaphiodon (synapomorphy 74).

13. 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, in the region where they extend ventrally of the longitudinal axis of the shaft of the vomer. Some variation at 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, almost to 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 just until the posterior half of the extension 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, since there are no bony plates extending ventral of the longitudinal axis of the shaft of the vomer. As already mentioned, the vomer of Distichodus fasciolatus, is similar to that of Cynodon, with continuous bony plates along all its lateral extension.

In characiforms outgroups that have the 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 from its posterior to the anterior portion 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 contributes to make this portion of the bone wide. 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 for these outgroups was, therefore, coded as a missing entry. According to the scheme of cynodontine relationships hypothesized in cladogram 1 , the condition described for Cynodon is hypothesized as derived and for this genus (B_4). In cladogram 2 the condition described for Rhaphiodon and Hydrolycus species is that hypothesized as derived and synapomorphic for that assemblage (H_1).

14. 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, and this is usually a relatively loose type of contact. In ctenoluciids the articular surface of the vomer is situated at its lateral portion between the anterior and posterior edges of the vomer. 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 the 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 that are 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 have two large articular surfaces in the vomer that are in contact with the palatine. These articular surfaces are somewhat posterior in the vomer but are also oriented ventrally, and 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 being hypothesized as a synapomorphy for the latter group (Machado-Allison, 1983:163). The phylogenetic relationships of the Serrasalminae remains unresolved. Machado-Allison (1983) discussed the problem and mentioned characters in common between serrasalmines and Brycon. Lucena's (1993) study on the 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 portion at the posterior edge of the vomer to which the cartilaginous surface of the anterior portion of the palatine contacts, this also being a condition similar to cynodontines. Hepsetus is hypothesized as being closely related to the Ctenoluciidae and Erytrhinidae, families with a different type of vomer-palatine contact. The vomer-palatine type of articulation found in these characiforms outgroups is, therefore, most parsimoniously hypothesized as having originated independently from that in cynodontines, and therefore, the condition in the latter taxa is hypothesized as synapomorphic in cladograms 1 and 2 (synapomorphy 12).

15. Vomer-maxilla articulation.

The maxilla of cynodontines articulates with the lateral surface of the vomer at the anteroventral portion of the latter ossification. At this area of contact, the vomer has developed a shallow depression. Anterodorsally, this depression is roofed by the anteroventral portions of the ventral diverging lamella of the mesethmoid (see character 10 above), and posteroventral portions of the lateral wing of the mesethmoid. The latter serves as areas for ligamentous attachment of the maxilla to the neurocranium (see character 11 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 slightly intermediate between that of Cynodon and Hydrolycus. Ontogenetic variation is observed in this feature. In a small specimen of Rhaphiodon (BMNH 1935.6.4:33-39, 96.8 mm SL) the depression is not evident, whereas in a larger individual (MZUSP 32812, 191.0 mm SL) it is clearly distinct. In very large specimens of Hydrolycus armatus the depression in the vomer becomes very developed and it is very deep, like a fossa (this was 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. But because of the ontogenetic variation observed within species and the continuous variation among species, the definition of discrete character states is complicated and was not pursued at this time. The presence of a depression of varying degrees of development in the lateral surface of the vomer associated with the articulation of the maxilla was, however, not encountered outside the Cynodontinae among characiforms and, therefore, is hypothesized as an additional synapomorphy for the assemblage in cladograms 1 and 2 (synapomorphy 13).

16. Ridge on lateral surface of the 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. n. sp. 1 (VR in fig. 4), and H. n. sp. 2 of approximately 150 mm SL. In H. armatus it absent in a specimen 136.0 mm SL (LACM 43295-36), and in a specimen 151.0 mm SL (MZUSP 32607) it is only very slightly developed, and being represented by a thickening of bone in the area where the ridge is present in larger specimens. It is well developed in a 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 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. This character was, therefore, 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 position medially, in the large specimens.

No such ridge on the lateral surface of the vomer was observed in any of the specimens of Cynodon examined. 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. A 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.

In cladogram 1, the condition described for Hydrolycus is hypothesized as synapomorphic with the missing entry coded for Rhaphiodon being optimized as "0" (absent of a ridge) (C_4). In cladogram 2 the presence of the ridge on the vomer is hypothesized as a synapomorphy for Hydrolycus and Rhaphiodon (with the missing entry coded for Rhaphiodon optimized as "1", presence of a ridge) (H_2).

17. Rhinosphenoid.

All Hydrolycus species and Rhaphiodon have a rhinosphenoid (RS in figs. 3-5, and 7). 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 in all Hydrolycus species except H. scomberoides, the rhinosphenoid is in the form of a flat and wide curved rod. Anteriorly, it attaches to the midsagittal portion of the lateral ethmoids. Posteriorly it connects the medial portion of the orbitosphenoid. 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 laterodorsal portion of each side of the orbitosphenoid develops a process that extends anteriorly and medially where it meets 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 in ontogeny than the remaining of the ossification. Specimens of Hydrolycus armatus smaller than 151.0 mm SL (MZUSP 32607) and Rhaphiodon vulpinus 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. 4 and 5). A specimen of Hydrolycus n. sp. 2 (MZUSP 32630, 151.2 mm SL) has the dorsal extension of the rhinosphenoid well developed.

In H. scomberoides the rhinosphenoid is reduced compared to the remaining cynodontines with this ossification. The dorsal extension is lacking in all specimens prepared for osteological examination (fig. 3), the largest being 241.0 mm SL (AMNH 40087SD, dry skeleton). The ventral portion of the rhinosphenoid in H. scomberoides is also reduced, and it consists of a small curved rod filling the space between the orbitosphenoid and lateral ethmoids just dorsal to the parasphenoid.

The rhinosphenoid is an ossification that has been reported only for 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, among others.

In Acestrorhynchus the rhinosphenoid is in contact with the parasphenoid and this feature has been considered as unique for this genus (Menezes and Géry, 1983). In small specimens this contact is made through cartilage in between these two ossifications. In larger specimens the bones are in direct contact. In Hydrolycus species and Rhaphiodon vulpinus the rhinosphenoid also contacts the parasphenoid through cartilage, with a 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 losses (synapomorphy 41).

18. 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 (LEP in fig. 6). 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 mm SL, dry skeleton), the contact between the lateral-ethmoid and orbitosphenoid is extended by the dorsal growth of these two elements, and together with the growth of the ventral lamella of the frontal, the dorsolateral portion of the anteriomedian opening of the orbitosphenoid is completely covered. The ventral portion of the lateral-ethmoid process extends medially almost to meet the medial outgrowth of the same process of the other side (I was unable to determine whether or not the process from each side meet 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 seems that the entire 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, 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, however, less developed in the latter two species.

The contact between the orbitosphenoid and lateral ethmoid in the majority of the groups mentioned 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). Citharinids have a dorsal contact between these two elements that is similar to cynodontines, but have a second articulation between them that is formed mainly by an anterior extension of the orbitosphenoid (Vari, op. cit.). In the Alestinae and Hydrocynus the process between the lateral ethmoid and orbitosphenoid is formed entirely by the latter element and it 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 formed by a dorsal and a 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, in cladogram 1, as derived for the clade formed by Cynodon and Rhaphiodon vulpinus (synapomorphy 31) with an independent origin in Hydrolycus scomberoides (autapomorphy 53). In cladogram 2 two equally parsimonious explanations are possible. In the first, a lateral ethmoid - orbitosphenoid contact is hypothesized as a synapomorphy for the Cynodontinae (J_1) with a reversal to a condition of lack of contact between these two elements in Hydrolycus n. sp. 1 and the clade formed by H. n. sp. 2 and H. armatus. Under the alternative explanation the lateral ethmoid - orbitosphenoid contact is hypothesized as independent acquisitions in Cynodon (K_1), Rhaphiodon (L_2), and Hydrolycus scomberoides (M_1).

19. Orbitosphenoid - parasphenoid distance.

All cynodontines have the orbitosphenoid in direct contact with the parasphenoid. The distance between the main portion of the orbitosphenoid and the parasphenoid, however, differs among them. Hydrolycus n. sp. 1, H. n. sp. 2 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. 4 and 5). 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 6 and 7). 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, but it is relatively more so than in Cynodon and Rhaphiodon. Therefore, the condition in Hydrolycus scomberoides was coded as a missing entry.

Many characiforms have the parasphenoid and orbitosphenoid remote from each other (e.g. Brycon, Roestes, Gilbertolus, Charax, the Heterocharacini, Acestrocephalus, Acestrorhynchus, and Serrasalmus). This was listed as one of the distinguishing features for the Characinae (Weitzman, 1962:48), and it 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, the prochilodontids Semaprochilodus and Prochilodus (Roberts, 1973:217). Galeocharax is more closely related to characids such as Acestrocephalus (Menezes, 1976) and Charax (Lucena, 1993), and Semaprochilodus and Prochilodus to a monophyletic assemblage formed by the Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae, 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 "Relationships of the Cynodontinae with other characiforms"), all taxa with the orbitosphenoid well separated from the parasphenoid, the condition in Cynodon and Rhaphiodon is hypothesized as derived.

In cladogram 1 an orbitosphenoid close to the parasphenoid is hypothesized as a synapomorphy for the clade formed by Cynodon and Rhaphiodon (synapomorphy 36). In cladogram 2, the same condition is hypothesized as having independent origins in the two genera (synapomorphies 78 and 82).

20. 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). According to this author, in all three cynodontine genera the dilatator operculi muscle has two origins. One is dorsally from the frontal - sphenotic groove which extends on to the cranial roof, and the other is ventrally from the deep cavity which 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 and the indentation provides a sharp dorsal rim for the dilatator groove. The muscle takes its origin 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, also discusses variation of this pattern; Howes, 1976). In characiforms with this pattern of the dilatator groove (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) the dilatator muscle does not extend anteriorly on the dorsal surface of the cranial roof more than the dorsoposterior edge of the orbit. Only in cynodontines is the dilatator fossa greatly expanded anteriorly, covering most of the dorsal surface of the frontal. An expanded dilatator groove reaching 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, this condition being unique among characiforms and considered as synapomorphic in both cladograms 1 and 2 (synapomorphy 14).

Different modifications in the region 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 portion 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 21 below). The second relates to the differing degree of development of the dorsal portion of the sphenotic spine (character 22 below).

21. Frontal shelf at posterodorsal edge of orbit.

In the majority of characiforms with a primitive form of the dilatator fossa the portion of the frontal at the posterodorsal edge of the orbit has developed a lateral shelf that is continuous with the dorsal portion 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 portion of the frontal shelf is probably associated with the type of insertion of the dilatator muscle which, according to Howes (1976:215), has two origins, one on the dorsal surface of the frontal and a second from the cavity 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 edge of the orbit occurs also in Acestrocephalus sardina, Acanthocharax microlepis, and Gnathocharax among examined characiform outgroups. However, the dilatator muscle in these species does not seem to have a ventral origin as in cynodontines (Howes, 1976:235).

In Hydrolycus n. sp. 2 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 (coded as 1). A further reduction of the shelf of the frontal occurs in Cynodon, Rhaphiodon, Hydrolycus n. sp. 1, and H. scomberoides (coded as 2)(figs., 3,4,6 and 7). In these taxa such a 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 a derived condition (synapomorphy 15), with a partial secondary reversal to a small shelf in Hydrolycus n. sp. 2 and H. armatus as a derived character for the clade formed by these two species (synapomorphy 52).

22. 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. 3, 6, and 7). 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 common to ctenoluciids, erythrinids, and lebiasinines. However, this reduction is accompanied by a longitudinal expansion of the remainder of the spine, this causing a restructure of the spine (Vari, 1995:14). No such restructure 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, 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 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 derived under the scheme of relationships presented in cladogram 1, and most parsimoniously hypothesized as synapomorphic for the clade formed by Cynodon and Rhaphiodon with an independent acquisition in Hydrolycus scomberoides. In cladogram 2, two alternative equally most parsimonious hypotheses can account for the distribution of this character. In the first case, the reduction of the dorsal portion of the sphenotic spine is synapomorphic for the Cynodontinae with a subsequent reversal to the primitive condition in Hydrolycus n. sp. 1 and the clade formed by H. n. sp. 2 and H. armatus. In the alternative hypothesis the reduction of the dorsal portion of the sphenotic spine is regarded as independent acquisitions in Cynodon, Rhaphiodon, and Hydrolycus scomberoides.

23. 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 covers the dorsal surface of the lateral ethmoids, extending laterally relative to the longitudinal axis of the body. The anterior portion of the frontal shelf is wider in larger specimens. In smaller specimens (LACM 43295-36 135.9 mm SL; MZUSP 32607, 2 specimens, 151.4-200 mm SL) it is represented by a very narrow bony platform. In Hydrolycus n. sp. 2 the anterior shelf of the frontal is similar to that in H. armatus, although relatively less pronounced. The largest specimen of H. n. sp. 2 prepared for osteological examination (MZUSP 32632, 257.0 mm SL) has a narrower shelf than smaller specimens of H. armatus. In Hydrolycus n. sp. 1 the anterior shelf of the frontal is completely absent (largest specimen prepared for osteological examination MZUSP 32638, 163.0 mm SL). In Hydrolycus armatus this shelf is considerably more developed in relatively large specimens (examined in dry skeletons preparations, AMNH 91342SD, 450 mm SL). Hydrolycus n. sp. 2 reaches sizes comparable to that of H. armatus, so it is possible that the shelf also is more developed in larger specimens. Hydrolycus n. sp. 1 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 shelf of the frontal 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 Hydrolycus armatus the area between these two elements is shallower and more open. In H. scomberoides the anterior frontal shelf is truncated at the midline of the orbit. In Rhaphiodon and Cynodon the shelf continues forward to the anterior portion of the sphenotics. In Rhaphiodon the margin of the anterior shelf of the frontal is straight ventrally, whereas in Cynodon it has a curved edge. The different conditions of the anterior shelf of the frontal in cynodontines are partially shown in figures 3-7.

A frontal bone with an expanded platform located lateral to the supraorbital canal and projecting over the lateral ethmoid bone was noted by Buckup (1991:215) for some characiforms e.g. Charax, Cynopotamus, Tetragonopterus, Bryconops, Oligosarcus and Phenacogaster . The condition resembles that of Hydrolycus armatus within cynodontines and was also noted for Roestes, and Gilbertolus.

According to the scheme of cynodontine relationships derived from cladogram 1, the different conditions of the anterior portion of the frontal shelf within cynodontines are most parsimoniously hypothesized as having originated independently in Hydrolycus

n. sp. 1 (the lack of an anterior frontal shelf, synapomorphy 60) and H. scomberoides (truncated frontal shelf synapomorphy 55). A ventral expanded frontal shelf in Cynodon and Rhaphiodon can be hypothesized as derived for this clade (synapomorphy 33). The differences in the margin of the frontal shelf of Cynodon and Rhaphiodon are ambiguous under any kind of optimization. In cladogram 2, each of the modifications described above is most parsimoniously hypothesized as having originated independently Hydrolycus n. sp. 1, H. scomberoides, Cynodon, and Rhaphiodon (autapomorphies 58, 53, 74, and 83, respectively) .

24. 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), 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, the Heterocharacini (Géry, 1966), 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 at a higher level of inclusiveness (see discussion in previous section).

25. Dorsal posttemporal fossa.

Cynodon species lack the dorsal posttemporal fossa which is bordered by the supraoccipital, parietal, and epioccipital in characiform outgroups. The lack of this fossa, also occurs in the citharinids Citharinus and Citharidium and 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 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). The lack of the dorsal posttemporal fossa is, therefore, hypothesized as independent losses in citharinids, gasteropelecids, and Cynodon with the condition in the latter genus hypothesized as synapomorphic in both cladograms 1 and 2 (synapomorphy 43).

26. 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 cranio-vertebral joint as described for cynodontines is unique to this assemblage among examined outgroups and hypothesized as a synapomorphy in cladograms 1 and 2 (synapomorphy 23).

Suspensorium and hyoid arch

27. 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. 8A). 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. 8B), 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 in cladogram 1. The first is the acquisition of the process in the ancestor of the Cynodontinae clade, with its subsequent loss in Cynodon (A_1). Alternatively, the process may have arisen independently in the genus Hydrolycus and Rhaphiodon (C_1 and F_1). In cladogram 2, the process of the hyomandibula as described above is hypothesized as a synapomorphy for Hydrolycus species and Rhaphiodon (synapomorphy 72).

28. Symplectic.

The symplectic in cynodontines is fairly elongate, its posterior portion bears an elongate blade-like 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. 9A). This groove in the hyomandibula 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. 9B) 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 towards and contacts the metapterygoid (a slight contact of a lamellar process of the symplectic with the metapterygoid was also observed in Boulengerella lateristriga in ctenoluciids). The symplectic process and the hyomandibula are in slight contact along their margins. The symplectic in Hoplias (fig. 9C), in addition to contacting the metapterygoid, extends dorsally to contact also 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, 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 hypothesized to be synapomorphic for the subfamily (synapomorphy 2).

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.

29. 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. Metapterygoid teeth are present also 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 sized specimen (143.4 mm SL, mentioned above) lacks teeth on the metapterygoid. Rather it seems that there is intraspecific 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, being 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 the form of 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 appearing late in ontogeny which fuse to each other and with the metapterygoid.

The presence of teeth in the metapterygoid of Hydrolycus species and Rhaphiodon vulpinus is a unique condition in characiforms and there are two equally parsimonious explanations for the distribution of this character in cladogram 1. The first is the acquisition of metapterygoid teeth in the ancestor of the Cynodontinae clade, with its subsequent loss in Cynodon (A_2). Alternatively, metapterygoid teeth may have had independent origins in the genus Hydrolycus and Rhaphiodon vulpinus (C_2 and F_2). In cladogram 2, the presence of teeth in the metapterygoid is hypothesized as a synapomorphy for Hydrolycus and Rhaphiodon (synapomorphy 73).

30. Mesopterygoid teeth.

Cynodontines possess a broad patch of very small teeth, which covers the buccal surface of the mesopterygoid almost entirely.

Teeth on the mesopterygoid are present only in a few characiforms: they were observed in a few (but not all) Acestrorhynchus species; in Lebiasina bimaculata (coded as absent by Vari, 1995:7); within ctenoluciids, Vari (1995:24) mentions 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 (pers. communication) 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 tooth plate 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, Gilbertolus, Gnathocharax, and the Heterocharacini, but present in most Acestrorhynchus species. As previously discussed, there is stronger evidence supporting a hypothesis of a close relationship between Roestes plus Gilbertolus, and the Cynodontinae, in which case the presence of mesopterygoid teeth could be hypothesized as being derived for cynodontines. However, with the present evidence, a relationship of Acestrorhynchus to the Cynodontinae, at a higher level of universality, cannot be completely discarded, in which case an alternative interpretation in which mesopterygoid teeth would represent a secondary loss in the taxa immediately related to cynodontines, is possible. 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 more parsimoniously interpreted as independent acquisitions relative to cynodontines.

31. Ectopterygoid teeth.

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

Teeth on the ectopterygoid occur in diverse characiforms including Acestrorhynchus (Menezes, 1969:35), 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.

The morphology and pattern of teeth arrangement in the ectopterygoid bone, seems however, 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 conical the 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 differences in the size and distribution of teeth on the ectopterygoid bone are also present. No differences in ectopterygoid teeth pattern was 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 a most parsimoniously interpreted as independent acquisitions, with the condition in the latter taxa hypothesized as synapomorphic in cladograms 1 and 2 (synapomorphy 4).

32. 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) and, 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 in cladograms 1 and 2 (synapomorphy 5).

33. Ectopterygoid - mesethmoid contact.

All cynodontines have longitudinally elongate ectopterygoids, extending well beyond the anterior portion of the palatine, 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, its anteriormost tip does not contact the mesethmoid as it does in Cynodon. They are in close contact with the ventral surface of the vomer (see character 12).

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 these taxa the palatine bone constitutes the anteriormost portion of the palatine arch, 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 antero-ventral 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 lineage (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 of that in cynodontines. The condition observed in Cynodon is hypothesized as derived for cynodontines and autapomorphic for the genus (synapomorphy 38).

34. Branchiostegal rays.

All cynodontines have five branchiostegal rays. Among examined characiforms outgroups, five branchiostegal rays is also present also in erythrinids (Weitzman, 1964:147), in the characidiin Characidium fasciatum (Buckup, 1992:1069), and in some hemiodontids 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 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 (pyrrhulinines, Weitzman, 1964:150, and some anostomids of the genera Pseudanos and Anostomus (Winterbottom, 1980:39).

All the groups 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, five branchiostegal rays is most parsimoniously interpreted as having independent origins in all these taxa. The presence of five branchiostegal rays is, as a consequence, hypothesized as a synapomorphy for the Cynodontinae in cladograms 1 and 2 (synapomorphy 6).

35. Branchiostegal rays.

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 hypothesized as being independently acquired in Ctenolucius and cynodontines.

The situation with respect to Acestrorhynchus is complicated in view of the uncertainty of its relationships with the Cynodontinae (see "Relationships of the Cynodontinae with other characiforms"). Evidence currently available (Lucena and Menezes, in prep.), points toward a hypothesis of a close relationship between cynodontines and Gilbertolus and Roestes. Given that hypothesis, and also considering a hypothesis of Acestrorhynchus being related to these taxa at the next inclusive level, the presence of five branchiostegal rays might be then explained as either being homoplastically present in Acestrorhynchus and the Cynodontinae or it can be synapomorphic for all these taxa with a reversal to the primitive condition in Gilbertolus and Roestes. As a consequence, 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

36. 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). The possession of enlarged dentary canines is not restricted to cynodontines. Relatively pronounced dentary canines occur also in Acestrorhynchus, Hydrocynus, Hepsetus, Ichthyborus, the

Heterocharacini, the Erythrinidae, and the Cynopotaminae. In some of these taxa, the canines can get 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 is a number of relatively large canines similar in 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 n. sp. 2, H. scomberoides, and H. armatus. In these species the dentary canine is much more developed than in Cynodon, Hydrolycus n. sp. 1, and Rhaphiodon (fig. 10). In the latter three species only the dorsalmost tip of the dentary canine extends dorsally to reach the snout opening, while in Hydrolycus n. sp. 2, H. scomberoides, and H. armatus it extends far dorsally into the snout opening. The highly developed dentary canines of Hydrolycus n. sp. 2, H. scomberoides, and H. armatus represents a unique condition within characiforms and is synapomorphic for this assemblage in cladogram 1 and 2 (synapomorphy 49).

37. Foramen in anterior portion of snout for the 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 n. sp. 2, H. scomberoides, and H. armatus extends 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 in the latter taxa the ascending process of the maxilla passes posterior to the dentary canine while in Roestes, Gilbertolus, and Agoniates this process lies anterior to the dentary canine. The ascending process of the maxilla in the latter three taxa rests on the posterior surface of the premaxilla, the typical condition 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 in cladograms 1 and 2 (synapomorphy 26).

38. Replacement tooth trenches.

There is considerable variation in the morphology of replacement tooth trenches in characiforms. Monod (1950) and Roberts (1967) described different types of replacement tooth trenches in the order. According to the latter author 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 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 positioned 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 teeth 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° degree angle relative to the functional teeth, in a horizontal plane 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 condition in the latter taxa being synapomorphic for the clade in cladogram 1 and 2 (synapomorphy 27).

Branchial arches

39. 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. 12). This condition is present only in Acestrorhynchus (illustrated in 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 rakers, reduced, similar in shape as 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-raker 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.

The utilization of gill raker morphology as either a synapomorphy for the Cynodontinae (with an independent acquisition in Acestrorhynchus) or as a synapomorphy for a clade including these two taxa still depends on further studies clarifying the relationships of Acestrorhynchus. Following the same line of argumentation provided above for character 34, the presence of small, flat gill rakers along the leading portion of the first ceratobranchial cannot be unambiguously proposed as an additional synapomorphy for the Cynodontinae at this time.

40. Gillrakers.

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 gillrakers of the first ceratobranchial were observed in Cynodon and Hydrolycus n. sp. 1 (fig. 12A). These spines are considerably larger than the remaining spines that cover the surface of the gill-raker. Usually one of the spines is distinctly larger, with its length more than half of the vertical length of the bony plate of the gillraker. Enlarged spines are more evident on the gillrakers situated towards the posterior end of the first ceratobranchial. Hydrolycus n. sp. 2, 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 gillraker, being only slightly larger than the latter.

Acestrorhynchus species, the only other characiform taxa that have short, flattened gillrakers covering the entire first ceratobranchial, have considerably enlarged spines on the free upper edge of the gillrakers. In all examined species except A. falcirostris and A. nasutus, there are one or more prominent spine larger than the others. The latter two species lack a single, more prominent, spine on the dorsal margin of the gillrakers, with all spines on the free upper edge of the gillraker similar in size (Menezes, 1969:61,74-75). Nevertheless, the latter spines in these species are also considerably larger than the ones on the surface of the gill rakers. In view of the current uncertainty about the relationships of Acestrorhynchus, it is not possible to hypothesize whether the condition of the spines on the first ceratobranchial gill-rakers in Acestrorhynchus provides any information about the polarity of the character states observed within cynodontines. Ontogenetic information, is however, available for this character. In juveniles of both Cynodon (AMNH 32485SW, 35 mm SL) and Rhaphiodon (USNM 231549 41.7-50.1 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 of the gill-raker. No juvenile of any Hydrolycus species was available for the examination of this character, but the condition observed in Rhaphiodon provide 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, being hypothesized as derived.

In cladogram 1 this character is most parsimoniously hypothesized as synapomorphic for the clade formed by Hydrolycus n. sp. 2, H. scomberoides, H. armatus (synapomorphy 50) with an independent origin in Rhaphiodon (autapomorphy

71). In cladogram 2 this character is hypothesized as a synapomorphy for the clade formed by Hydrolycus n. sp. 2, H. scomberoides, H. armatus and Rhaphiodon (synapomorphy 76).

41. 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 to be primitive members of the order (Fink and Fink, 1981). Unelaborated hypobranchials have been hypothesized to be 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 H_1 is much shorter and less curved than in cynodontines. In Serrasalmus, in addition, the process is dorso-ventrally flattened with no associated articular surface.

The condition observed in cynodontines is unique within characiforms and hypothesized as synapomorphic in cladogram 1 and 2 (synapomorphy 9).

42. 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 the latter 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, 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 (synapomorphy 10) with its further enlargement in Cynodon, hypothesized as a synapomorphy for the genus in cladogram 1 and 2 (synapomorphy 40).

Anterior vertebrae

43. 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 26), 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 already present on the ventral surface of the first centrum.

In one specimen of Hydrolycus n. sp. 1 (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 in Cynodon but are much less developed than in the that genus. Weakly developed processes were observed also 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 Hydrolycus n. sp. 2, 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 the presence of well developed processes on the ventral surface of the first centrum in Cynodon species will be considered as indicative of the presence of these processes due to the lack of more specimens of Hydrolycus n. sp. 1 and Hydrolycus n. sp. 2 for examination of this feature. Examination of a larger number of 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 developed condition of these processes unique to Cynodon can be considered a synapomorphy for this genus in cladogram 1 and 2 (synapomorphy 44).

44. 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 to 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 a synapomorphy for the group in cladogram 1 and 2 (synapomorphy 17).

In all cynodontines the transverse processes of the second and third vertebrae contact each other in an interdigitating pattern which 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 45 and 47).

45. Second vertebra.

The second vertebra of cynodontines bears a lateral process designated as "transverse process" by Nelson (1949). This process is highly developed and slightly dorsoposteriorly oriented. It is bifurcated distally into two short processes that clasp the transverse process of the third neural arch (TP_2 in figs. 14-16).

The presence of a "transverse process" in the second centrum is not unique to cynodontines among examined characiforms. Such a process occurs in the erythrinids, ctenoluciids, Hepsetus, Heterocharacini, Gnathocharax, Roestes, Gilbertolus, and in some Acestrorhynchus species. However, in all these taxa the is process only slightly developed and 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 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 in cladograms 1 and 2 (synapomorphy 18).

The determination whether the short posterodorsal process on the second vertebra in outgroups is homologous to the process in cynodontines remains to be shown by a phylogenetic analysis including all the taxa involved.

46. Second vertebra.

The lateral process of the second vertebra (LP-C_2) 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 (e.g. Weitzman, 1962:36 for Brycon meeki).

Within cynodontines a number of differences from the generalized characiform condition is observed. Cynodon and Hydrolycus species (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 at its proximal end and then turns posteriorly at its distal portion. Ventrally, at its tip, the process possesses an articular surface for the attachment of ligamentous tissue connecting with the pectoral girdle. The posterolateral margin of the process ends in two short processes (figs. 14 and 15). Ligamentous tissue attaches to this 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 flat and posteriorly directed. The distal end of the process possesses an articular 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 as in the groups just mentioned, this articular 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 and 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 described for the remaining cynodontines. The condition in this latter species has been previously briefly described by Weitzman (1962:36) and illustrated by Nelson (1949:517). From a dorsal view there is a triangular-shaped flat sheet of bone extending laterally and posteriorly under the tripus. Ventrally it has a short process extending 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 hypothesized as synapomorphic in cladograms 1 and 2 (synapomorphy 19), with the conditions in H. scomberoides and Rhaphiodon vulpinus constituting autapomorphies for these two species autapomorphies 55 and 60, respectively).

47. Third vertebra.

All cynodontine species except Hydrolycus n. sp. 1 possess a lateral process on the third vertebra (LP-C_3) 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 the third vertebra. In Rhaphiodon, Hydrolycus n. sp. 2, and H. armatus, the process is relatively well developed, originating just ventral to the lateral portion of the "transverse process" of the second vertebra. The process 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 n. sp. 2, and H. armatus and seems to originate posteriorly to the portion of the "transverse process" of the second vertebra that is in contact with the transverse process of the third neural arch (fig. 14), rather than ventral to it as in Rhaphiodon, Hydrolycus n. sp. 2, and H. armatus. This process is lacking as a separate element in the two cleared and stained specimens of Hydrolycus n. sp. 1. Among examined characiform outgroups, only Ctenolucius has a process similar to that described for Rhaphiodon, Hydrolycus n. sp. 2, and H. armatus.

In cladogram 1 of cynodontine intrarelationships, the explanations for the distribution of this character are equivocal under any type of optimization used. In cladogram 2, a ventral origin of the lateral process of the third centrum is hypothesized as derived for Rhaphiodon, Hydrolycus n. sp. 2, H. armatus, and H. scomberoides, with a further modification to a posterior origin of such a process in the latter species. The condition in Cynodon is hypothesized as having originated independently from that in Hydrolycus scomberoides. It is my opinion that the ambiguity in the interpretation of the distribution of this character is partly a consequence of the poor understanding of the anatomy of this lateral process of the third vertebra. 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 n. sp. 1 to confirm the absence of the process from this species. It was not possible to carry out a more detailed study of this character 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 bifurcated process of the second vertebra with the processes of the third vertebra described under characters 45 and 47 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 the interdigitating 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 (specially H. armatus and Hydrolycus n. sp. 1) having a slightly more elongate process. Variation of this feature within cynodontines will not be taken into further consideration at this time because of the difficulty of establishing discrete units unambiguously to account for this variation.

48. Third vertebra.

The tripus (TR) 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 surface 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 the latter family, however, 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 5 below).

The anteriorly elongate blade portion of the tripus in Rhaphiodon vulpinus is unique among examined characiforms and hypothesized as autapomorphic for the species (autapomorphy 69).

49. Third vertebra.

The posterior section of the tripus that terminates in the transformator process is distinct in Rhaphiodon vulpinus from that in the remaining cynodontines and among characiform outgroups. In the typical characiform condition the transformation process of the tripus is a thin curved process continuous with the posterior portion of the tripus with no modifications at its median end (Fink and Fink, 1981:331). In Rhaphiodon vulpinus the posterior portion of the tripus extends posteriorly being almost horizontally aligned relative to the longitudinal axis of the body. At the region medial to the lateral portion of the fused fourth pleural rib plus parapophysis the tripus becomes a much thinner process, 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 (autapomorphy 70).

50. Fourth pleural rib + parapophysis.

The fused fourth pleural rib and parapophysis (PRP_4) in Cynodon and Rhaphiodon differ notably from those of Hydrolycus. In the latter genus the fused pleural rib and parapophysis extend laterally in a flat, thin dorsoventrally oriented process (fig. 15). This condition is similar to the condition observed in characiform outgroups and described and figured by Weitzman (1962:36, 68).

In Cynodon and Rhaphiodon the process is very enlarged, extending anteriorly and ventrally, and covering the posterolateral portion of the tripus (fig. 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 by Nelson (1949:500) for Rhaphiodon vulpinus 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 at the region of the articulation of the cleithrum and supracleithrum. In order to understand the type of connection between the elements of the Weberian apparatus and the pectoral girdle in cynodontines, a much more detailed study of these connections should be carried out in an attempt to isolate all 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 under cladogram 1 (synapomorphy 34). In cladogram 2 this feature is hypothesized as having independent origins in Rhaphiodon and Cynodon (synapomorphies 78 and 81).

51. 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 laterally and posteriorly with ligamentous attachments originating from both its dorsal and ventral surfaces (LP-C_4). Ligaments from the dorsal surface of the process of the fourth vertebra attach to a process extending anteriorly and laterally from the anterior 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 may sometimes has another process (see character 52 below).

Although modifications of the fourth and fifth vertebrae to form an articulation between these two elements is found in some of the examined outgroups, in none of them is the condition similar to 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 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 bend the head upward, studied 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 52 below), the presence of such an articulation in the remaining species may imply that they may demonstrate at least some degree of bending.

The type of articulation between the fourth and fifth vertebra in Cynodontines is unique among characiforms and hypothesized as synapomorphic in cladogram 1 and 2 (synapomorphy 20).

52. Articulation between fourth and fifth vertebrae.

The anteroventral portion of the fifth vertebra in cynodontines is laterally expanded, extending ventral to the lateral process of the fourth centrum that forms the articulation between the fourth and fifth vertebrae (fig. 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 (LP-C_5). The latter process is more evident in larger specimens, in which it is more pronounced laterally and extends more ventrally to the process of the fourth vertebra. In Hydrolycus scomberoides the process seems to be less pronounced than in the remaining cynodontines. It is 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. The difference in the degree of expansion of the ventral portion of the fifth centrum in H. scomberoides will not be coded as an additional condition of this character for cynodontines until more specimens are examined to check for the variation in the relative degree of development of this feature.

In Rhaphiodon vulpinus the ventral process of the fifth vertebra is further enlarged relative to 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 ventral process of the fifth vertebra is smaller than the other process of the fifth vertebra in the remaining cynodontines). The process is therefore more conspicuous when observed either from a ventral and/or lateral view (fig. 16) than in the remaining cynodontine species. The process 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 autapomorphic for this species (synapomorphies 21 and 61).

53. Pleural ribs.

The fifth and to a certain extent the sixth and seventh pleural ribs (PR) 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 not as conspicuous with some variation in different specimens. 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. The rib is slender along its entire length and possesses a very short medially directed process in its the dorsal portion which is, however, less developed than that in Rhaphiodon. The dorsoposterior process present in Rhaphiodon is absent from the remaining cynodontines. A process on the medial portion of the fifth rib also occur in some characiform outgroups (e.g., Gilbertolus, Roestes, Acestrorhynchus, Agoniates, Gnathocharax, and the Heterocharacini), and was described and figured by Roberts (1969:426, fig. 46,47) (see also Buckup (1991:226), and Lucena (1993:56) for distribution of this feature in characiforms) and they are similar to those of Cynodon and Hydrolycus. In all these taxa the rib is not conspicuously flat in its proximal half as in Rhaphiodon and is approximately the same length relative to 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 (synapomorphy 68).

54. 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 and 15). The enlargement of the parapophyses is greater in the anterior vertebrae gradually becoming less pronounced posteriorly.

The parapophyses of the vertebrae of 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 fossa 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 ventrally and slightly anteriorly, reaching the anteroventral portion of the vertebra but not extending beyond it to reach the anterior vertebra. The fossa 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 fossa with which the parapophyses of the anterior precaudal vertebrae articulates is 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 a component of Alestes (Brewster, 1986:192), a genus in which there is no 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 in cladograms 1 and 2 (synapomorphy 22).

55. Baudelot's ligament.

In all cynodontine species (except Rhaphiodon vulpinus, see comments below) 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 the basioccipital and the posteriorly to the pectoral girdle. Rhaphiodon seems to have a somewhat different condition from the remaining cynodontines. In Rhaphiodon Baudelot's ligament is not as well developed as in the remaining cynodontines 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.

An attachment of Baudelot's ligament with the lateral process of the second vertebra is most parsimoniously hypothesized as synapomorphic for the Cynodontinae, with a secondary loss of the attachment in Rhaphiodon vulpinus (synapomorphy 29). The condition in the latter species is interpreted as an autapomorphy (autapomorphy 63).

Pectoral girdle

56. Postcleithrum 2.

A lack of postcleithrum 2 is common to all cynodontines. This feature is not, however, unique to this group of fishes among characiforms. 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 siluroids (Fink and Fink, 1980:334), and it was interpreted by those authors as specializations which have evolved independently in these various lineages.

In view of the current evidence for a close relationship between the Cynodontinae and Gilbertolus plus Roestes, (see previous section), 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 hypothesized as an independent loss in Gilbertolus and the Cynodontinae. A future analysis of the relationships of Gnathocharax might also show that the lack of postcleithrum 2 is phylogenetically informative at a higher level of universality.

57. 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).

The same arguments discussed above under character 56 for the lack of postcleithrum 2 apply for the lack of postcleithrum 3, with the exception that in this case, the latter feature could be unequivocally hypothesized as derived feature for a clade formed by Roestes, Gilbertolus and the Cynodontinae. Also, a future analysis of the relationships of Gnathocharax might also show that the lack of postcleithrum 3 is phylogenetically informative at a higher level of universality.

58. Coracoid.

The posterodorsal portion of the coracoid in all cynodontine species is perforated by a very large foramen (CORF in figs. 17 and 18). This foramen is 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 (1930:23) 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. Therefore, the presence of the foramen per se cannot be used to hypothesize relationships between Gilbertolus and cynodontines. 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 (fig.19) is intermediate in size between that of Gilbertolus and cynodontines, and that in the remaining characiforms in which the foramen is present. However, there is also variation in the size of the foramen in the remaining characiform outgroups, rendering the delimitation of discrete states to account for the variation of this feature problematic. Therefore, only the highly developed size of the foramen in cynodontines and Gilbertolus versus the presence or absence of this condition in the remaining outgroups was considered in the present analysis.

The possibility of a close relationship between Gilbertolus and Roestes to the Cynodontinae was discussed in the previous section. If further studies substantiate this hypothesis the highly developed foramen on the posterodorsal portion of the coracoid might be hypothesized as synapomorphic for these taxa with a further modification in Roestes or, alternatively as independently originated in Gilbertolus and cynodontines.

59. Coracoid.

Cynodontines possess relatively enlarged coracoids (COR), a feature shared with a number of other characiforms such as the Gasteropelecidae, Triportheus, Agoniates, and Gnathocharax. Weitzman (1954:230) and Roberts (1969:426) mentioned the presence of enlarged coracoids, in addition, in Pseudocorynopoma and Clupeacharax, respectively. The shape of the expanded coracoids differs in all the examined characiforms outgroups that possess them. The coracoids more developed in the Gasteropelecidae and Triportheus than in the Cynodontinae. In the former family they are fan-shaped with a rounded ventral profile (Weitzman, 1954); whereas in Triportheus and Gnathocharax the expansion of the coracoids takes place mainly at 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 the use of that feature to propose relationships. These authors also proposed an independent origin of this feature 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 potential sister groups to the Cynodontinae (e.g. Roestes, Gilbertolus, Acestrorhynchus) do not have expanded coracoids. The presence of this feature in cynodontines is hypothesized as synapomorphic for the group (synapomorphy 25).

60. Coracoid.

In all cynodontines the coracoids are closely applied to each other along their entire midline. In Cynodon species and Rhaphiodon vulpinus the coracoids are fused to each other along a large portion of the area of contact between the contralateral coracoids, with the region of the fusion between the two ossifications being densely corrugated. All attempts to separate the left and right elements, resulted in breaking of one coracoid around the corrugated area. Fusion between the contralateral coracoids and the corrugated pattern is present in juveniles of Rhaphiodon vulpinus 50 mm in SL (USNM 231549), 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 coracoid located ventral to the dorsal margin of the ossification that forms the ventral edge of the large foramen formed by the cleithrum and coracoid is formed only by one coracoid. This feature was observed in all examined Rhaphiodon vulpinus specimens prepared for osteological examination 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 was discussed above.

The condition of partially fused and corrugated coracoids described for Rhaphiodon and Cynodon is hypothesized as a synapomorphy for these genera under the scheme of cynodontine relationships derived from cladogram 1 (synapomorphy 35). In cladogram 2, this feature is most parsimoniously explained as independent acquisitions in Cynodon and Rhaphiodon (synapomorphies 79 and 82).

61. Mesocoracoid.

The mesocoracoid (MEC) in cynodontines is very enlarged relative to the condition in the majority of examined outgroups. The typical condition of the mesocoracoid in characiforms (fig. 19) 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 its articular surfaces with the surrounding bones are broader (fig. 17). The mesocoracoid 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 of 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 midlength 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 midlength 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. In view of the current evidence of a possible sister group relationship between the Cynodontinae and Gilbertolus plus Roestes (Howes, 1976; Lucena and Menezes, in prep.; see also discussion in the previous section), two alternative, equally parsimonious, explanations are possible for the presence of the enlarged mesocoracoid in these taxa. In the first, the presence of the enlarged mesocoracoid would be a synapomorphy for a clade formed by the Cynodontinae, Gilbertolus and Roestes, with a reversal to a condition of a small mesocoracoid in the latter genus. In the second alternative the presence of the enlarged mesocoracoid would be considered as independently derived in the Cynodontinae and Gilbertolus. Under any other hypothesis of sister group relationships to the Cynodontinae, the hypothesis of an independent origin of this feature would be the most parsimonious explanation for the origin of this feature in the Cynodontinae.

62. Scapula (SCA)

The scapular foramen in the Cynodontinae is almost entirely exposed when examined from a lateral view of the pectoral girdle (fig. 18). In the majority of examined characiform outgroups the scapular foramen is covered laterally by the cleithrum and not exposed in lateral view (fig. 20). The condition observed in cynodontines seems to be the result of a posterior shifting in the articulation of the scapula and the mesocoracoid relative to the medial surface of the cleithrum. In cynodontines the enlarged mesocoracoid articulates with the cleithrum in the middle of the medial surface of this latter 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 lie more anterior in the medial surface of the cleithrum (Roberts, 1969: figs. 48-52; Weitzman 1962: fig. 19) with the consequence that the scapular foramen is completely covered by the posterior portion of the cleithrum. As a consequence of the posterior shifting of the articulation of the scapula with the cleithrum, the insertion of the pectoral girdle is also shifted posteriorly so that a vertical through the base of the unbranched pectoral-fin ray is situated posterior to a vertical 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. In the Gasteropelecidae also the scapular foramen is exposed from a lateral view. However, in the latter family the pectoral girdle show 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. The condition of the articulation of the scapula and mesocoracoid in the Cynodontinae and Gilbertolus can be explained by the same two alternative hypothesis discussed under character 58 and 59 above.

63. Cleithrum (CL).

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 (fig. 20). Lucena's (1993) study on the family Characidae provided some support for a hypothesis about the relationships of Agoniates. As discussed in the previous section, 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), 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. The condition in cynodontines is therefore, hypothesized as synapomorphic (synapomorphy 24).

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 of the anterior tip of the cleithrum 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 (autapomorphy 64).

The cleithrum shows some differences among cynodontines, the most pronounced occurring at the posteroventral margin of this ossification. 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 there is a continuous margin along the entire posterior and ventral margins of the cleithrum, with the posteroventral margin of the cleithrum not being fused to and continuous with the scapula. The condition in

Hydrolycus and Cynodon is that widespread for characiforms, with the condition in Rhaphiodon occurring only in gasteropelecids, among examined outgroups, and hypothesized as independently acquired in these two taxa.

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 being 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 due to variation of this portion of the ossification in the examined cynodontines. As a consequence this feature was not proposed as an additional character of phylogenetic interest at this time.

Pelvic fins

64. Pelvic fin insertion.

The pelvic fin in Hydrolycus scomberoides is distinctly dorsal of the ventral profile of the abdomen. As a consequence the ventral profile of the abdomen is continuous, with no 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 insertion of the pelvic fins, this being 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 far from the ventral profile of the abdomen in Hydrolycus scomberoides is hypothesized as autapomorphic for this species (autapomorphy 58).

Anal fin

65. 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 within 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, Lucena and Menezes, in prep.). The presence of 60 or more branched anal-fin rays is unique to Cynodon among characiforms and hypothesized as derived (synapomorphy 45).

Caudal fin

66. Hypurals (HYP)

Cynodon and Hydrolycus species have hypurals 1-3 fused into a single unit which is articulated with the $PU_1 + U_1$ (fig. 21). In Rhaphiodon 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 towards $PU_1 + U_1$. 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 96.8 mm SL (BMNH 1935.6.4:33-39). Hypurals 1-3 are already fused in a specimen of Cynodon gibbus 102.4 mm SL (LACM 43295-89).

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 seems 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 although they closely contact along at their 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.

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.

The uncertainty in the understanding the phylogenetic relationships of the Cynodontinae complicates the interpretation of the fusion of hypurals 1-3 in cynodontines and Acestrorhynchus. However, since hypurals 1-3 are fused only in some Acestorhychus species, and the evidence toward a closer relationship of Gilbertolus and Roestes to the Cynodontinae, the fusion of hypurals 1-3 is hypothesized as independent events in the Cynodontinae and some of Acestrorhynchus species (detailed above). According to the most parsimonious hypothesis arrived at in the present study fusion of hypurals 1-3 is synapomorphic for cynodontines (synapomorphy 28) with the fused hypurals 2-3, and hypural 1 as a separate element in Rhaphiodon vulpinus representing partial reversal to the primitive condition of the hypural fan, and therefore, autapomorphic (autapomorphy

65).

Intermuscular bones

67. 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 (synapomorphy 16).

68. Myorhabdoi.

Rhaphiodon vulpinus possesses highly developed myorhabdoi (name coined by 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 specially developed in the anterodorsal portion of the body, where they are almost horizontally aligned. At 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) describe 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) mentions 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 gasteropelecids some of the intermuscular bones attach also 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 discarded by Weitzman (1954: 230). The latter author 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 (autapomorphy 66). Lesiuk and Lindsey (1979) hypothesize that the epaxial musculature pulling on this bundle of intermuscular bones, described by them as forming a cablelike tendon (labeled as 'T" in their figure 2), provides the force to rotate the head upwards.

Miscellaneous

69. Scales.

The scales of Hydrolycus scomberoides are characterized by serrations on their exposed portion (fig. 22) (as opposed to cycloid scales in the remaining cynodontine species). This kind of scales was termed spinoid scales by Roberts (1993:62). The term "ctenoid scales" usually employed for any kind of serration present on scales was restricted by that author to scales in which the spines along the margin of the scale 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 that author the various characiforms that possess spinoid scales have been hypothesized as being 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 resembles 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 hypothesized as autapomorphic for H. scomberoides (autapomorphy 57).

70. Gasbladder.

The gasbladder of Rhaphiodon vulpinus was described in detail and figured by Nelson (1949) and Lesiuk and Lindsey (1979). The most distinctive feature of the gasbladder in this species is the presence of a series of fringe-like appendices along the length of the lateral surface of the posterior chamber. These appendices extend laterally into the body wall into which they penetrate. 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 (1979) noted the proximity between the appendices in the swim bladder to the pores scales on the lateral-line.

Cynodon and Hydrolycus species lack appendices in the gas bladder. The condition in Rhaphiodon vulpinus is unique among characiforms and hypothesized autapomorphic (autapomorphy 67).

Comments on functional morphology

The anatomical peculiarities presented by cynodontines have raised interest about their functional morphology. Certain aspects of these anatomical peculiarities, mainly those related to feeding behavior, have been addressed by a few authors using different approaches. The studies of Howes (1976) and Lesiuk and Lindsey (1978), were based on observations of preserved and fresh specimens of Rhaphiodon vulpinus. Lesiuk and Lindsey (1978) provide comments on the possible function of some osteological modifications in Rhaphiodon that may be involved in the feeding mechanism, and Howes (1976) proposed the action of the muscles involved. More recently, Alfaro and Westneat (1996) studied prey capture in Rhaphiodon and Hydrolycus by means of kinematic and electromyographic analysis, and high speed cinematography.

All these studies confirmed the ability of these fish to raise the neurocranium upwards as much as approximately 40 degrees. The lower jaw also opens ventrally producing a large gape, enabling the fish to accommodate large prey. The enlarged dentary canines are used to pierce and hold the prey. The enlarged pectoral fin is also part of the feeding system providing rapid anterodorsal thrust for prey capture. According to Alfaro and Westneat (1996) cynodontines utilize a rapid strike to capture the prey, with capture being initiated from below the prey item. These authors propose that suction feeding may also be utilized to catch the prey as suggested by timing of kinematic and neuromuscular activity patterns. A more recent study (Arendt, 1997) of aquarium kept specimens described in detail the feeding action of Hydrolycus scomberoides and Rhaphiodon vulpinus.

Modifications of the Weberian apparatus and the swim bladder relative to these structures in other characiforms was described for Rhaphiodon vulpinus by Nelson

(1949). Modifications of the Weberian apparatus are also described in the present study for the remaining cynodontine species. A study of the function of the Weberian apparatus in cynodontines has not, however, been the subject of a detailed study. Nelson (1949) suggested that a possible function for the appendices present in the swim bladder of Rhaphiodon vulpinus was a refinement of the reception of vibrations associated with the overall functioning of the swim bladder and Weberian apparatus in hearing and hydrostatic perception. That author stressed the need for research using modern equipment in order to ascertain their true function. Lesiuk and Lindsey (1978) noted the proximity between the appendices of the swim bladder and latter line and proposed a number of possible functions for this proximity.

PHYLOGENETIC RESULTS

Analysis of cynodontine relationships, using Roestes and Gilbertolus as outgroups with multistate characters left unordered, resulted in two equally most parsimonious cladograms (79 steps; CI= 0.87; RI= 0.88; RC=0.77). The two cladograms (designated as cladogram 1 and cladogram 2, figs.23 and 24, respectively), differ in placement of Rhaphiodon vulpinus. In cladogram 1 Rhaphiodon is hypothesized as the sister group to Cynodon, together these form the sister group to the clade formed by the remaining four cynodontines. In cladogram 2 Rhaphiodon is hypothesized as the sister group to the clade formed by Hydrolycus n. sp. 2, H. armatus, and H. scomberoides. Hydrolycus n. sp. 1 is the sister group to the latter clade in cladogram 2, and Cynodon is the sister group to the clade formed by Rhaphiodon and Hydrolycus species.

Seven characters (3, 18, 19, 22, 23, 50, and 60) support a hypothesis of a sister-group relationship between Rhaphiodon and Cynodon in cladogram 1, with four of these characters (3, 19, 50, and 60) representing unique synapomorphies for this clade. Characters 18 and 22 are hypothesized as having independent origin in Hydrolycus scomberoides. Character 23 is ambiguous at this node under any kind of optimization.

The clade formed by Hydrolycus species and hypothesized in cladogram 1 to be the sister group to the clade formed by Cynodon and Rhaphiodon is supported by five characters (4, 12, 16, 27, and 29), with only character 4 representing a unique synapomorphy. Although character 16 is also hypothesized as a unique synapomorphy for this clade, it was coded as "?" for Rhaphiodon in the matrix, and was optimized as

"0" in cladogram 1, therefore, rendering it apomorphic for Hydrolycus. Characters 12, 27, and 29, are all optimization dependent and can be equally parsimoniously hypothesized as a synapomorphy for Hydrolycus species with an independent origin in Rhaphiodon, or, alternatively they can be considered synapomorphic for the Cynodontinae with a reversal to the primitive condition in Cynodon.

Three characters (8, 40, and 47) support the hypothesis of a sister group relationship between Rhaphiodon and the clade formed by Hydrolycus n. sp. 2, H. armatus, and H. scomberoides in cladogram 2, with only character 40 representing a unique derived feature for the clade. Character 8 is coded as "?" in the outgroup and it is optimized as "1" in the analysis, therefore, rendering the character synapomorphic for this clade. In cladogram 1, character 8 is ambiguous under any kind of optimization. Character 47 is a multistate character, and state 1 is hypothesized as a synapomorphy for the clade formed by Rhaphiodon and Hydrolycus n. sp. 2, H. armatus, and H. scomberoides in cladogram 2, with state 2 representing a further autapomorphic modification in H. scomberoides that is independently acquired in Cynodon. Hydrolycus n. sp. 1 has a condition coded as "0", the same for the outgroups. This character is ambiguous under any kind of optimization in cladogram 1.

The clade formed by Rhaphiodon and all Hydrolycus species, in cladogram 2, is supported by six characters (4, 12, 13, 16, 27, 29,) four of which (4, 12, 27, and 29) constitute unique synapomorphies. Character 13 is coded as "?" in the outgroup, and the results of the analysis allow for one of the possible optimizations of this character to be an additional synapomorphy for the clade formed by Rhaphiodon and Hydrolycus species. However, the alternative hypothesis in which the other state of character 13 is hypothesized as synapomorphic for Cynodon is equally parsimonious. Character 16 coded as "?" in Rhaphiodon is optimized as "1" rendering it synapomorphic for this clade.

While in cladogram 1 a close relationship between Rhaphiodon and Cynodon is supported by four unique synapomorphies, in cladogram 2 the relationship of Rhaphiodon to the clade formed by Hydrolycus n. sp. 2, H. armatus, and H. scomberoides is supported by only one unique synapomorphy. On the other hand in cladogram 1 only one unique synapomorphy supports the clade formed by Hydrolycus species and in cladogram 2 the addition of Rhaphiodon to the clade formed by Hydrolycus species, is supported by four unique synapomorphies.

Of the three non-unique characters supporting the relationships of Rhaphiodon with Cynodon in cladogram 1, two of them also have independent origins in H. scomberoides (characters 18 and 22), with the third (23) being ambiguous. Of the two non-unique characters supporting the relationships of Rhaphiodon to the clade formed by Hydrolycus n. sp. 2, H. armatus, and H. scomberoides, character 8 is coded as "?" in the outgroup and 47 is, as discussed in "Character description and analysis" section, poorly understood at the present time. As a test to see the influence of the latter two characters in determining the final most parsimonious cladograms, the analysis was performed excluding these characters one at a time and then, both at the same time. In all three cases the analyses resulted in only one most parsimonious cladogram equal to cladogram 1.

Character 8 seems worthy of closer examination. In cladogram 2, state "1" of the character is assigned to the outgroup by the program, and therefore, state "0" is optimized as a synapomorphy for Rhaphiodon, Hydrolycus n. sp. 2, H. armatus, and H. scomberoides. However, assigning either state "1" or "0" to the outgroup is inappropriate since the character is inapplicable to these taxa (see Platnick at al., 1991 for a discussion on the implications of missing entries in cladistic analysis). It is possible that information from some other source (e.g. ontogeny) might prove useful in determining the polarity of this character. In the case in which this additional source of information assigns state "0" as primitive state then cladogram 1 will be the outcome of the analysis. Alternatively, if state "1" is hypothesized as the primitive state than this character will not be decisive, and two cladograms (1 and 2) will result from the analysis. The ambiguous nature of character 8, is one of the sources of the conflicts observed in the results of the analysis, i.e. only cladogram 1 results from the analysis in which character 8 is excluded, with two cladograms resulting when character 8 is included in the analysis with the outgroup coded as "?". It should be emphasized that, had character 8 not been ambiguous, or had it not been discovered and included in the analysis, the program would have generated only a single most parsimonious, fully resolved cladogram, and the fact that the data would be very sensitive to even minor changes might have gone unnoticed.

As mentioned above, character 40 is the only character that unambiguously relates Rhaphiodon to Hydrolycus n. sp. 2, H. armatus, and H. scomberoides. This character was previously coded the same way as character 8, discussed above, with "?" assigned to the outgroup. Additional evidence (i.e. ontogenetic, see "Character description and analysis" section) assigned state "0" as primitive for this character and when this information is added into the analysis the result is two equally parsimonious cladograms equal to cladogram 1 and 2. In this case resolving the ambiguity of character 40 did not eliminate the conflict between the two alternative hypothesis provided by cladogram 1 and 2. If state 1 had been assigned as the primitive state than the analysis would have resulted in only one most parsimonious cladogram, equal to cladogram 1.

Characters 7 and 13 were also coded as "?" in the outgroups, however, when they are excluded from the matrix one at a time or both at the same time, the analysis always resulted in both cladograms 1 and 2. The states coded as "?" in the outgroups, allow for different optimizations for each of the characters in the ingroup (i.e. state "1" can be the primitive state, or alternatively state "0" can be primitive), and therefore, a large number of combinations can be tested separately and the results compared. A number of different combinations (but not all) was tried in the present study and the results vary from either two equally parsimonious cladograms (cladogram 1 and 2), or only cladogram 1. Excluding all characters coded as "?" in the outgroups resulted in one most parsimonious cladogram equal to cladogram 1.

In summary, the data as presented are not completely decisive in fully resolving the relationships of Rhaphiodon. The source of the conflicts may be partially explained by the ambiguity present in a few characters. This ambiguity might be resolved with additional evidence, but depending on how they are resolved, the conflicts between the hypotheses of cynodontine relationships can still persist (e.g. see discussion of character 40 above). In the latter case, however, one of the causes of the conflict (i.e. ambiguity) has been eliminated, reducing the number of variables that have to be accounted for when evaluating the results of the analysis.

When the outgroup is changed to Acestrorhynchus, there is no change in the results. Two equally most parsimonious cladograms with the same topologies of cladograms 1 and 2 are obtained. There are a few differences in character coding between the outgroups used (see Table 1). Acestrorhynchus is coded as "?" for characters 12, 21, and 22 (coded as 0 in Roestes and Gilbertolus). Characters 56, 58, 61, and 62 are coded as "0" in Acestrorhynchus (coded as "0" in Roestes and "1" in Gilbertolus). Characters 9, 23, and 39 are coded as "1" in Acestrorhynchus (coded as "0" in Roestes and Gilbertolus). Characters 57 and 66 are coded as "0&1" in Acestrorhynchus and as "1" and "0" respectively, in Roestes and Gilbertolus). These changes do not seem to have a major effect in the resulting cladograms. The tests that were performed in the analysis using Roestes and Gilbertolus as outgroups arrived at the same results when the outgroup was changed to Acestrorhynchus (e.g., excluding character 8 yield to a single most parsimonious cladogram equal to cladogram 1, the same with character 47, see above). Therefore, it seems that in this case the ambiguity of these characters are also playing a role in the results. Excluding only characters 12, 21, and 22 (characters coded as "?" in the analysis using Acestrorhynchus as the outgroup, with unambiguous states assigned in the analysis using Roestes and Gilbertolus as outgroups) did not affect the results and both cladograms 1 and 2 were obtained.

When Acestrorhynchus, Roestes, and Gilbertolus were simultaneously used as outgroups, the analysis resulted in a single most parsimonious cladogram equal to cladogram 1. Removing characters, 7, 8,and 13 (characters coded as "?" in all outgroup taxa) one at a time and then all at the same time did not affect the results. When Roestes, Gilbertolus, the Heterocharacini and Gnathocharax were used as outgroups the analysis resulted in two equally most parsimonious cladograms equal to cladograms 1 and 2. The few differences in character coding in these taxa, relative to Gilbertolus and Roestes are in character 9 coded as "1" in Lonchogenys ("0" in the remaining outgroup taxa), character 24 coded as "0" in Hoplocharax ("1" in the remaining outgroups); and characters 56, 57, and 59 coded as "1" in Gnathocharax (with Gilbertolus also coded as "1" for characters 56 and 57 and "0" in the remaining outgroups). The various tests carried out with taxa coded as "?" (described above) arrived at the same results as when performed using only Roestes and Gilbertolus as outgroups.

The changing of outgroups did not, as may be concluded from the discussion above, have a major impact in the outcoming results. This is not surprising considering that there are no considerable differences in the coding of the characters in the various outgroup taxa, with some of those occurring in characters that did not have an significant influence in determining the differences in the two resulting cladograms, and with those coded as "?" in one outgroup, being coded "?" in all the remaining outgroups. The fact that when Acestrorhynchus, Roestes, and Gilbertolus are simultaneously used as outgroups, the analysis results in only one cladogram as compared to two cladograms when they are separately used as outgroups may imply that the addition of outgroups at a more inclusive level may help solve some of the conflicts in the two resulting hypothesis. Evidence for that will come from additional studies focusing on the analysis of relationships at a higher level of universality (see "Relationships of the Cynodontinae with other Characiforms").

When characters 3, 42, and 52 were ordered with the remaining multistate characters left unordered, the analysis resulted in only a single most parsimonious cladogram, equal to cladogram 1. In order to see whether the change of the results were due to a specific character, each of characters 3, 42, and 52 was ordered individually, with the others left unordered. The change in the number of resulting cladograms occurs if only character 3 is ordered, with both cladograms 1 and 2 resulting from the analysis in which either 42 or 52 are ordered.

Three clades remained unchanged in the two equally most parsimonious cladograms that resulted from all the analyses. Some of the characters supporting each of these nodes have changed from one hypothesis to the other due to differences in optimization, but most of the characters supporting these clades constitute unique synapomorphies.

The first clade is formed by Hydrolycus n. sp. 2 and H. armatus and it is supported by characters 1 and 21 (state "1") in both cladograms. The second clade formed by the two species just mentioned and H. scomberoides, is supported in both cladograms by three unique characters, 5, 11, and 36. In cladogram 1 characters 16 and 40 constitute additional synapomorphies for the clade, with character 40 being homoplastic in Rhaphiodon. Character 16 was coded as "?" in the latter genus and it was optimized as "0" by the program (see discussion above). The third clade is formed by Cynodon n. sp. 1 and C. gibbus and is supported by 9 unique synapomorphies:

characters 3 (state "2"), 10, 17, 23 (state "2"), 25, 33, 42 (state "2"), 43, and 65. Characters 12, 27, and 29, in cladogram 1 may by hypothesized as reversals for this clade, therefore constituting three additional synapomorphies, however, these characters are ambiguous in this cladogram with an equally parsimonious optimization which interprets the characters as an apomorphy for Hydrolycus with an independent origin in Rhaphiodon. Character 13 is coded as "?" in the outgroups, and one of its possible optimizations considers it to be a reversal in Cynodon; however, all other possible optimizations are equally parsimonious. In cladogram 2, characters 3, 50, 60, 77, and 78 constitute additional apomorphies for Cynodon with an independent origin in Rhaphiodon.

The monophyly of the Cynodontinae was corroborated by 27 unique derived features. Six additional ambiguous features have been identified for this clade, with three of them being optimization dependent (i.e. can also be hypothesized as independently originated in less inclusive clades within the Cynodontinae, characters 27, 29 and 12) and the remaining being dependent on which taxa is the sister group to the Cynodontinae (characters 30, 35, and 39).

SYNAPOMORPHY LIST

The following synapomorphy list refers to the hypothesis presented in cladogram 1. Following this first list is an additional list discussing the synapomorphies for the clades in cladogram 2. Numbers in parentheses indicate character number in "Character description and analysis".

Cladogram 1:

Monophyly of the Cynodontinae:

1. Contact between antorbital and lateral margin of the lateral ethmoid (2).
2. Dorsal elongation of posterior portion of symplectic to fit into a groove in the medial face of lower arm of the hyomadibula (28).
3. Mesopterygoid teeth (dependent on outgroup) (30).
4. Ectopterygoid teeth arranged in patch covering most or the entire surface of the ectopterygoid (31).
5. Attachment between the posterior portion of ectopterygoid and the anteroventral portion of metapterygoid (32).
6. Five branchiostegal rays on the ceratohyal (34).
7. Two branchiostegal rays on the posterior ceratohyal (outgroup dependent) (35).
8. Gillrakers on leading portion of first ceratobranchial all short, flattened, tooth-bearing bony plates (outgroup dependent) (39).

9. Anterior portion of first hypobranchial anteroventrally prolonged, into a prong-shaped process extending from the ventrolateral margin of its main body 9 (41).
10. Anterior portion of first ceratobranchial curved dorsally, forming an angle relative to the longitudinal axis of the remaining portion of that ossification (42).
11. Presence of two processes on ventral portion of the mesethmoid (6).
12. Articulation between anterior portion of palatine and posterior portion of vomer (14).
13. Shallow depression on lateral surface of vomer for the articulation of maxilla (15).
14. Great expansion of dilatator fossa to cover most of the dorsal surface of frontal (20).
15. Lack of shelf of frontal at the posterodorsal edge of orbit (partially reversed in Hydrolycus n. sp. 1 and H. armatus) (21).
16. Medial branch of one of anterior epineurals contacting the neural complex of Weberian apparatus (67).
17. Lack of a direct contact between the neural complex of Weberian apparatus and posterior margin of neurocranium (44).
18. Transverse process of the second vertebra bifurcated at its distal end into two short processes that clasp the transverse process of third centrum (45).
19. Highly modified lateral process of second vertebra (further modified in Hydrolycus scomberoides and Rhaphiodon vulpinus) (46).
20. Possession of a process on fourth centrum attached by ligaments to a process on anterior portion of fifth centrum (51).

21. Second process on ventral portion of fifth vertebra extending ventral to process of fourth vertebra (52).

22. Elongate parapophyses of precaudal vertebrae, with paraphysis of one vertebra extending anteriorly and articulating with the vertebra anterior to it (54).

23. Portion of basioccipital that articulates with the vertebral column flared posteriorly forming a receptacle for first centrum (26).

24. Anterior portion of cleithrum ending in a vertically elongate process that articulates with anterior portion of the enlarged coracoids (63).

25. Enlarged coracoids (59).

26. Foramen for the 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 the foramen (37).

27. Teeth horizontally aligned in mandibular replacement trench, with tips of replacement teeth projecting posteriorly (25).

28. Hypurals 1-3 fused into a single unit (with hypurals 2-3 fused in Rhaphiodon vulpinus) (66).

29. Attachment of Baudelot's ligament to the ventral portion of the enlarged lateral process of the second vertebra (secondarily reversed in Rhaphiodon) (55).

Ambiguous features for this clade:

A_1. Process on the shaft of hyomandibula (secondarily reversed in Cynodon) (27) (synapomorphy 71 in cladogram 2).

A_2. metapterygoid teeth (secondary reversed in Cynodon) (29) (synapomorphy 72 in cladogram 2).

A_3. Crest on ventral surface of vomer (secondarily reversed in Cynodon) (12) (synapomorphy 73 in cladogram 2)..

Monophyly of Rhaphiodon and Cynodon:

30. Process, extending medially, on posterior margin of antorbital (3) (synapomorphy 77 and 83 in cladogram 2) .
31. Lateral-ethmoid-orbitosphenoid contact (independently acquired in Hydrolycus scomberoides) (18) (J_1 and K_1 in cladogram 2).
32. Reduced dorsal portion of sphenotic spine, no longer contacting ventrolateral margin of frontal (independently acquired in Hydrolycus scomberoides) (22) (J_2 and K_2 in cladogram 2).
33. Ventrally expanded shelf of frontal, continuous to anterior portion of sphenotics (23).
34. Enlargement of fourth pleural rib + parapophysis (50) (synapomorphies 77 and 80 in cladogram 2).
35. Fusion and corrugated pattern of coracoids (60) (synapomorphies 78 and 81 in cladogram 2).
36. Reduced distance between the orbitosphenoid and parasphenoid (19) (synapomorphies 79 and 83 in cladogram 2).

Monophyly of Cynodon:

37. Further medial elongation of posterior margin of antorbital (3) (synapomorphy 77 in cladogram 2).

38. Contact between anterior tip of ectopterygoid and posterior portion of mesethmoid (33).

39. Lack of a crest on ventral surface of vomer (as a secondary shift to the primitive condition) (12).

40. Further dorsal elongation of anterior portion of first ceratobranchial (42).

41. Posterior extension of triangular portion of ventral diverging lamella of mesethmoid reaching posteroventral margin of vomer (10).

42. Lack of a rhinosphenoid (17).

43. Lack of a dorsal posttemporal fossa, bordered by supraoccipital, parietal and epioccipital (25).

44. Processes on the ventral surface of first centrum (43).

45. Anal fin with 61 or more branched rays (65).

Ambiguous features for this clade:

B_1. Lack of a process on shaft of hyomandibula (as a shift to the primitive condition) (27).

B_2. Lack of metapterygoid teeth (as a shift to the primitive condition) (29).

B_3. Lack of contact of vomer with posterior portion of ventral processes of mesethmoid (independently acquired in Hydrolycus n. sp. 1 (derived condition of character, dependent on condition in outgroup, coded as missing entry) (8).

B_4. Lateral bony plates of vomer continuous to anterior portion of vomer (derived condition of character, dependent on condition in outgroup, coded as missing entry) (13).

B_5. Additional lateral process of third centrum having a posterior origin (see discussion in "Character description list and analysis") (47).

Monophyly of Hydrolycus:

46. Dorsoventral enlargement of mesethmoid spine being almost round in shape from a lateral view (4) (synapomorphy 72 in cladogram 2)..

Ambiguous features for this clade:

C_1. Process on shaft of hyomandibula (also present in Rhaphiodon) (27) (synapomorphy 71 in cladogram 2)..

C_2. Metapterygoid teeth (secondary reversed in Cynodon) (29) (synapomorphy 72 in cladogram 2)..

C_3. Crest on ventral surface of vomer (also present in Rhaphiodon) (12) (synapomorphy 73 in cladogram 2).

C_4 Ridge on lateral surface of vomer (16) (feature dependent on optimization in Rhaphiodon vulpinus coded as missing entry).

Monophyly of Hydrolycus n. sp. 2, H. armatus, and H. scomberoides:

47. Upturned mesethmoid spine, with anterodorsal surface of mesethmoid interrupted by a notch (5).

48. Posterior orientation of portion of lateral wing of mesethmoid where part of the ligamentous tissues from the maxilla attach (11).

49. Possession of highly enlarged dentary canines with their tips extending through the nasal opening when mouth is closed (36).

50. Spines on dorsal margin of gillrakers on first ceratobranchial not conspicuously larger than spines on lateral surface of gillraker (independently acquired in Rhaphiodon vulpinus (40) (synapomorphy 75 in cladogram 2)..

Monophyly of Hydrolycus n. sp. 2 and H. armatus:

51. Reduced fifth infraorbital, with a contact between fourth and sixth infraorbitals (1).

52. Reduced shelf of frontal bone at posterodorsal edge of orbit (as a partial secondary reacquisition of shelf lost at higher level, see 15 above). (21).

Autapomorphies of Hydrolycus scomberoides:

53. Lateral-ethmoid-orbitosphenoid contact (independently acquired in the clade formed by Rhaphiodon and Cynodon) (18).

54. Reduced dorsal portion of sphenotic spine, no longer contacting ventrolateral margin of frontal (independently acquired in the clade formed by Rhaphiodon and Cynodon) (22).

55. Anterior portion of the frontal shelf truncated at the midline of the orbit (23).

56. Dorsoventrally flat and laterally-directed lateral process of the second vertebra (46).

57. Serrations on exposed portion of scales (69).

58. Insertion of pelvic fins far from ventral profile of body (64).

59. Reduction of ventral lamella of mesethmoid (9).

Ambiguous features for this species:

D_1. Additional lateral process of the third centrum having a posterior origin (see discussion in "Character description list and analysis") (42).

Autapomorphies for <u>Hydrolycus</u> n. sp. 1:

60. Lack of an anterior shelf of frontal (23).

Ambiguous features for this species:

E_1. Lack of contact between vomer and posterior portion of ventral processes of mesethmoid (independently acquired in <u>Cynodon</u> (derived condition of character, dependent on condition in outgroup, coded as missing entry) (8).

E_2. Ventral processes of mesethmoid anteriorly-directed (derived condition of character, dependent on condition in outgroup, coded as missing entry) (7).

E_3. Lack of additional lateral process in third centrum (as a secondary shift to plesiomorphic condition) (see discussion in "Character description list and analysis") (47).

Autapomorphies of Rhaphiodon vulpinus:

61. Highly modified lateral process of second vertebra (46).

62. Further enlargement of ventral process of fifth vertebra (52).

63. Lack of attachment of Baudelot's ligament to lateral process of second vertebra (as a secondary reversal to the primitive condition) (55).

64. Lack of an anterodorsal projection at anterior portion of cleithrum (63).

65. Fusion of hypurals 2-3 (as a partial reversal of fusion of hypural 1-3 at higher level) (66).

66. Presence of myorhabdoi (68).

67. Presence of fringe-like appendices along lateral surface of the posterior chamber of gasbladder (70).

68. Highly modified fifth pleural rib (53).

69. Anterior elongation of blade-like portion of tripus (67).

70. Posterior portion of transformator process of tripus forming a 90° angle with its anterior portion, and ending in an enlarged rectangular bony plate (49).

71. Spines on dorsal margin of gillrakers on first ceratobranchial not conspicuously larger than spines on lateral surface of the gillraker (independently acquired in the clade formed by Hydrolycus n. sp. 2, H. armatus, H. scomberoides) (40) (synapomorphy 75 in cladogram 2).

Ambiguous features for this species:

F_1. Process on shaft of hyomandibula (also present in Hydrolycus) (27) (synapomorphy

71 in cladogram 2).

F_2. Metapterygoid teeth (also present in Hydrolycus (29) (synapomorphy 72 in cladogram 2).

F_3. Crest on ventral surface of vomer (also present in Hydrolycus) (12) (synapomorphy 73 in cladogram 2).

Cladogram 2:

Clades formed by the same species in cladogram 1 and 2 are supported by the same characters excepted as noted below. To avoid confusion synapomorphies are numbered sequentially from those in cladogram 1.

Monophyly of the Cynodontinae:

Ambiguous features for this clade:

G1. Lateral-ethmoid-orbitosphenoid contact (secondarily reversed to the primitive condition in Hydrolycus n. sp. 1 and the clade formed by Hydrolycus n. sp. 2 and H. armatus) (synapomorphy 31 in cladogram 1)

G2. Reduced dorsal portion of sphenotic spine, no longer contacting ventrolateral margin of frontal (secondarily reversed to the primitive condition in Hydrolycus n. sp. 1 and the clade formed by Hydrolycus n. sp. 2 and H. armatus (synapomorphy 32 in cladogram 1).

Monophyly of Rhaphiodon and Hydrolycus:

72. Process on shaft of hyomandibula (27) (A_1, C_1. and G_1 in cladogram 1).

73. Metapterygoid teeth (29) (A_2, C_2, and G_2 in cladogram 1).

74. Crest on ventral surface of vomer (12) (A_3, C_3, and G_3 in cladogram 1).

75. Dorsoventral enlargement of mesethmoid spine being almost round in shape from a lateral view (with a secondary reversal to the primitive condition in Rhaphiodon vulpinus (4) (synapomorphy 46 in cladogram 1).

Ambiguous features for this clade:

H_1. Lack of continuity of the lateral bony plates of vomer to anterior portion of vomer (derived condition of character dependent on condition in outgroup which was coded as missing entry) (13).

H_2. Ridge on the lateral surface of vomer (feature dependent on the optimization in Rhaphiodon vulpinus coded as missing entry) (16) (C_4 in cladogram 1).

Monophyly of Rhaphiodon and Hydrolycus n. sp. 2, H. armatus, and H. scomberoides :

76. Spines on dorsal margin of gillrakers on first ceratobranchial not conspicuously larger than spines on lateral surface of gillraker (40) (D_1 in cladogram 1).

Ambiguous features for this clade:

I_1. Contact between vomer and posterior portion of ventral processes of mesethmoid (derived condition of character, dependent on condition in outgroup, coded as missing entry) (8).

I_2. Additional lateral process of third centrum having a ventral origin (with further modification to a posterior origin in Hydrolycus scomberoides (see discussion in "Character description list and analysis") (47).

Monophyly of Cynodon:

77. Ventrally expanded frontal shelf with a curved margin (23).,

78. Presence of an enlarged process, extending medially, on posterior margin of antorbital (3) (synapomorphy 30 in cladogram 1).

79. Enlargement of fourth pleural rib + parapophysis (50) (independent origin in Rhaphiodon vulpinus) (synapomorphy 34 in cladogram 1).

80. Fusion and corrugated pattern of coracoids (60) (independent origin in Rhaphiodon vulpinus) (synapomorphy 35 in cladogram 1).

81. Short distance between orbitosphenoid and parasphenoid (19) (independently acquired in Rhaphiodon) (synapomorphy 36 in cladogram 1).

Ambiguous features for this clade:

K_1. Lateral-ethmoid-orbitosphenoid contact (independent acquisition in Rhaphiodon and Hydrolycus scomberoides) (synapomorphy 31 in cladogram 1)

K_2. Reduced dorsal portion of sphenotic spine, no longer contacting ventrolateral margin of frontal (independent acquisition in Hydrolycus n. sp. 1 and clade formed by

Hydrolycus n. sp. 2 and H. armatus (synapomorphy 32 in cladogram 1).

Autapomorphies for Rhaphiodon vulpinus:

82. Enlargement of fourth pleural rib + parapophysis (50) (independent origin in Cynodon) (synapomorphy 34 in cladogram 1).
83. Fusion and corrugated pattern of coracoids (60) (independent origin in Cynodon) (synapomorphy 35 in cladogram 1).
84. Process, extending medially, on posterior margin of antorbital (3) (synapomorphy 30 in cladogram 1).
85. Short distance between orbitosphenoid and parasphenoid (19) (independently acquired in Cynodon) (synapomorphy 36 in cladogram 1).
86. Straight margin of ventrally expanded frontal shelf (23).

Ambiguous features for this species:

L_1. Pointed mesethmoid spine (as a secondary reversal to the primitive condition) (4).

L_2. Lateral-ethmoid-orbitosphenoid contact (independent acquisition in Cynodon and Hydrolycus scomberoides) (synapomorphy 31 in cladogram 1)

Autapomorphies for Hydrolycus scomberoides:

Ambiguous features for this species:

M1. Lateral-ethmoid-orbitosphenoid contact (independent acquisition in Cynodon and Rhaphiodon) (synapomorphy 31 in cladogram 1).

CLASSIFICATION

The subfamily name Cynodontinae was created by Eigenmann (1907) to include Cynodon, Rhaphiodon, and Hydrolycus. Travassos (1946) created the name Rhaphiodontinae as a substitute for Cynodontinae, based on the argument that Cynodon was an objective synonym of Rhaphiodon. The nomenclatural problems regarding the genus names Cynodon and Rhaphiodon have been discussed by Toledo-Piza and Lazara (MS, see Appendix) as part of a petition sent to the Commission on Zoological Nomenclature in order to stabilize the usage of both Cynodon and Rhaphiodon. Rhaphiodontinae is herein considered a junior synonym of Cynodontinae.

The clade formed by Cynodon, Rhaphiodon, and Hydrolycus has also been assigned to various ranks depending on differing ideas about phylogenetic relationships of the group to other characiforms. The group was raised to familial rank, Cynodontidae, by Greenwood et al. (1966) and lowered to tribal rank, Cynodontini, by Howes (1976) (in which he also included the genus Roestes in addition to the three genera mentioned above). Cynodontidae and Cynodontinae are the most commonly used names to refer to the group. Available evidence (discussed in a previous section) provides support for a close relationship between cynodontines and members of the Characidae (Lucena, 1993). Therefore, the use of the name Cynodontinae for the clade formed by Cynodon, Rhaphiodon, and Hydrolycus seems to be the most appropriate name to be used at this time.

Names for suprageneric groupings within the Cynodontinae were proposed by

Fowler (1958:10), at the tribal rank: Cynodonidi and Hydrolycidi. That author refers to the sub-family name as Cynodoninae. The correct names are Cynodontinae for the latter name and Cynodontini for the tribe name as proposed by him, following the rules for the formation of names in the International Code of Zoological Nomenclature (ICZN: Article 29i).

At the generic level, Cynodon, previously a monotypic genus (C. gibbus), has now a second species assigned to it (Cynodon n. sp. 1). Rhaphiodon is monotypic, with its single species R. vulpinus. Four species are herein assigned to the genus Hydrolycus. Two of them were previously described (H. scomberoides and H. armatus) and together with Hydrolycus n. sp. 2 form a well supported group (see discussion in "Phylogenetic results"). The third new cynodontine species (referred to as Hydrolycus n, sp. 1) was conservatively assigned to the genus Hydrolycus in the present study. The reasons for this action are discussed below.

The phylogenetic analysis undertaken in the present study resulted in two equally most parsimonious cladograms (cladogram 1 and 2, respectively figs. 23 and 24). In cladogram 1 the assignment of the new species to the genus Hydrolycus is consistent with the hypothesized scheme of relationships. In cladogram 2 Hydrolycus n. sp. 1 is the sister group to the clade formed by Rhaphiodon and the remaining Hydrolycus species. According to such scheme of relationships, assigning Hydrolycus n. sp. 1 to the latter genus would render it paraphyletic.

As discussed under the "Phylogenetic results" section, at this time there is no way to resolve the conflicts generated by the two alternative hypothesis of cynodontine relationships. Moreover, the source of the conflicts was shown to be at least partially explained by ambiguity present in the data (i.e. in the form of missing entries in the outgroup taxa). Future studies may be able to resolve the conflict about the phylogenetic placement of Rhaphiodon. In case additional evidence corroborates the hypothesis of a sister group relationship between Rhaphiodon and Cynodon, then all four Hydrolycus species will constitute a clade and no further nomenclatural action would need to be taken. In case the hypothesis of a clade formed by Rhaphiodon, Hydrolycus n. sp. 2, H. armatus, and H. scomberoides is corroborated, than the creation of a new genus name for the species herein assigned to Hydrolycus n. sp. 1 will be justifiable (the alternative option of synonymizing Hydrolycus with Rhaphiodon - the latter being the senior name - is not suggested due to the long history of usage of both names).

Another alternative is the creation of a new genus for the species herein assigned to Hydrolycus n. sp. 1, at this time. This would be in agreement with both hypotheses of cynodontine relationships generated by the data. I do not believe it to be the appropriate action to be taken at this time, because it is an attempt to resolve a conflict generated by lack of decisive data rather than being based on a well corroborated hypothesis. Thus, it would conceal rather than reveal the real nature of the problem and future studies might prove it was unnecessary.

Subfamily CYNODONTINAE Eigenmann, 1907

Rhaphiodontinae: Travassos, 1946:136.

Cynodoninae: Fowler, 1958:10.

Cynodontidae: Greenwood et al. 1966:395

Cynodontini: Howes, 1976:206.

Diagnosis: The Cynodontinae are distinguished within characiforms by a series of derived features (see "Synapomorphy list"). Externally cynodontines can be readily diagnosed by their oblique mouth and a pair of highly developed dentary canines.

Key to Hydrolycus Müller and Troschel, Cynodon Agassiz, and Rhaphiodon Agassiz

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 to 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 to 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 the ICZN 1990:76)

Key to Species of Hydrolycus Müller and Troschel, 1844

1. Serrations present on the exposed field of scales in all specimens other than juveniles (under ~100 mm SL); base of pelvic fin distinctly dorsal of the ventral profile of the body; black spot at the base of the innermost pectoral-fin rays (Rio Amazonas and its tributaries above mouth of Rio Tapajós) . . H. scomberoides

- No serrations on the exposed field of scales; base of pelvic fin inserted at level of ventral profile of body; no black spot at the base of the innermost pectoral-fin rays 2

2. Anal-fin rays not covered by scales; 36 to 43 branched anal-fin rays; length of largest dentary canine 11.6 to 17.3 of HL; ground coloration of body and fins black (Rio Negro and upper Río Orinoco basins). . . . . Hydrolycus n. sp. 1

- Anal-fin rays covered by scales to approximately one half of their length; 27 to 37 branched anal-fin rays; length of largest dentary canine 18.2 to 29.0 of HL; ground coloration of body silvery or yellowish-tan 3

3. Perforated lateral-line scales 121 to 154; 30 to 42 rows of scales between lateral-line and dorsal fin origin; rows of scales between lateral line and anal-fin origin; and 32 to 41 rows of scales around caudal peduncle; very conspicuous black spot on adipose fin; dark pigmentation on distal portions of caudal- and anal-fin rays forming well defined band (eastern portions of Rio Amazonas basin including Rio Negro drainage and tributaries below its mouth, Rio Tocantins and Rio Capim drainages, Essequibo River in Guyana, and Río Orinoco basin) . H. armatus

- Perforated lateral-line scales 102 to 119; 20 to 29 rows of scales between lateral-line and dorsal-fin origin; 14 to 22 rows of scales between lateral line and anal-fin origin; and 25 to 33 rows of scales around caudal peduncle; dark pigmentation on adipose fin not forming conspicuous spot, dark pigmentation on distal portions of caudal and anal fins diffuse (eastern portions of Rio Amazonas basin including Rio Negro drainage and tributaries below its mouth, Rio Tocantins and Rio Capim drainges, Essequibo River drainage in Guyana, and upper portions of Río Orinoco basin) . . . . Hydrolycus n. sp. 2

Hydrolycus scomberoides (Cuvier, 1819)

Figures 22-30; tables 2-5.

Hydrocynus scomberoides Cuvier, 1816:168 (named in a footnote to the description with generic name all in lower case; indicated as a new species originating in Brazil, see "Remarks" for details concerning date of publication).

Hydrocyon scomberoides: Cuvier, 1819:357, pl. 27, fig. 2 (more extensive description with generic name all in lower case, first letter of generic name capitalized in figure; specimen presumably the same as in Cuvier, 1816).

Cynodon scomberoides: Valenciennes, 1849:324 (in part: only dry specimen, not specimens in alcohol; for remaining specimens see under synonymy of Hydrolycus n. sp. 2 and H. armatus; description). Kner, 1859:45, not fig.16b (in part: not dry specimens [not examined]; Brazil; description). Steindachner, 1883:15 (description, Río Amazonas, Iquitos).

Cynodon pectoralis Günther, 1866:30 (original description, type locality: upper Amazon); 1868:247 (Peru, Xeberos [=Jeberos]). Boulenger, 1898:426 (Brazil, Rio Juruá). Pellegrin, 1909:150 (Brazil, Teffé [=Tefé]).

Cynodon scombroides: (species name misspelled): (not Peters, 1877:472; see synonymy of Hydrolycus armatus).

Hydrolycus pectoralis: Cope, 1878:688 (Peru, Nauta). Eigenmann and Eigenmann, 1891:59 (list of species). Fowler, 1906:466 (Peru: description); 1945:156, fig. 48 (literature compilation); 1950:330 (literature compilation, references in part).

Eigennman and Ogle, 1907:31 (Brazil; Bolivia; [Río Mamoré]). Eigenmann, 1910:444 (literature compilation). Starks, 1913:20 (Brazil; mouth of Rio Madeira: description). LaMonte, 1935:7 (Brazil, Rio Purus). Schultz, 1944:272 (in key to species of genus); 1950:46 (Brazil, Bolivia and Peru: brief description). Howes, 1976:205, fig. 1B (specimens at the Natural History Museum, London). Ortega and Vari, 1986:10 (in list of freshwater fishes of Peru). Goulding et al., 1988:123 (Brazil, Rio Negro: listed).

Hydrolycus scomberoides: Eigenmann and Eigenmann, 1891:59 (in part: only Peru, Iquitos, not in Río Orinoco, Guiana, Rio Capin [=Capim], Araguay [=Araguaia]; list of species). Fowler, 1939: 267 (Peru, Contamana: description); 1945:157 (literature compilation: geographic distribution information in part: only Peru and Amazonas, not Río Orinoco, Guayanas [=Guianas], Paraguay); 1950:331, not fig. 389 (literature compilation, references in part; common name). Bertin, 1948:8 (type depository, in part: only MNHN A 8659: holotype of *Hydrocyon scomberoides* Cuvier, 1816, not specimens designated as paratypes, for the latter see synonymy of *Hydrolycus* n. sp. 2 and *H*. *armatus*). Lauzanne and Loubens, 1985:55, fig. 51 (in key to characiform species of Rio Mamoré, Bolivia). Géry, 1986:62 (*Cynodon pectoralis* Günther, 1866 proposed as a synonym of *C*. *scomberoides*). Ortega and Vari, 1986:10 (in list of freshwater fishes of Peru). Goulding et al., 1988:127 (Brazil, Rio Negro: listed). International Commission of Zoological Nomenclature, 1990:Opinion 1581 (name *scomberoides* Cuvier, 1819, confirmed as type species of *Hydrolycus*, and placed on the Official List of Specific names in Zoology). (not Howes, 1976:205; Schultz, 1944:272; Mendes dos Santos et al., 1984:39; Taphorn, 1992:433; Taphorn and Lilyestrom, 1984:70: see under synonymy of Hydrolycus armatus).

Hydrolicus scomberoides: (genus name misspelled): Eigenmann and Allen, 1942:273 (Peru and Brazil). Campos, 1945:474, fig. 6 (Brazil, Rio Amazonas: redescription). Fowler, 1975:279 (listed, common name). Barriga, 1991:30 (in list of freshwater fishes of Ecuador: common name). (not Mago-Leccia, 1970:263; Cala, 1977:8; Novoa, 1982:275, fig. 11; Lasso, 1988:132; see under synonymy of Hydrolycus armatus).

Hydrolicus pectoralis: (genus name misspelled): Eigenmann and Allen, 1942:273 (literature compilation). Campos, 1945:475 (literature compilation). Fowler, 1975:279 (listed). Barriga, 1991:30 (in list of freshwater fishes of Ecuador, common name).

Hydrolichus scomberoides: (genus name misspelled):(not Machado-Allison, 1987:134; see under synonymy of Hydrolycus armatus)

Hydrolycus sp.: Padovani, 1988:98 (Peru).

Following is a list of references that cite the species scomberoides and pectoralis that, could not be unambiguously assigned to any Hydrolycus species because I was unable to examine the specimen, that were the basis for the report which did not provide sufficient information for species determination. In most cases, the species in question would be identified as either H. armatus, or Hydrolycus n. sp. 2 and in one case (H. cf pectoralis , see below) the species in question is either Hydrolycus n. sp 1 or Hydrolycus n. sp. 2.

Hydrolycus scomberoides: Müller and Troschel, 1844:93 (Guiana [=Guyana]); 1845:19 (identical to Müller and Troschel, 1844). Eigenmann and Eigenmann, 1891:59 (in part: Río Orinoco, Guiana, Rio Capin [=Capim], Araguay [=Araguaia]; list of species). Fowler, 1906:466 (brief description); 1950:331 (literature compilation; references in part only). Eigenmann, 1910:444 (literature compilation); 1912 (specimen in the Berlin Museum specimen collected on Gluck Island). Di Caporiacco, 1935:66 (Guiana: Essequibo River: Rockstone). Géry and Planquette, 1982:75 (Guyane [=French Guyana]; list of species). Ferreira, 1984:356 (Brazil, Pará, Rio Curuá-Una). Le Bail et al., 1984:11 (Guyane [=French Guyana]; key to species). Ferreira et al., 1988:344 (Brazil, Roraima, Rio Mucajaí). Goulding et al., 1988:127 (Brazil, Amazonas, Rio Negro);

Cynodon scombroides: Goeldi, 1898:484 (Brazil, Pará, Rio Capim). Regan, 1905:190 (based on Wallace's drawings of fishes from the Rio Negro).

Cynodon scomberoides: Puyo, 1949:139 (Guyane Française [=French Guyana].

Hydrolicus cf. pectoralis: Royero et al., 1992:51 (Venezuela, Río Atabapo).

Diagnosis: Hydrolycus scomberoides can be readily distinguished from all other cynodontines by at least 3 features: 1) the presence of serrations on the exposed portion of the scales (fig. 22) in specimens at least 95 mm SL (two smaller specimens, 45.0 and

67.8 mm SL, had this feature absent); 2) the presence of a small black spot on the base of the innermost pectoral-fin rays (faint in some specimens) (figs. 25 and 26); and 3) base of pelvic fins distinctly dorsal of the ventral profile of the body (figs. 25 and 27).

Description: Body compressed laterally, deep anteriorly, greatest body depth at vertical situated between pectoral and pelvic fins, relative depth decreasing posteriorly. Dorsal profile of head slightly concave at interorbital region. Predorsal body profile curved, forming slight to pronounced hump at vertical through posterior border of orbit; straight and slightly posteroventrally slanted at dorsal-fin base, proportionally less slanted 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 specimens under 68 mm dorsal profile of body slightly concave from tip of snout to vertical through pelvic-fin origin (fig. 26); then slightly convex to dorsal-fin origin. Ventral profile of body conspicuously convex to anal-fin origin; straight and posterodorsally slanted at anal-fin base, then straight to origin of ventralmost procurrent caudal-fin ray. Ventral surface of body with median keel from isthmus to anus; keel anteriorly supported by expanded coracoids.

Posterior margin of preopercle ventral to point where it contacts ventral portion of opercle, posterior margin of interopercle, and to a lesser extent posterior margin of subopercle and fifth branchiostegal ray serrate; serrations more pronounced in larger individuals, not present in specimens smaller than 70 mm SL. Infraorbitals and opercular bones, with laterosensory canal system highly branched; canals more pronounced in larger individuals.

Mouth obliquely aligned relatively to horizontal axis of body, with upper jaw very long relative to head length; posterior tip of maxilla extending posteriorly slightly beyond vertical through posterior tip of second infraorbital; relatively more elongate in smaller individuals. Third infraorbital not in contact with preopercle posteriorly and ventrally. Snout shorter than orbital diameter. 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. Premaxillary dentition delimited by one canine anteriorly and one canine, similar in size, posteriorly. One large conical tooth located anterior to posteriormost canine and separated from it by usually 2 (sometimes 1 or 3) small conical teeth. Several small conical teeth lie between anteriormost canine and large conical tooth, decreasing in size toward the middle portion of the tooth row. Anterior portion of maxilla with large conical teeth interspaced among smaller ones; teeth gradually get smaller and more similar in size posteriorly. Dentary with one very well developed canine, extending through snout when mouth is closed, tip of canine reaching nostrils anteriorly. Canine larger relative to head length in larger specimens. One very small conical tooth anterior to largest canine. Canines posterior to largest canine separated by small conical teeth and varying in size, third largest; teeth gradually decrease in size posteriorly. Teeth on ectopterygoid, mesopterygoid, and metapterygoid (latter observed in one of two cleared and stained specimens) small and conical.

Scales with distinctly serrated posterior margin and serrae over exposed field.

Scales of specimens under 70 mm SL with smooth posterior margin and exposed field. Scales smaller on dorsal and ventral portions of body. Scales along pre-dorsal midline arranged in somewhat irregular rows. Scales below lateral line obliquely arranged. Lateral-line scales larger than those of rest of body, with many divergent branches of the lateral-line canal. Divergent branches more pronounced in larger individuals; no branches of the lateral-line canal present in specimen of 45 mm SL; specimen of 68 mm SL with ventrally directed branch of lateral-line canal, beginning of dorsally directed branch observed in some scales, branches pronounced in 95 mm SL specimen. Number of scales along lateral-line series 93-106. Lateral-line canal extending to posterior tip of middle caudal-fin rays.

Dorsal-fin rays ii,10 (rarely 9, 11 in only one specimen). Dorsal-fin origin notably in front of vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 17th or 18th (rarely 19th) vertebrae (table 3). Distal margin of dorsal fin slightly convex. Specimens over 95 mm SL with diminute scales on dorsal-fin base, extending onto membrane between fin rays about one fifth length of middle rays, to less extent on remaining rays. Anal-fin rays iii (rarely iv), 39-47. First anal-fin pterygiophore inserting behind hemal spine of 26th or 27th vertebrae (table 3). Distal margin of anal fin straight. Anal fin almost entirely covered with scales in specimens over 95 mm SL. Pectoral-fin rays i,15-19, pointed distally. Posterior tip of longest pectoral-fin ray extends to, or not quite to, vertical through dorsal-fin origin, and reaches vertical through tip of longest pelvic-fin ray. Pelvic-fin rays i,8 (rarely 9, 7 in only one specimen). Pelvic fin pointed distally, with first and second branched rays longest. Base of pelvic fin inserted distinctly dorsal of ventral profile of abdomen. Caudal fin rounded, covered with scales for at least two-thirds of length of the rays in specimens over 70 mm SL.

Vertebrae: 48(2), 49(18), 50(22), 51(3).

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 on tip of lower jaw. Specimens lacking guanine with yellowish-tan ground coloration on sides of body and head, slightly darker dorsally. Slight dark pigmentation on anterior region of body dorsal to pectoral fin, and on opercular region. Specimens show varying degrees of guanine retention. A few specimens (MZUSP 32616 - 1 specimen; MZUSP 32093 - 2 specimens) 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 of 45 and 68 mm SL having light-tan ground body coloration with tip of lower jaw and ventral margin of dentary covered by dark chromatophores.

Spot of dark pigmentation on posteriormost portion of supracleithrum. Very small dark spot at base of innermost pectoral-fin ray (faint and, therefore, difficult to observe in many specimens).

Specimens retaining pigmentation on fins with dorsal fin dusky and distal half of pelvic fins and dorsal portion of pectoral fins (specially unbranched pectoral-fin ray) covered with dark chromatophores. Distal half of anal fin with band of dark chromatophores. Caudal fin dusky from base to midline of fin-rays, pigmentation less intense toward distal portion of fin-rays. Adipose fin with very conspicuous spot of dark pigmentation. Distal profile of adipose fin hyaline.

Geographic distribution: Rio Amazonas and its tributaries above mouth of Rio Tapajós (fig. 28). Taphorn (1992) reports a cynodontine species with ctenoid scales in the Río Apure system in the Río Orinoco system of Venezuela. Specimens from this area and other portions of the Río Orinoco system were examined, but H. scomberoides was not found in that river drainage. The three other species of Hydrolycus occur in the Río Orinoco system, and the number of anal-fin rays in the form reported by Taphorn (1992) agree with those in both Hydrolycus n. sp. 2 and H. armatus.

Remarks: Under Opinion 1581 of the International Commission of Zoological Nomenclature (1990:76) the name scomberoides Cuvier, 1819 was placed on the Official list of specific Names in Zoology. As a consequence, 1819 is the official date of the publication of the species name and not Cuvier (1816)(see synonymy list above).

As is obvious from the synonymy lists of H. scomberoides, H. armatus, Hydrolycus n. sp. 1, and Hydrolycus n. sp. 2 there has been significant confusion in the usage of the names associated with these forms. Géry (1986) and Géry and Mahnert (1988) resolved part of the confusion by showing that H. scomberoides (Cuvier, 1819) and H. pectoralis (Günther, 1866) apply to the same form and should, therefore, be treated as synonyms. They also pointed out that the specimen identified as H. scomberoides by Müller and Troschel (1844) at the time they established the genus Hydrolycus was misidentified (it is actually either H. armatus or Hydrolycus n. sp. 2, see discussion under "remarks" of the former species accounts). In addition, they demonstrated that Valenciennes (1849) based his redescription of H. scomberoides (Cuvier, 1819) on 4 specimens, 3 of which belong to different species (Hydrolycus n. sp. 2 and H. armatus). All available specimens pertinent to the above discussion, in particular the holotypes of Hydrocynus scomberoides Cuvier, 1816 (fig. 29) and Cynodon pectoralis Günther, 1866 (fig. 30) were examined in the present study. The former is a dry specimen, this accounting for some of the variation observed in a few morphometric characters, especially those related to body depth (table 4). The remaining morphometric characters showed no, or very little, variation between the two specimens. The few meristic characters that could be accurately taken in the holotype of Hydrocyon scomberoides showed no difference relative to the type of Cynodon pectoralis (table 5). Günther (1866), distinguished the latter species from Hydrolycus scomberoides based on the number of anal-fin rays and proportional pectoral-fin length, two features that could not be examined on the holotype of Hydrocyon scomberoides Cuvier, 1819, due to the poor condition of this specimen. However, examination of a large number of specimens showed that it is not possible to unambiguously distinguish different forms based on these features. Hydrolycus pectoralis is, therefore, considered a junior subjective synonym of H. scomberoides, this being in agreement with the conclusions of Géry (1986) and Géry and Mahnert (1988).

Material examined: 183 specimens (59, 45.0-284):

Type material: Hydrocyon scomberoides Cuvier, 1819, holotype: MNHN A8659 (211.0 mm SL, dry specimen), Brazil; Cynodon pectoralis Günther, 1866, holotype: BMNH 1866.2.15.22 (1, 145.5 mm SL), upper Amazon.

Other material examined: **BOLIVIA**. *El Beni*: AMNH 40048 (mixed lot) (2, 190.0-240.0) Río Baures, above mouth, 6 km SW Costa Marques, Brazil; MNHN 1989 1458 (3, 161.0-168.0) Trinidad, Río Mocovi; USNM 5686 (1, 184.0) Río Mamoré; UMMZ 204857 (5, 217.0-257.0) Río Baurés, 2 km above mouth; *Santa Cruz*: AMNH 77538 (1, 142.5) Río Mamoré, ca. 2 km N of Boca Chapare. **BRAZIL**. *Acre*: AMNH 12542* mixed lot (1, 203.0); USNM 94669 (1, 161.0) Vicinity of Rio Macaua, tributary of Río Iaco, which is a tributary of Rio Purus, near Sena Madureira; *Amazonas*: BMNH 1893.4.24:29 (1, 210.0); BMNH 1929.11.18:4 (1, 160.0); MNHN 4542 (1, 156.0) Manaus; NMW 57109 (1) Barra do Rio Negro (=Manaus); CAS 154740 (1, 184.0); CAS 70317 (1, 241.0) market at Manaus; USNM 229153 (1, 137.0) near Manaus, Camaleão, Ilha da Marchantaria; MZUSP 6144 (1) Rio Negro, above Manaus; MZUSP 6195 (3) Igarapé Jaraqui, left margin of Rio Negro, above Manaus; MZUSP 32620 (2) Rio Negro, Anavilhanas; MZUSP 32616 (8, 168.0-200.0) Rio Branco, Marará; MZUSP 6014 (2); MZUSP 6379 (3, 192.0-270.0); Lago Beruri, Rio Purus; MZUSP 27337 (1) mouth of Rio Purus, Rio Solimões, District of Coari; MZUSP 6320 (2, 154.0-166.0) Lago Castro, mouth of Rio Purus; BMNH 1927.2.2:4-6 * (3, 156.0-229.0) Rio Solimões - Rio Tonantins; MZUSP 24937 (3, 182.0-254.0) Lago Janauacá and surroundings, Rio Solimões; MZUSP 27338 (3) mouth of Rio Içá, Rio Solimões; USNM 163777 (1, 168.0)

Porto América, mouth of Rio Içá, from lagoon on island; BMNH 1925.10.28:125-127 (3, 200.0-238.0) Manacapuru, Rio Solimões; USNM 310692 (1, 172.0) Rio Solimões, near Tefé, Cayman Station; MZUSP 36094 (1) channel at Lago Amanã, mouth of Rio Japurá; BMNH 1897.12.1:182-183 (2, 137.6-201.0) Rio Juruá; MNHN 1909 0155 (1, 160.0) Rio Tefé; CAS 12077 (1, 178.0) Rio Madeira at its mouth into Rio Amazonas; MZUSP 23434 (1) Igarapé Tomé, Ati-Paraná, NW of Fonte Boa; MZUSP 6098 (2) Lago Puraquequara, mouth of Rio Puraquequara; MZUSP 7639 (1, 252.0) mouth of Lago José Açu, Pairintins; *Pará*: CAS 70318 (2, 200.0-209.0), CAS 163589 (1, 141.0) market at Santarém; CAS 70321 (1, 205.0), CAS 70316 (1, 210.0), CAS 70321 (1, 205.0) Santarém river; MZUSP 47982 (1) Rio Trombetas, Cuminá; MZUSP 47983 (23, 190.0-237.0) Rio Trombetas, 20 km above its mouth; *Rondônia*: MZUSP 13899-13901 (3, 235.0-273.0), MZUSP 32609 (2); Rio Machado, Lago do Paraíso; MZUSP 14010 (1, 249.0) Rio Machado, Lago do Cururu; MZUSP 32093 (32, 140.0-257.0) Rio Madeira, Calama; MZUSP 32610 (1) Rio Madeira, Cachoeira do Teotônio; MZUSP 3122 (2) Amazonas and Pará; NMW 57107 (3) Amazonem Strom (=Rio Amazonas); NMW 68728 (1, 224.0) Bananeira (=Rio Bananeira ?); MNHN 1909 0317 (1, 150.0); USNM 39402 (1) Brazil. **ECUADOR.** *Napo*: FMNH 103381 (2, 255.0-274.0) Río Tiputini, near mouth in Río Napo and Quebradas; FMNH 103383 (2, 203.2) Río Aguarico at destacamento Zancudo and mouth of Quebrada Zancudo Cocha; FMNH 103385 (1, 252.0) Quebrada Zancudo Cocha, about 1 km from mouth in Río Aguarico. PERU. *Loreto:* CAS 159463 (1, 156.0), CAS 134790 (1, 179.0 mm SL) Río Ampiyacu, near Pebas; CAS 134791 (1, 67.8) Caño del Chancho, near Pebas; USNM 124882 (1, 181.0), USNM 124946 (1, 204.0) Río Ampiyacu; BMNH 1867.6.13.39 (1, 191.0) Xeberos (=Jeberos); CAS 79262 (7, 148.0-261.0), NMW 69447 (1, 152.0) Iquitos; MZUSP 15222 (1, 180.0); MZUSP 15223 (1, 167.0) Cocha Aguajal, Iquitos; CAS 15729 (1, 250.0) Gosulimacocha, cutoff channel of the Río Morona; CAS 70319 (2, 165.0-166.0) sandbars of Río Ucayali near Orellana; CAS 70323 (1, 181.0) Lago Sanango, large cutoff lake connected with Río Huallaga by a narrow channel, above Yurimaguas; MZUSP 26379 (1, 123.0) Supaycocha (?), Jenaro Herrera; USNM 167774 (1, 219.0) Lago Cashiboya; *Amazonas*: LACM 39947-17 (1, 284.0) Quebrada Pastazillo, tributary to Río Santiago; LACM 41738-3 (1, 220.0) Río Marañon; *Ucayali*: MZUSP 26177 (5, 95.3-134.3) Río Ucayali, Bagazán; MZUSP 26727 (2, 144.0-156.0) Río Ucayali, Pucallpa.

Hydrolycus n. sp. 1

Figures 31-36; tables 2-5

Cynodon pectoralis: Regan, 1905:189 (based on the drawings presented by A. R. Wallace to the Natural History Museum, London, fig. 31).

Diagnosis: The lack of scales covering the anal-fin rays in Hydrolycus n. sp. 1 distinguishes it from all its congeners greater than 95 mm SL (for H. scomberoides) and at least 130 mm SL for Hydrolycus n. sp. 2 and H. armatus. Hydrolycus n. sp. 1 can be further distinguished from Hydrolycus n. sp. 2 and H. armatus in the number of branched anal-fin rays (36-43 in Hydrolycus n. sp. 1 versus 27-37 in the latter two combined), lateral-line scales (89-99 versus 102-154, respectively). The lack of serrations on the exposed field of the scales and the placement of the pelvic fins at the level of the ventral profile of the abdomen further separates Hydrolycus n. sp. 1 from H. scomberoides.

The dentary canine is also much less developed in Hydrolycus n. sp. 1 relative to congeners being 11.6-17.3 of HL compared with 14.6-26.9 in the remaining species combined (fig 10). The lowest value observed in the latter range are four juveniles less than 69 mm SL. If only specimens of Hydrolycus n. sp. 1 within same size range as its congeners are compared (fig. 32), then there is no overlap in the relative length of the dentary canine (11.6-17.3 versus 18.5-26.9, respectively). The orbital diameter is larger in Hydrolycus n. sp. 1 (35.5-43.3 of HL versus 20.8-38.9 in the remaining species combined). The overlap in the range is limited to 5 specimens (out of a total of 171) of Hydrolycus n. sp. 2 (see discussion under geographic variation of this species account) that show proportionally larger orbital diameters.

The dark body and fin coloration (figs. 33-35) also separates Hydrolycus n. sp. 1 from its congeners which have silverish to yellowish-tan ground coloration with dark pigmentation covering only parts of the fins either forming bands, or more scatterred towards their distal portions.

Description: Body compressed laterally, deep anteriorly, greatest body depth at vertical situated slightly posterior to base of innermost pectoral-fin ray, depth decreasing posteriorly. Dorsal profile of head concave at interorbital region. Predorsal body profile strongly convex, forming pronounced hump at vertical through posterior margin of orbit; straight and slightly posteroventrally slanted at dorsal-fin base, proportionally less slanted and slightly convex 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. Ventral profile of body convex to anal-fin origin, convexity more pronounced anterior to pelvic-fin origin. Ventral profile of body with notch at vertical through base of innermost pelvic-fin ray, less convex from there to anal-fin origin and straight and posterodorsally slanted along anal-fin base, then straight to origin of ventralmost procurrent caudal-fin ray. Ventral surface of body with keel from isthmus to anus; keel interrupted at vertical through base of pelvic fin. Keel anteriorly supported by expanded coracoids, interrupted at vertical through base of innermost pelvic-fin ray, then continuing from that point to anus.

Posterior margin of opercular bones not serrated. Laterosensory canal system in infraorbitals and opercular bones highly branched; canals more pronounced 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; dorsal half of third infraorbital in contact posteriorly with preopercle in individuals larger than 115 mm SL. Snout shorter than orbital diameter. 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 portions; sometimes slightly smaller third canine located anterior to posteriormost canine and separated from it by usually 3 or 4 small conical teeth; several small conical teeth between anteriomost and middle canines. Premaxillary canines relatively smaller than in H. scomberoides. Anterior portion of maxilla with slightly enlarged conical teeth separated by smaller teeth; teeth gradually get smaller and more similar in size posteriorly. Dentary with well developed canine (relatively smaller than that of H. scomberoides), extending into snout when mouth is closed, tooth tip reaching nostrils anteriorly. One smaller canine, about half the size of the largest, located anteriorly; this followed by one very small conical tooth anteriorly. Canine teeth posterior to largest canine progressively decreasing in size posteriorly, anterior tooth about half size of largest canine. Canines separated by conical teeth varying in size; teeth gradually decrease in size posteriorly. Teeth on ectopterygoid, mesopterygoid, and metapterygoid small and conical.

Scales without distinct serrations. Scales small on dorsal portions of body, increasing in size laterally; largest scales on lateral region of body dorsal to pectoral fin; scales on region dorsal to anal fin small. Scales along pre-dorsal midline very small; arranged in somewhat irregular rows. Row of scales forming keel from posterior portion of coracoid to anus less rounded in shape than those of covering body. Scales below lateral line obliquely arranged. Lateral-line scales similar in size as those of lateral region of body, with many divergent branches in the lateral-line canal. Divergent branches more pronounced in larger individuals; absent in 70.5 mm SL specimen. Specimen of 114 mm SL with one ventrally and one dorsally directed branch of lateral-line canal, more branches present in larger specimens. Number of scales along lateral-line series 88-99. Lateral-line canal extending to posterior tip of longest middle caudal-fin ray.

Dorsal-fin rays ii,10. Dorsal-fin origin notably in front of vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 17th to 19th vertebrae (table 2). Distal margin of dorsal fin straight to somewhat concave. Diminute scales on base of dorsal fin. Anal-fin rays iii (rarely iv), 36-43. First anal-fin pterygiophore inserting behind hemal spine of 25th or 26th vertebrae (table 3). Distal margin of anal fin straight in smaller individuals, slightly falcate in larger ones. Scales restricted to base of fin rays, not covering anal-fin rays. Pectoral-fin rays i,16-18, fin pointed distally. Posterior tip of longest pectoral-fin ray extends to or not quite to vertical through dorsal-fin origin, and reaches vertical through midlength to tip of longest pelvic-fin ray. Pelvic-fin rays i,8 (rarely 9, 7, or 6 (latter in only one specimen)). Pelvic-fin pointed distally with first branched ray longest. Base of pelvic fin inserted at level of ventral profile of abdomen. Caudal fin forked, middle caudal-fin ray very elongate, its tip extending to or beyond vertical through tip of dorsalmost principal ray; distal margin of upper lobe somewhat concave, and that of lower lobe rounded. Scales covering only basal portion of caudal-fin rays, not extending onto branched portions.

Vertebrae: 50(9), 51(34), 52(2).

Color in alcohol: Overall ground body and head coloration much darker than that in remaining Hydrolycus species (figs. 33-35). Dorsal portion of body and head quite dark, blackish, in many individuals greyish to dark brown; getting lighter ventrally, more so in region anterior to pelvic fin. Lateral surface of body with dusky pattern predominating in few individuals; in others ground coloration tan with dark pigmentation homogeneously scattered. Dark pigmentation on head extending ventrally onto opercular region and first and second infraorbitals. Pigmentation on region of third and fourth infraorbitals less prominent and with some guanine retention in few individuals. Elongate blotch of dark pigmentation extending from posterior portion of posttemporal, covering most of supracleithrum and posterior portion of cleithrum. Scales at base of anal fin somewhat darker than remaining scales of this region of body, forming narrow, diffuse band. Band of dark pigmentation on ventral keel, extending from isthmus to pelvic fin; reaching to anus in few individuals. All fins dark; basal and dorsal portion of pectoral-fin rays usually darker than ventral. Adipose fin dusky.

One specimen (CAS 24685) without any dark pigmentation. Overall ground coloration of head and body light tan; blotch of dark pigmentation remaining on posterior portion of supracleithrum. All fins hyaline.

Geographic distribution: Rio Negro and its tributaries, Río Casiquiare, and upper portions of the Río Orinoco drainage (fig. 36).

Hydrolycus n. sp. 1 is found in sympatry with Hydrolycus n. sp. 2 throughout most of its distributional range. It is also sympatric with H. scomberoides in the lower portions of the Rio Branco, Brazil and with Hydrolycus armatus in the upper portions of the Río Orinoco drainage.

Remarks: A drawing of Hydrolycus n. sp. 1 is included in a series of pencil-sketches of fishes of the Rio Negro and its tributaries, made by A. R. Wallace, and currently deposited in the library of the Natural History Museum, London. The existence of these drawings was reported by Regan (1905) who identified the specimen as Cynodon pectoralis. The drawing (fig. 31) clearly is of Hydrolycus n. sp. 1.

A brief account on A. R. Wallace's life and work is found in Nelson (1995). Wallace spent four years in the Amazon (1848-1852) collecting and preparing sketches of animals and plants. He traveled mainly up the Rio Negro, to San Carlos and west into the Rio Uaupés. All his collection, except for a few notes and the sketches of palm trees and fishes, were lost when a fire destroyed the ship on her way back to England.

One specimen of Hydrolycus n. sp. 1 (CAS 24685) was subsequently collected in 1925. Additional specimens deposited at MZUSP, FMNH, MCNG were collected in 1979 and later.

Material examined: 120 specimens (70.5-335.0):

Type material: Holotype: **BRAZIL**. *Amazonas*: MZUSP 00000 (286.00) Rio Negro, Ilha de Tamaquaré; Parataypes: **BRAZIL**. *Amazonas*: MZUSP 32645 (34, 224.0-

288.0) all taken with holotype.

Other material examined: **BRAZIL.** *Amazonas*: MZUSP 32636 (2, 233.0-283.0); MZUSP 32637 (15, 214.0-267.0) Rio Arirará, near mouth; MZUSP 31276 (1, 239.0), MZUSP 32638 (6, 152.2-235.0) Rio Negro, below Daraá; MZUSP 31130 (1, 312.0), MZUSP 32641 (1, 281.0) Rio Negro, Cuiuni; MZUSP 32644 (21, 210.0-307.0), MZUSP 32646 (10, 222.0-297.0) Rio Negro, Ilha de Tamaquaré; MZUSP 32645 (35, 220.0-294.0) Rio Negro, Mandiquié; MZUSP 32634 (16, 213.0-297.0) Rio Marié, Lago Curiá-muru; MZUSP 32640 (1, 291.0) Rio Negro, São Pedro; MZUSP 32639 (1, 247.0) Rio Daraá, Cachoeira do Aracu; *Roraima*: MZUSP 32642 (1) Rio Branco, Xeriuni; CAS 24685 (1, 223.0) Rio Negro, sandbank at Cucui; **VENEZUELA.** *Amazonas*: FMNH 103660 (1, 113.8) Río Sipapo, 1 km above mouth of Río Cuao; FMNH 103662 (1, 128.9) Río Sipapo at rocks just above mouth in Río Cuao; FMNH 103663 (1, 237.0) mouth of small caño, ca 200 m above base camp on Río Cuao; FMNH 103661 (15, 279.0-322.0) Río Autana at Playa Cucurito in front of caño Cucurito; FMNH 104993 (1, 233.0) Río Ventuari at beach in front of small caño ca 5 hr. by falca above mouth in Río Orinoco; MCNG 21545 (1, 70.5) Río Guainia at Maroa; MCNG 21901 (1, 335.0) Caño Chimita, 3-15 km from confluence with Río Atacavi; MCNG 22349 (1, 139.9) Río Atabapo in San Fernando de Atabapo; MCNG 26207 (1, 271.0) Caño Guaripoco, tributary of Río Casiquiare, 2 km below El Porvenir; MBUCVV 6004 (1).

Hydrolycus armatus (Schomburgk, 1841)

Figures 37-40; tables 2,3,6-8

Hydrocyon ? armatus, 1841:249, pl. 25 (see also comments under "Remarks") (original description, type locality Guiana [=Guyana]).

Cynodon scomberoides: Valenciennes, 1849:324 (in part: only 1 of 2 specimens from the Essequibo River presented by Schomburgk; and specimen collected by Castelnau; for remaining specimens see synonymy of Hydrolycus n. sp. 2 and H. scomberoides). Günther, 1864:358 (in part: only specimen from River Capin (=Rio Capim), for other specimen see synonymy for Hydrolycus n. sp. 2). Kner, 1859:45 (in part: dry specimen only, for other specimens see synonymy for H. scomberoides).

Cynodon scombroides: (species name misspelled): Peters, 1877:472 (Venezuela, identification based on location, misidentification).

Hydrolycus scomberoides: Bertin, 1948:8 (type depository, in part: only MNHN A. 9854 (1 of 2) and MNHN A. 8549, for remaining specimens see synonymy for Hydrolycus n. sp. 2 and H. scomberoides). Lowe-McConnell, 1964:110 (in part: see also synonymy of Hydrolycus n. sp. 2). Misidentification: Howes, 1976:205 (BMNH 1972.7.27:46-49; dry skeletons not examined). Schultz, 1944:272 (Venezuela, Guarico); 1950:47 (Venezuela, Guarico). Mendes dos Santos et al., 1984:39 (Brazil, Rio Tocantins). Taphorn, 1992:433 (Venezuela, Apure). Taphorn and Lilyestrom, 1984:70 (Venezuela, Apure).

Hydrolicus scomberoides: (genus name misspelled): (misidentification) Cala, 1977:8 (Colombia, Río Orinoco basin, identification based on location). Lasso, 1988:132 (Venezuela, lower Río Orinoco, identification based on location).

Hydrolicus scomberoides: (genus name misspelled): (misidentification) Mago-Leccia, 1970:263 (Venezuela; figure). Novoa, 1982:275, fig. 11 (Venezuela, Río Orinoco).

Hydrolicus sp : (generic name misspelled): Roman, 1983:113 (photograph, Venezuela).

Hydrolichus scomberoides: (genus name misspelled) Machado-Allison, 1987:134 (Venezuela, los Llanos, misidentification).

Diagnosis: Hydrolycus armatus can be distinguished from its congeners by the number of lateral-line scales (121-154 versus 89-119, respectively), scales above the lateral line (30-42 versus 16-29, respectively), scale below the lateral line (24-38 versus 12-25, respectively), and scales around the caudal peduncle (32-41 versus 24-33, respectively). It is further separated from H. scomberoides in the lack of serrations on the exposed field of the scales and by the placement of the pelvic fins at the level of the ventral profile of the abdomen (fig 37, 38). It is, in turn, distinguished from Hydrolycus n. sp. 1 in the number of anal-fin rays (27-35 versus 36-43 in Hydrolycus n. sp. 1), and color pattern.

Among all its congeners, Hydrolycus armatus most closely resembles Hydrolycus n. sp. 2 from which it can be distinguished based on scale counts (see above and table 7). The two species also differ in coloration. Specimens of Hydrolycus armatus which retain coloration have the black spot in the adipose fin very conspicuous and well defined while in Hydrolycus n. sp. 2 the spot is rather diffuse (compare figures 37 and 43). The same difference occurs in the dark pigmentation pattern in the anal and caudal fins which forms a more defined black band in H. armatus and it is somewhat diffuse in Hydrolycus n. sp. 2. Figures 38 and 41 show photographs of specimens shortly after collection, prior to preservation. In these specimens the differences in color pattern are more evident than in preserved specimens.

Description: Body compressed laterally, deep anteriorly, greatest body depth at vertical situated between pectoral and pelvic fins, depth decreasing posteriorly. Dorsal profile of head slightly concave at interorbital region. Predorsal body profile curved, forming slight to pronounced hump at vertical line through posterior border of orbit; straight and slightly posteroventrally slanted along dorsal-fin base, proportionally less slanted and somewhat convex 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. Ventral profile of body convex to anus, convexity in region of the coracoids less pronounced than in other Hydrolycus species; profile with notch at vertical through base of innermost pelvic-fin ray; then posterodorsally slanted at anal-fin base, followed by straight profile to origin of ventralmost procurrent caudal-fin ray. Ventral surface of body with median keel from isthmus to anus, interrupted at vertical through pelvic-fin base; keel anteriorly supported by expanded coracoids.

Posterior margin of opercular bones not serrated. Laterosensory canal system in infraorbitals and opercular bones, highly branched; canals more pronounced in larger individuals.

Mouth obliquely aligned relative to horizontal axis of body, angle less pronounced relative to other Hydrolycus species. Upper jaw very long relative to head length; posterior tip of maxilla extending posteriorly to vertical through posterior tip of second infraorbital. Third infraorbital in contact with preopercle posteriorly but not ventrally. Snout shorter than orbital diameter in specimens smaller than 442.0 mm SL, longer in larger specimens. 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. Premaxillary dentition delimited by one canine anteriorly and one similar-sized canine, posteriorly; one large conical tooth located anterior to posteriormost canine and separated from it usually by 2 (sometimes 1 or 3) small conical teeth; several small conical teeth located in between anteriomost canine and large conical tooth, size of these teeth decreasing towards middle portion of teeth row. Anterior portion of maxilla with large conical teeth interspaced among smaller ones; teeth gradually get smaller and more similar in size posteriorly. Dentary with one very well developed canine, extending through snout when mouth is closed, tip of canine reaching nostrils anteriorly. One small conical tooth anterior to largest canine (sometimes second smaller one anteriorly); canine teeth posterior to largest canine varying in size, third largest; canines separated by small conical teeth; teeth gradually decreasing in size posteriorly. Most, but not all, individuals with one (sometimes more) very small conical teeth near symphyses of dentary, posterior to first small conical teeth on dentary. Teeth on ectopterygoid, mesopterygoid, and metapterygoid small and conical.

Scales without distinct serration. Scales smaller on dorsal and ventral portions of body, larger laterally at level of lateral line, and in region between pectoral and pelvic fins. Scales along pre-dorsal midline arranged in somewhat irregular rows. Scales below lateral line obliquely arranged. Lateral-line scales with many divergent lateral-line canal branches; branches more pronounced in larger individuals. Number of scales along lateral-line series 121-154. Lateral-line canal extending to posterior tip of middle caudal-fin rays.

Dorsal-fin rays ii,10. Dorsal-fin origin notably in front of vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 18th or 19th vertebrae (table 2). Distal margin of dorsal fin slightly convex. Anal-fin rays iv, 27-35. First anal-fin pterygiophore inserting behind hemal spine of 27th to 29th vertebrae (table 3). Distal margin of anal fin straight to slightly falcate. Scales covering one-third to one-half length of anal-fin rays. Pectoral-fin rays i,15-17 (13 and 14 in one specimen each), pointed distally. Posterior tip of longest pectoral-fin ray extends to or not quite to vertical through dorsal-fin origin, and reaches vertical through middle (or slightly beyond) of longest pelvic-fin ray. Pelvic-fin rays i,8 (rarely 9, 7 in two specimens). Pelvic fin pointed distally with first and second branched rays longest. Base of pelvic fin inserted at level of ventral profile of abdomen. Caudal fin with dorsal lobe somewhat straight, ventral lobe slightly rounded. In few individuals, middle caudal-fin ray slightly lengthened with tip extending posteriorly to vertical through tip of dorsalmost principal ray. Scales covering only basal portion of caudal-fin rays, not extending onto their branched portions.

Vertebrae: 44(1), 45(5), 46(12), 49(3), 50(4), 51(2).

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. Pigmentation darker dorsally, including tip of lower jaw. Specimens lacking guanine with yellowish-tan ground coloration on sides of body and head, slightly darker dorsally. Specimens show varying degrees of guanine retention. Elongate blotch of dark pigmentation extending from posterior portion of posttemporal, over most of the supracleithrum, and posterior and dorsal portions of cleithrum.

Specimens retaining pigmentation on fins with distal half of dorsal and pelvic fins and dorsal portion of pectoral fins (specially unbranched pectoral-fin ray) covered with dark chromatophores. Distal half of anal and caudal fins covered with dark chromatophores forming a well defined band, fin tips unpigmented. Adipose fin with very conspicuous black spot. Specimens lacking pigmentation on fins with all fins light-tan to hyaline.

Geographic distribution: Eastern and central portions of the Amazon basin including Rios Capim, Xingu, Tapajós, Trombetas, Branco, and Madeira drainages, and Rio Tocantins basin. Its is also distributed throughout the Río Orinoco basin, from its mouth to its upper reaches, and in Essequibo River in the Guyana (fig. 39).

Hydrolycus armatus is found in sympatry with Hydrolycus n. sp. 2 throughout most of its distributional range including the easternmost portion of the Amazon basin, the Essequibo River, and upper portion of the Río Orinoco drainage. It is also found in sympatry with Hydrolycus n. sp. 1 in the upper portions of the Río Orinoco drainage, and with H. scomberoides in the central portion of the Amazon basin at the mouth of Rio Japurá, state of Amazonas, Brazil.

Geographic variation: Specimens from the Río Orinoco basin differ in numbers of vertebrae from specimens from the Amazon basin and Guyana. Of 20 specimens from the Río Orinoco basin in which vertebral counts were available 18 have 44-46 vertebrae with two having 51 vertebrae. Vertebral counts of specimens from the Amazon basin and Guyana were available only from a small sample of 7 specimens and range from 49-50 vertebrae (table 8). The two specimens from the Río Orinoco basin with 51 vertebrae (AMNH 91342 and 91344, dry skeletons) were collected at the upper portions of Río Caroni along the face of Cerro Guaiquinima. The latter localities are included within the Gran Sabana region of Venezuela (Lasso et al., 1989). According to the these authors the ichthyofauna from the Gran Sabana is more closely related to that of the Cuyuní-Essequibo river systems. The pattern of distribution of vertebral counts of Hydrolycus armatus is congruent with this hypothesis suggesting that specimens of H. armatus from the Río Orinoco (including only the lower portions of the Río Caroni), and from the Gran Sabana region and Essequibo river might constitute different forms. Future studies should focus on a more detailed comparison of specimens from these two geographical areas.

Remarks: Hydrocyon armatus Schomburgk, 1841, was described for a form originating in the rivers of the Guyana. This species name, however, was subsequently only employed by Eigenmann (1912:396) who placed Hydrocyon armatus as a synonym of Hydrolycus scomberoides. Géry (1986) sorted out the problems of species identity in Hydrolycus (see also "Remarks" under H. scomberoides) and proposes that H. armatus is an available name to be used for the form from Guyana based on his belief that only one species of Hydrolycus occurs in that area (Géry, 1986:62). The present study, however, recognizes two distinct forms as occurring in the rivers of Guyana. They are found in sympatry at the Manari ponds, near Takutu River (BMNH 7.27:46-49) and in the Essequibo River (MNHN A 9854, locality not precisely located). A total of 14 specimens from Guyana were examined, 5 of which were assigned to Hydrolycus armatus, 8 to H. n. sp. 2 and one that was impossible to identify. Three of these specimens (MNHN A 9854, 2 spec. and BMNH -registration uncertain, 1 spec.) were collected by Robert Schomburgk, and comprise two different forms. As already mentioned elsewhere (Toledo-Piza and Menezes, 1996) it is uncertain whether the specimens collected by Schomburgk are from his first or second trip to Guyana, and therefore, potential types. Determining which of the two forms correspond to what was described as Hydrocyon armatus is further complicated by the fact that the provided description (Schomburgk, 1841) and associated drawing (plate 25; note in some editions of the "Fishes of Guiana Schomburgk, 1841, there are two plates numbered 25. Only the second one refers to the description, see Menezes (1969) for a comment on this question) are very vague. Géry (1986) subsequently cited it as species inquirenda. Both anal- and pectoral-fin ray counts provided in the original description (19 and 8 respectively) seem aberrant, being notably outside the range observed in the present study for both forms combined (27-37 and 14-18 respectively, table 7). The number of vertebrae provided by Schomburgk (1841) (48) cannot be compared with those provided in the present study, since there is no mention as to which vertebrae were included in the count (i.e. whether it includes the four vertebrae of the Weberian apparatus or not, as well as the PU1 + U1 element).

Some evidence was found, however, to indicate which form Schomburgk was referring to in his description of Hydrocyon armatus. A series of anonymous drawings was discovered deposited in the library of the Natural History Museum, London and entitled "1841 - Original drawings - SA freshwater fishes. Coloured from Mr. Schomburgk's drawings". One of the plates (fig. 40) illustrates a specimen of Hydrolycus that can be identified as the form herein assigned to Hydrolycus armatus, based on color pattern (i.e., the caudal and anal fins with a conspicuous band of dark pigmentation and white tips, and the conspicuous black spot on the adipose fin). In addition, the ventral keel at the region of the coracoids is not so pronounced as in the form assigned to Hydrolycus n. sp 2 (compare figure 40 with figures 38 and 41).

In light of the discussion above and in order to stabilize the nomenclature of Hydrolycus armatus a neotype will be designated following the examination of additional specimens from Guyana.

Material examined: 176 specimens (67, 132.1-656.0):

Type material: see discussion above under "Remarks".

Material examined: **BRAZIL.** *Amazonas*: CAS 70320 (1, 223.0) market at Manaus; *Pará*: BMNH 1849.11.8:44 (1, 137.4) Rio Capim; MZUSP 23893 (1, 213.0) Lago Jurunundéua, Rio Capim; MZUSP 24161 (3, 200.0-218.0) Rio Tocantins, lagoon near Canal do Capitariauara, near Jatobal; MZUSP 24094 (2, 215.0-230.0) Rio Tocantins, mouth of Igarapé Espirito Santo, below Tucuruí; MZUSP 32618 (3, 438.0-516.0); MZUSP 32619 (2, 503.0-575.0) Rio Itacaiunas, Caldeirão; MZUSP 25495 (1, 540.0) Rio Tapajós, left margin, in front of National Park headquarters; MZUSP 25561 (1, 507.0) Santo Antônio (or Pau-Rosa), left margin of Rio Tapajós (ca km 83 of highway BR-230), National Park; MZUSP 32608 (3, 217.0-229.0) Rio Tapajós, between Itaituba and São Luís; MZUSP 32608 (3, 217.0-229.0) Rio Tapajós, between Itaituba and São Luís; MZUSP 32607 (30, 155.0-420.0) Rio Xingu, Belo Monte; MZUSP 32611 (1, 507.0) Rio Xingu, confluence of Rio Culuene and Sete de Setembro; MZUSP 32633 (1, 376.0) Rio Trombetas, 20 km above mouth; MZUSP 48006 (1, 380.0) Rio Trombetas, Cuminá; NMW 57106 (1, 194.0) Santarém; *Roraima*: MZUSP 22552 (2) Rio Mucajaí, south of Boa Vista; MZUSP 22552 (2) Rio Mucajaí, south of Boa Vista; MZUSP 32615 (8, 344.0-395.0) Rio Branco, Cachoeira do Bem-Querer; NMW 57100 (1, 203.0); NMW 57101 (1, 185.0) Rio Branco, Boa Vista; NMW 57108 (3, 132.0-158.0) lagoon at Rio Branco, Boa Vista; NMW 57102 (1, 214.0) Rio Branco, Conceição; *Mato Grosso*:

MZUSP 32612 (2, 461.0-628.0) Rio Arinos, Porto dos Gaúchos; USNM 310734 (1, 275.0) Rio Batovi; USNM 310737* (mixed lot) (1); USNM 310733 (1, 255.0 mm SL) small tributary of Rio Batovi; USNM 310738 (1, 242.0) Rio Batovi, at Waura Indian Village; USNM 194404 (1, 569.0 mm SL); USNM 194405 (1, 462.0) upper Juruena; *Goiás*: MZUSP 40774 (1, 612.0) "Fecho" of Rio Paranã, below mouth of Rio São Domingos, Nova Roma; MZUSP 4841 (1, 302.0) Rio Araguaia, Aruanã; MNHN A8549 (1, 532.0) Amazone (=Amazonas); **COLOMBIA.** *Meta*: CAS 153816 (1, 505.0) Cordillera Macarena, junction of Ríos Duda and Losada, into Rio Guyabero; **GUYANA.** FMNH 59278 (1,515 mm SL) Wismar; MNHN A 9854* (mixed lot) (1, 411.0) Essequibo; BMNH 1972.7.27:46-49 (mixed lot) (3, 192.0-201) Manari ponds, near Takata River; **VENEZUELA.** *Apure*: AMNH 77801 (1, 260.0); MZUSP 27957 (1, 226.0); USNM 260138 (7, 205.0-226.0) side channel of Río Apure, ca. 5 km west of San Fernando de Apure; CAS 56693 (1, 211.0) San Fernando de Apure; USNM 257559 (1, 209.0) Río Apure ca. 2 km E of bridge at San Fernando de Apure; CAS 64321 (2, 188.0-189.0), south of Bruzual, borrow pit on E side of highway; *Guarico*: MZUSP 27877 (2, 218.0-253.0) Río Orituco, at highway Calabozo - Paso del Caballo; USNM 258158 (3, 284.0-357.0) Río Orituco, where crossed by road from Calabozo; UMMZ 214838 (4, 262.0-294.0) Río San José, ca 10 km N of confluence of San Jose and Río Guariquito; USNM 121385 (1, 236.0) Río Paya, tributary of Río Guarico; *Amazonas*: CAS 164372 (1, 253.0) Río Orinoco bifurcation at Playa Tama Tama; FMNH 105000 (1, 487.0) Río Orinoco, mouth of small caño, ca. 200 m above base camp on Río Cuao; *Monagas*: LACM 43381-1 (1, 400.0) Caño El Jobal, upstream of Caño Guargapo and

Barrancas, 147 n mi from sea buoy; LACM 43399-27 (3, 140.5-160.0) Caño Chivera, Isla Chivera, near Barrancas, 142 n mi from sea buoy; UMMZ 211283 (3, 157.0-198.0) lagoon of Río Orinoco, n mi. 163 between Pt Ordaz (Pt Palua) and Barrancas, at Los Costillito, Isla Iatatupa; UMMZ 211283 (3, 157.0-198.0) lagoon of Río Orinoco, n mi. 163 between Pt. Ordaz (Pt. Palua) and Barrancas, at Los Costillito, Isla Iatatupa; *Delta Amacuro*: LACM 43382-24 (4, 187.0-189.0) Río Orinoco, secondary caño about 500 m from its mouth in Caño Guarguapo; USNM 222866 (2, 486.0-489.0) Río Orinoco, Caño El Consejo, 134 n mi upstream from sea buoy; USNM 222877 (1, 365.0) Río Orinoco, N shore Brazo Imataca, 93 n mi upstream from sea buoy; USNM 222907 (2, 256.0-442.0) Río Orinoco, first small cano on W side of Caño Paloma 100 m above its mouth, 92 n mi upstream of sea buoy; CAS 50786 (1, 240.0 mm SL) Delta Amacuro; *Bolivar*: AMNH 91342 (1, dry skeleton) Río Lima, tributary of Río Carapo, along face of Cerro Guaiquinima; AMNH 91344 (1, dry skeleton) Río Caroni; USNM 270329 (4, 174.0-177.0) small caño connecting with Río Orinoco immediately south of El Burro; LACM 43295-36 (48), Río Orinoco, on N shore at Isla Portuguesa;

Hydrolycus n. sp. 2

Figures 41-44; tables 2,3,6-8

Cynodon scomberoides: Valenciennes, 1849:324 [in part: only 1 of 2 specimens from the Essequibo presented by Schomburgk; for remaining specimens see synonymy for Hydrolycus scomberoides and H. armatus]. Günther, 1864:358 [in part: only specimen from British Guiana [=Guyana]; for other specimen see synonymy list for Hydrolycus armatus).

Hydrolycus scomberoides: Eigenmann, 1912:396 (Guiana [=Guyana]: specimen presented by Robert Schomburgk, at the BMNH; other specimens not identified, see synonymy of H. scomberoides). Bertin, 1948:8 [type depository, in part: only MNHN A. 9854 (1 of 2); MNHN A. 1713, for remaining specimens see synonymy for H. scomberoides and H. armatus]. Lowe McConnell, 1964:110 [in part: see synonymy for Hydrolycus armatus].

Diagnosis: Hydrolycus n. sp. 2 can be distinguished from H. scomberoides by the lack of serrations on the exposed field of the scales and the placement of the pelvic fins at the level of the ventral profile of the abdomen; it can be distinguished from Hydrolycus n. sp. 1 in the number of anal-fin rays (29-37 versus 36-43 in Hydrolycus n. sp. 1), and number of lateral-line scales (102-119 versus 89-99, respectively).

Among all its congeners, Hydrolycus mostly resembles H. armatus but it can be separated from the latter species in the number of lateral-line scales (102-119 versus 121-154, respectively); scales above (20-29 versus 30-42, respectively), and below the lateral line (14-22 versus 24-38, respectively), scales around the caudal peduncle (25-33 versus 32-41 respectively), and coloration (see diagnosis of H. armatus). Differences in color pattern between the two species are much more evident in freshly preserved specimens (figs. 38 and 41). Hydrolycus n. sp. 2 has the proximal half of the caudal-fin rays (and to a certain extent the anal-fin rays) orange to red whereas in H. armatus they are yellowish to hyaline. Note also the very conspicuous dark spot on the adipose fin of H. armatus, when compared to Hydrolycus n. sp. 2.

Description: Body compressed laterally, deep anteriorly, greatest body depth at vertical situated between pectoral and pelvic fins, depth decreasing posteriorly. Dorsal profile of head slightly concave at interorbital region. Predorsal body profile curved, forming slight to pronounced hump at vertical through posterior margin of orbit; straight and slightly posteroventrally slanted at base of dorsal fin, proportionally less slanted and somewhat convex 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. Ventral profile of body convex to anus, convexity more pronounced anterior to pelvic-fin origin, notch present at vertical through base of innermost pelvic-fin ray. Profile less convex to anus; straight in very short region from anus to anal-fin origin; posterodorsally slanted at anal-fin base, then 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.

Posterior margin of opercular bones not serrated. Laterosensory canal system in infraorbitals and opercular bones, highly branched; canals more pronounced in larger individuals.

Mouth obliquely aligned relatively to horizontal axis of body, with upper jaw very long relative to head length; posterior tip of maxilla extending posteriorly to vertical through posterior tip of second infraorbital. Third infraorbital in contact with preopercle posteriorly but not ventrally. Snout shorter than orbital diameter. 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. Premaxillary delimited by one canine anteriorly and one similar sized canine, posteriorly; one large conical tooth anterior to posteriormost canine separated from it usually by 2 (sometimes 1 or 3) small conical teeth; several small conical teeth between anteriomost canine and large conical tooth, these teeth decreasing in size towards middle portion of teeth row. Anterior portion of maxilla with several large conical teeth separated by smaller teeth; teeth gradually get smaller and of more similar size posteriorly. Dentary with one very well developed canine, extending through snout when mouth is closed with tip reaching nostrils anteriorly. One very small conical tooth anterior to largest dentary canine; canine teeth posterior to largest canine varying in size, third largest, canines separated by small conical teeth. Dentary teeth gradually decreasing in size posteriorly; most individuals with one (sometimes 2) very small conical teeth at dentary symphyses, posterior to first small conical teeth on dentary. Teeth on ectopterygoid, mesopterygoid, and metapterygoid small and conical.

Scales without distinct serration. Scales smaller on dorsal and ventral portions of body, larger laterally at level of lateral line. Scales along pre-dorsal midline arranged in somewhat irregular rows. Scales below lateral line obliquely arranged. Lateral-line scales larger than those on rest of body, with many divergent branches of lateral-line canal. Divergent branches more pronounced in larger individuals; individuals 145 mm SL and smaller with only one dorsally and one ventrally directed branch of lateral-line canal. Number of scales along lateral-line series 93-119. Lateral-line canal extending to posterior tip of middle caudal-fin rays.

Dorsal-fin rays ii,10 (9 and 11 in only one specimen). Dorsal-fin origin notably in front of vertical through anal-fin origin. First basal dorsal-fin pterygiophore inserting behind neural spine of 19th to 20th vertebrae (table 2). Distal margin of dorsal fin slightly convex. Anal-fin rays iv, 29-43. First anal-fin pterygiophore inserting behind hemal spine of 29th to 30th vertebrae (table 3). Distal margin of anal fin straight to slightly falcate. Scales covering one-third to one-half length of anal-fin rays. Pectoral-fin rays i,15-18. Pectoral fin pointed distally. Posterior tip of longest pectoral-fin ray extends to or nearly to vertical through dorsal-fin origin, and reaches to, or slightly beyond vertical through middle of longest pelvic-fin ray. Pelvic-fin rays i,8 (rarely 7, 9 in only one specimen). Pelvic fin pointed distally with first and second branched rays longest. Base of pelvic fin inserted at level of ventral profile of abdomen. Caudal fin with dorsal lobe somewhat straight, ventral lobe slightly rounded. Few individuals with middle caudal-fin ray very elongate, tip extending posterior to vertical through tip of dorsalmost principal ray; scales covering only basal portion of caudal-fin rays, not extending onto their branched portions.

Vertebrae: 50(1), 51(14), 52(19), 53(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. Head and body darker dorsally, including tip of lower jaw. Specimens lacking guanine with yellowish-tan ground coloration on sides of body and head, slightly darker dorsally. Specimens show varying degrees of guanine retention. One specimen (MZUSP 32627, 398 mm SL) from the Rio Negro basin with darker overall body coloration. Elongate blotch of dark pigmentation extending from posterior portion of posttemporal, covering most of the supracleithrum, and posterior and dorsal portions of cleithrum.

Specimens retaining pigmentation on fins with distal half of dorsal and pelvic fins and dorsal portion of pectoral fins (especially unbranched pectoral-fin ray) covered with dark chromatophores. Distal half of anal- and caudal fins covered with dark chromatophores forming diffuse band. Adipose fin with diffuse black spot.

Geographic distribution: Eastern and central portions of the Rio Amazonas basin including Rios Capim, Xingu, Tapajós, Trombetas, Negro, and Branco drainages, and Rio Tocantins basin (fig. 44). Three specimens were collected at Lago Amanã, mouth of Rio Japurá, the latter representing the most westerly locality for this species along the main Amazon. The species also occurs in upper drainages of Río Orinoco with specimens collected in the Río Siapa, Mavaca and Ventuari, the latter being the northernmost range of the species in the Río Orinoco drainage. This species is also found in the Rupununi and Essequibo rivers in Guyana. Hydrolycus n. sp. 2 is found in sympatry with H. armatus, H. n. sp. 1, and H. scomberoides in different parts of the distributional range of these species.

Geographic variation: Three specimens from the Essequibo River in Guyana (BMNH 1976.6.18:7-9), have a relatively large orbital diameter (37.1-38.9 of HL) when compared to remaining specimens of this species (27.8-37.0 of HL). All other counts and measurements fall within the range of Hydrolycus n. sp. 2.

Remarks: See nomenclatural notes under "Remarks" of Hydrolycus armatus.

Material examined: 243 specimens (50, 136.5-445.0 mm SL):

Type material: Holotype: **BRAZIL**. *Pará*: MZUSP 00000(268.0) Rio Xingu, Belo Monte; Parataypes: **BRAZIL**. *Pará* MZUSP 48005 (29, 244.0-445.0) all taken with holotype.

Other material examined: **BRAZIL**. *Amazonas*: MZUSP 00000 (1, 233.0 mm SL) Rio Negro, below Rio Daraá; MZUSP 32621 (5, 198.0-330.0) Rio Negro, Ilha de Tamaquaré; MZUSP 32624 (3, 209.0-297.0) Rio Negro, São Gabriel da Cachoeira; MZUSP 32625 (1, 215.0) Rio Negro, Barcelos; MZUSP 32627 (2, 398.0-412.0) Rio Negro, São Pedro; MZUSP 32631 (3, 159.0-179.0) Rio Negro, Rosa Maria; MZUSP 32628 (1, 274.0), MZUSP 32629 (6, 146.0-186.0) Rio Marauiá, near its mouth; MZUSP 32630 (5, 152.0-240.0) Rio Marauiá, Cachoeira do Bicho-Açu; MZUSP 36095 (1, 224.0) Lago Amanã, mouth of Rio Japurá; MZUSP 36109 (1, 236.0) Igarapé Ubi, Lago Amanã, mouth of Rio Japurá; MZUSP 36120 (1, 232.0) Igarapé Cacau, Lago Amanã, mouth of Rio Japurá; MZUSP 31275 (1, 252.0) mouth of Rio Urubaxi; MZUSP 32622 (1, 264.0) Rio Marié, Lago do Curiá-Muru; *Pará*: BMNH 1897.11.26:6 (1, 300.0);

NMW 8964 (1, 340.0) Rio Capim; MZUSP 23871 (2, 235.0-253.0) Rio Capim, near Caranandéua; BMNH 1926.10.27:18 (1) Monte Alegre; CAS 70315 (1, 182.0 mm SL), CAS 70322 (1, 190.0); CAS 70324 (2, 205.0-209.0) market at Santarém; MZUSP 25008 (1, 258.0) Rio Muju, tributary of Rio Curuá-Una, Santarém; MZUSP 15640 (1, 310.0) mouth of Lago Leonardo, Reserva Biológica de Trombetas; MZUSP 32632 (128, 224.0-309.0) Rio Trombetas, Cuminá; MZUSP 5413 (3, 174.0-239.0) Rio Trombetas, Oriximiná; MZUSP 5520 (1, 222.0) Lago Jacupá, Oriximiná; MZUSP 3570 (1, 262.0) Rio Tapajós; MZUSP 21352 (1, 222.0) Rio Tapajós, Aveiro; MZUSP 22109 (6, 184.0-217.0); MZUSP 24329 (3, 191.0-236.0) Ilha da Barreirinha, Rio Tapajós, near São Luís; MZUSP 24266 (4, 171.0-200.0), PA, Rio Tapajós, São Luís; MZUSP 24313 (3, 244.0-262.0) lake at Ilha do Campinho, Rio Tapajós; MZUSP 51030 (83, 178.0-374.0) Rio Tapajós, between Itaituba and São Luís; NMW 68552 (1, 270.0) Rio Tapajoz (=Tapajós), Villa Braga; MZUSP 51033 (4, 262.0-416.0) Cachoeira do Espelho, Rio Xingu; MZUSP 48005 (29, 248.0-454.0) Rio Xingu, Belo Monte; MZUSP 35973 (2, 323.0-371.0) Rio Fresco, Aldeia Gorotire, São Felix do Xingu; MZUSP 24109 (1, 154.0) lagoon at Igarapé Muru, Rio Tocantins, below Tucuruí; MZUSP 24174 (1, 215.0) Laguinho, near Tucuruí, Rio Tocantins; *Roraima*: MZUSP 32613 (9, 179.0-313.0) Rio Branco, Xeriuini; MZUSP 32614 (13, 238.0-328.0); MZUSP 51032 (1, 228.0) Rio Branco, Cachoeira do Bem-Querer; *Goiás*: MZUSP 4841 (mixed lot) (1, 252.0) Rio Araguaia, Aruanã; *Mato Grosso*: USNM 194407 (1, 350.0), USNM 194416 (1, 376.0), USNM 194386 (1, 347.0) upper Rio Juruena; USNM 310737 (1, 171.0) small tributary of Rio Batovi, upper Rio Xingu; MZUSP 51031 (7, 232.0-369.0) Rio

Arinos, Porto dos Gaúchos; MZUSP 22811 (1, 115.0) Rio Araguaia, Santa Terezinha; MNHN 1713 (1, 240.0), Fleuve Amazone (=Rio Amazonas); MZUSP 2829 (1, 215.0), Amazonas and Pará. **GUYANA.** BMNH 1976.6.18:7-9 (3, 136.5-161.0 mm SL), Essequibo River, at Anarika; MNHN A 9854 (mixed lot) (1, 430.0) Essequibo River; BMNH -registration uncertain (1, 193.0) British Guiana (=Guyana); BMNH 1975.5.16:8 (1, 403.0) Guyana; BMNH 1972.7.27:50 (1, 251.0 mm SL) Rupununi River, Karanambo; **VENEZUELA.** *Amazonas*: AMNH 93068 (1, 230.0) Río Mavaca, at Tapirapeco base camp, near boat dock; CAS 148617 (2, 149.0-154.0) rock near mouth of Río Siapa, CAS 148618 (1, 150.6) Río Orinoco bifurcation, TamaTama Rock; CAS 155761 (1, 142.7) Kiratare; FMNH 103658 (1, 205.0) Río Ventuari at beach in front of small caño ca. 5 km by falca above mouth in Río Orinoco; MCNG 22895 (1, 210.0) Río Ventuari, 6 km above mouth of Río Yureba; MNHN 1887 0789 mixed lot (1, 155.0) Venezuela.

Genus Cynodon Agassiz, 1829

Cynodon Agassiz, 1829:77 (type species Cynodon gibbus, see Appendix).

Cynodon Cuvier, 1829:312 (see Appendix).

Camposichthys Travassos, 1946:132 (type species Cynodon gibbus by original designation).

Key to Species of Cynodon Agassiz, 1829

1. Branched pelvic-fin rays 8; band of dark pigmentation covering base of caudal fin (fig. 45); orbital diameter 24.9-33.8 of HL (Rio Amazonas and Río Orinoco basins, Rupununi river in Guyana, Rio Tocantins drainage and Rio Pindaré system of state of Maranhão in Brazil). . . . . C. gibbus

\- Branched pelvic-fin rays 7; no band of dark pigmentation covering base of caudal fin (fig. 50); 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). . . . . Cynodon n. sp. 1

Cynodon gibbus Agassiz, 1829

Figures 45-49; tables 9-12

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, Rio Essequibo, Dadanawa ponds). Howes, 1976:204 (specimens at the BMNH). Mendes dos Santos, 1984:40 (Brazil, Rio Tocantins). Taphorn and Lilyestrom, 1984: (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 (in list of freshwater fishes of Peru). Barriga, 1991:30 (list of freshwater fishes of Ecuador, common name). Taphorn, 1992:436 (Venezuela, Río Apure drainage). Ovchynnyk, 1967: Appendix A (list of freshwater fishes of Ecuador). (Not Eigenmann, 1912; Pellegrin, 1909; Di Caporiacco, 1935; Boeseman, 1952. See synonymy of Cynodon n. sp.1).

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

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

Diagnosis: Cynodon gibbus can be distinguished from Cynodon n. sp. 1 by the presence of a band of dark pigmentation that covers the base of the caudal fin rays (figs. 45, 46), the presence of eight (versus seven) branched rays in the pelvic fin, and by a relative smaller orbital diameter (24.9-33.8 versus 30.1-34.4 of HL), (fig. 47). See also comments under "Remarks".

Description: 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 (fig. 48), 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 by usually 2 or 3 small conical teeth; several small conical teeth between anteriomost 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 (similar in size to that in Hydrolycus n. sp. 2), extending up into snout when mouth is closed, tip of canine reaching nostrils anteriorly. Dentary with one smaller canine anterior to largest 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 decrease 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 towards lateral line; largest scales along lateral line; scales on region dorsal to anal fin small. Scales along pre-dorsal 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 of covering rest of body. Scales below lateral line obliquely arranged. Lateral-line scales with 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. Number of scales along lateral-line series 96-109. 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 vertebrae. Distal margin of dorsal fin straight to somewhat concave. Anal-fin rays, iii-iv, 65-80. First anal-fin pterygiophore inserting behind hemal spine of 22th 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 i,14-17, 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 (specially unbranched pectoral-fin ray) covered with dark chromatophores. Distal half portion 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 Ríos Marañon and Ucayali east to the drainages of Rio Purus, Madeira, Branco, Amazonas, Trombetas, Xingu, and Rio Tocantins basin (fig. 49). 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 mid 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 Cynodon n. sp. 1 in Rio Uatumã, a tributary of the Rio Amazonas, Brazil. In the Rio Branco, a tributary of Rio Negro in Brasil, the two species are found in proximate localities, Cynodon gibbus (MZUSP 32595) at Marará, and Cynodon n. sp. 1 (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 Rio Mapuera, whereas specimens of Cynodon n. sp. 1 examined were collected in Rio Mapuera (above Cachoeira da Porteira).

Remarks: The features that distinguishes Cynodon gibbus from its congener, Cynodon n. sp. 1, seem consistent throughout the samples examined. However, in a few instances some incongruences were observed. Table 9 shows that three specimens (AMNH 12542, MZUSP 32595, 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 9 specimens pelvic-fin ray counts could not be taken due to damage of the fins.

In spite of the significant difference in orbital diameter (fig. 47) this feature show a slight overlap between the two species (table 10). Specimens of Cynodon gibbus with relative orbital diameters larger than 30.5 of 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 post capture 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 river drainage where Cynodon n. sp. 1 does not occur. Given these facts and because these specimens showed some of the distinguishing features of Cynodon gibbus, they were tentatively 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 Spix and Agassiz, 1829:78). The specimens used in Agassiz's descriptions are housed at the MHNN, Neuchâtel (see, Rhaphiodon vulpinus, below). The remaining of Spix and Martius's specimens remained at the Zoologische Staatssammlung München but were destroyed during a bombing raid in 1944 (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 9 pelvic-rays ("pinnae pectoralis ventrales 9", Spix and Agassiz, 1829:78) in the original description can be used to identify the specimen he examined as Cynodon gibbus. As discussed above, Cynodon gibbus has i,8 pelvic-fin rays (total of nine) and Cynodon n. sp. 1 has i,7 (total of 8). A few specimens of Cynodon n. sp. 1 also have a total of 9 pelvic-fin rays (see discussion under "Remarks" of Cynodon n. sp. 1). The areas in Brazil sampled by Spix and Martius (Papavero, 1971, map 7 following page 66), where Cynodon occurs, encompasses the distribution of Cynodon gibbus and Cynodon n. sp. 1. Therefore, we cannot absolutely determine that the specimen examined by Agassiz was Cynodon gibbus or specimen of Cynodon n. sp. 1 with an aberrant number of pelvic-fin rays. Agassiz does not mention any pigmentation associated with the caudal fin, so this feature cannot be used to resolve the problem. But since only 3 out of 45 specimens of Cynodon n. sp. 2 had 9 pelvic-fin rays, the 9 pelvic-fin rays reported by Agassiz (in Spix and Agassiz, 1829:78) can be argued to be 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 neotype will be designated following the examination of additional specimens.

Material examined: 226 specimens (72, 77.0-280):

Type material: see discussion above under "Remarks".

Material examined: **BOLIVIA.** *El Beni*: AMNH 77340 (1, 85.7) mouth of Río Ibarre;

USNM 305368 (2, 169.0-261.0 mm SL) Ballivia, Río Cuiraba at 10 km NE El Porvenir Biol. Sta., 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; INPA 5328 (3, 191.0-200.0) Rio Amazonas, Ilha do Caieiro, Lago do Rei; INPA 5346 (mixed lot) (1, 198.0); INPA 5348 (1, 221.0) Rio Uatumã; MZUSP 13497 (1, 226.0) Rio Amazonas, Itacoatiara; MZUSP 21489 (1, 130.0) Pauini; 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; MZUSP 6539 (1, 146.0) Lago Manacapuru; *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-POLO 1035 (1, 128.0) Rio Mamoré, below Surpresa, and the mouth of Rio Guaporé; INPA-POLO 336 (2, 230.0) Rio Guaporé, Pimenteiras; INPA-POLO 530 (1, 280.0) Rio Jamari, à 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 Bem-Querer; MZUSP 32595 (4, 132.0-160.0) Rio Branco, Marará; 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 12542, mixed lot (2, 127.9-134.7) vicinity of Rio Macaua, tributary of Rio Iaco, a tributary of Rio Purus, near Sena Madureira; *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. **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*: 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), Loreto, 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, Dpto. 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; **VENEZUELA.** *Delta Amacuro*: CAS 50771 (1, 96.5) Delta Amacuro, in cove on shore; LACM 42282-22 (11, 77.6-123.4) Río Orinoco, secondary caño about 500 m from its mouth in caño Guarguapo; 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, naut. mi. 131; USNM 222855 (2, 136.0), USNM 233932 (1, 147.0) Delta Amacuro, Río Orinoco, small caño near mouth of Caño Socoroco, 11 n mi. 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; *Bolivar*: USNM 222848 (1, 212.0) Río Orinoco, cove at W end of Islote Fajardo, 182 naut. mi. upstream from sea buoy; *Guarico*: USNM 257564 (1, 208.0) Río Orituco where crossed by road from Calabozo.

Cynodon n. sp 1

Figures 50-51; tables 9-12

Cynodon gibbus: (misidentification): Eigenmann, 1912:395 (British Guiana [=Guyana]; description); 3 of 7 cited specimens examined). Pellegrin, 1909:148 (Brazil, Tonnantins [=Tonantins]). Di Caporiacco, 1935:66 (Guyana, Demerara River, identification based on location). Boeseman, 1952:191 (Suriname, Surinam River, identification based on location).

Cynodon gibbous: (species name misspelled): Heyde, 1986:140 (Suriname: common name, identif. based on location).

Cynodon aff. gibbus: Planquette et al., 1996:212-213 (French Guyana, Maroni, photograph).

Diagnosis: Cynodon n. sp. 1 lacks the band of dark pigmentation covering the base of the caudal fin rays that is characteristic of C. gibbus compare (figures 45 and 50). Some 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 seven (versus eight) branched pelvic-fin rays and the relatively larger orbital diameter (30.1-34.4 versus 24.9-33.8 of HL), also distinguishes Cynodon n. sp. 1 from C. gibbus (see comments under "Remarks" of these two species accounts).

Description: 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 along 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. 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, similar-sized canines, one in anterior and one in posteriormost portion; third canine sometimes slightly smaller, intermediate in position to 2 other canines and separated from posteriormost canine by usually 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 (similar in relative size to that in Hydrolycus n. sp. 1), extending up into snout when mouth is closed, tip of canine reaching nostrils anteriorly. One smaller dentary canine, about half size of largest located anteriorly followed by another smaller conical tooth anteriorly; canine teeth posterior to largest canine progressively decreasing in size posteriorly; dentary canines separated by conical teeth of various sizes. Teeth on ectopterygoid, 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; 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. Number of scales along lateral-line series 97-107. 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 21th vertebrae. Distal margin of dorsal fin straight to somewhat concave. Anal-fin rays , iii-iv (rarely ii), 61-76. First anal-fin pterygiophore inserting behind hemal spine of 22th 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 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 (specially unbranched pectoral-fin ray) covered with dark chromatophores. Distal half of anal fin with band of dark chromatophores. Adipose fin hyaline.

Geographic distribution: Cynodon n. sp. 1 occurs in the Rio Solimões/Amazonas drainage east of the mouth of Rio Içа (located close to the border of Brazil and Colombia), eastward into the Rios Negro, Branco, Trombetas, and Tapajós (fig. 51). One specimen (INPA 5334) from the Rio Tocantins, Brazil, represents the most easterly locality within the Amazon basin. Cynodon n. sp. 1 also occurs in the Essequibo and Demerara Rivers in Guyana. Cynodon n. sp.1 is found in sympatry with C. gibbus in a few localities within the Amazon basin (see geographic distribution of C. gibbus, for details).

Remarks: Planquette et al. (1996:212-213) provide a photograph of a specimen identified by those authors as Cynodon aff. gibbus. The picture clearly refers to Cynodon n. sp 1. In the accompanying description they distinguished this form from C. gibbus, based on relative greatest body depth and number of anal-fin rays. In the present study these two features showed a large degree of overlap between the two species (table 11). Table 12 shows the frequency distribution of branched anal-fin rays of Cynodon n. sp. 1 and C. gibbus. Although the former species tend to have fewer rays than Cynodon n. sp. 2 as suggested by Planquette et al (1996), there is a large overlap between the two species, making a distinction between these two forms based on this feature, problematic at best. Rather, the number of branched ventral-fin rays, color pattern, and relative orbital diameter (see "Diagnosis", above) are features which to distinguish these two forms (but see "Remarks" under Cynodon gibbus and comments below).

Three specimens (MZUSP 32597, 2 specimens and MZUSP 32585) of Cynodon n. sp. 1 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 8). 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 base of the caudal fin characteristic of C. gibbus and have relatively large orbital diameters, they were herein assigned to Cynodon n. sp. 1.

Material examined: 187 (51, 94.5-312):

Type material: Holotype: **BRAZIL.** *Amazonas*: MZUSP 00000 (238.0) Rio Tefé, Supiã-Pucu; Paratypes: **BRAZIL.** *Amazonas*: MZUSP 32590 (19, 204-247.0) all taken with holotype.

Other material examined: **BRAZIL.** *Amazonas*: INPA 5451 (1, 167.0) Rio Uatumã, at Balbina dam; INPA 5512 (1, 165.0) Rio Uatumã, Sumauma (=Samauma?); INPA 5347 (1, 212.0) Rio Uatumã, Igarapé Anauá; INPA 5346* (mixed lot) (3, 182.0-203.0) Rio Uatumã; 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; NMW 57111 (1, 171.0), mouth of Rio Negro; 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; MZUSP 21707 (4, 170.0-190.0) Lago Janauacá and surroundings, Rio Solimões; MZUSP 26933 (1, 212.0) Lago Janauacá and around Manaus; 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) AM 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 uncat1 (2, 109.6-140.5 mm SL); AMNH uncat2 (1, 229.0 mm SL); 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.

Genus Rhaphiodon Agassiz, 1829

Rhaphiodon Agassiz, 1829:59 (see Appendix).

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

Rhaphiodon vulpinus Agassiz, 1829

Figures 52-56; tables 13-16

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 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 fig.1-4 (description of juvenile teeth). Eletrosul, 1980:18 (Brazil: Rio Uruguai). Mendes dos Santos et al., 1984:40 (Brazil, Rio Tocantins; photograph, description). 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 cynodontin 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). Géry and Mahnert, 1984:174 (Ecuador, Río Napo 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, 1936:pl.12 (Ururguay). 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 (Ururguay, 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. 52-55) (pre-dorsal 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 latter point in Hydrolycus) and from Cynodon by the lower number of anal-fin rays (38-50 versus 61-80 in Cynodon).

Description: Body very elongate, compressed laterally, greatest body depth at vertical through pectoral-fin origin, depth decreasing posteriorly. Dorsal profile of head slightly concave, ranging from less concave to straight in specimens smaller than 50 mm SL (fig. 53); concavity varies depending on the 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 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. 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 base of anal fin, 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 plan varying depending on degree of flexure posterior to head at time specimen was preserved. 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.

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 variable sized conical teeth anteriorly, gradually becoming smaller and more similar in 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 pre-dorsal 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 180 mm SL with one ventrally and one dorsally directed branch of lateral-line canal. Number of scales along lateral-line series 122-152. 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; diminute scales on base of dorsal fin, extending onto membrane between fin rays about one-fifth length of middle rays, to lesser extent on remaining rays, scales not as extensive in individuals under 170 mm SL, absent in individuals under 60 mm SL. Anal-fin rays iv (rarely iii), 38-50. First basal anal-fin pterygiophore inserting behind hemal-spine of 36th (rarely 35) 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 i,12-17, fin pointed distally. Posterior tip of longest pectoral-fin ray extending to a point far anterior to vertical through dorsal- and 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 decreasingly towards 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, eastwards to Rio Capim in Brazil; 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. 56).

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 in, 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, see tables 13 and 14 for frequency distributions of these features), 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.

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 is inexact. Papavero (1971, map following page 66) describes the itinerary of Spix and Martius's 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, the possibility exists that the holotype of Rhaphiodon vulpinus originated in the Rio Paraná basin. Kottelat (1988) commented on the status of Spix and Martius specimens that Agassiz used as the basis for his descriptions and cited the 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. 54) 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 15). 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 55). 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 the larger size of this specimen. A few meristic features, present in Hydropardus rapax, also lie outside the range presented by the remaining Rhaphiodon vulpinus specimens (table 17). 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 towards lower values for the meristic features mentioned above for Hydropardus rapax, that could suggest that the latter would be a form distinct from Rhaphiodon vulpinus.

Rhaphiodon is the most widely distributed cynodontine genus, in South America and also the least speciose genus. 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. Two Cynodon species were recognized one 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 (1992) and Thoracocharax stellatus (Kner, 1859), see Weitzman (1960:220).

Material examined: 420 specimens (63:68.9-623 mm SL):

Type material: MHNN 822 (1, 303.0) Brazil; holotype of Rhaphiodon vulpinus Agassiz,

1829. ZMC 183 (1, 623.0) Montevideo, Uruguay; holotype of Hydropardus rapax Reinhardt, 1851.

Other material examined: 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*: 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 of Limoquije; MNHN 1989 1466 (1, 293.0) Trinidad, Laguna Capital; **BRAZIL.** *Amazonas*: 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; 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) 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 west 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; 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; 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), AM, Lago do Prego, in front of Santo Antônio do Içá; MZUSP 23518 (1, 280.0) Santo Antônio do Içá, mouth of Rio Içá; 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; 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; 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; MZUSP 24014 (2, 255.0-336.0) Paraná Samaúma, mouth of Rio Tocantins; MZUSP 32820 (1, 327.0) Rio Itacaiúnas, Serra dos Carajás, Igarapé Águas 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; *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, "repressed" (=represa, i.e. dammed up) Lagem Marsal brook into Rio Tocantins; *Goiás*: 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. **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 n. mi. 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 naut. mi. upstream from sea buoy; USNM 222880 (1, 265.0) Río Orinoco, N shore near San Felix, 176 naut. mi. upstream from sea buoy; UMMZ 211306 (2, 145.0-249.0) lagoon of Río Orinoco, naut. mi. 201; *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; *Monagas*: AMNH 47956 (1, 176.0) shore of Río Orinoco, Buoy 142 naut. mi. downstream from Barrancas, north side Isla Varader inlet; USNM 222863 (1, 227.0) Río Orinoco, small caño near mouth of Caño Guarguapo, 146 naut. mi. 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.

TABLES AND ILLUSTRATIONS

Table 1: Character matrix for species of the Cynodontinae and genera of proximate outgroups (number 9 indicates character coded as polymorphic -0&1).

Taxon	1-5	6-10	11-15	16-20	21-25	26-30	31-35
Hydrolycus armatus	11011	10000	11111	10001	10010	11111	11011
Hydrolycus n. sp. 2	11011	10000	11111	10001	10010	11111	11011
Hydrolycus n. sp. 1	01010	11100	01111	10001	20110	11111	11011
Hydrolycus scomberoides	01011	10010	11111	101?1	21410	11111	11011
Rhaphiodon vulpinus	01100	10000	01111	?0111	21310	11111	11011
Cynodon gibbus	01200	10101	00011	01111	21211	10101	11111
Cynodon n. sp. 1	01200	10101	00011	01111	21211	10101	11111
Roestes	00000	0??00	00?00	00000	00010	00000	00000
Gilbertolus	00000	0??00	00?00	00000	00010	00000	00000
Acestrorhynchus	00000	0??10	0??00	00000	??100	00009	00001
Hoplocharax	00000	0??00	00?00	00000	00000	00000	00000
Heterocharax	00000	0??00	00?00	00000	00010	00000	00000
Lonchogenys	00000	0??10	00?00	00000	00010	00000	00000
Gnathocharax	00000	0??00	00?00	00000	00010	00000	0.00

Table 1. (continued)

Taxon	36-40	41-45	46-50	51-55	56-60	61-65	66-70
Hydrolycus armatus	11111	11011	11000	11011	11110	11100	11000
Hydrolycus n. sp. 2	11111	11011	11000	11011	11110	11100	11000
Hydrolycus n. sp. 1	01110	11011	10000	11011	11110	11100	11000
Hydrolycus scomberoides	11111	11011	22000	11011	11110	11110	11010
Rhaphiodon vulpinus	01111	11011	31111	12110	11111	12100	21101
Cynodon gibbus	01110	12111	12001	11011	11111	11101	11000
Cynodon n. sp. 1	01110	12111	12001	11011	11111	11101	11000
Roestes	0000?	00000	00000	00000	01000	00000	00000
Gilbertolus	0000?	00000	00000	00000	11100	10000	00000
Acestrorhynchus	00011	00000	00000	00000	09000	00000	90000
Hoplocharax	0000?	00000	00000	00000	00000	00000	00000
Heterocharax	0000?	00000	00000	00000	00000	00000	00000
Lonchogenys	0000?	00000	00000	00000	00000	00000	00000
Gnathocharax	0000?	00000	00000	00000	11010	00000	00000

Table 1. Character summary:

1. Fifth infraorbital. 0, well developed, without contact between fourth and sixth infraorbitals; 1, greatly reduced, with the posteroventral margin of the sixth infraorbital in contact with the posterodorsal margin of the fourth infraorbital.
2. Antorbital. 0, no contact between antorbital and lateral ethmoid; 1, antorbital contacting ventral wing of lateral ethmoid along its entire lateral edge.
3. Antorbital. 0, flat, plate-like, without medial process; 1, with a short medial, vertically-aligned process at its posterior edge that extends along the posterior surface of the ventral wing of the lateral ethmoid; 2, with an enlarged medial, vertically-aligned process at its posterior edge that extends along the posterior surface of the ventral wing of the lateral ethmoid.
4. Mesethmoid spine. 1, conical, or with a different type of elaboration of its anterior portion (Vari, 1979:278-279); 1, dorso-ventrally developed, almost round in shape.
5. Anterodorsal surface of mesethmoid. 0, without a notch; 1, with a notch.
6. Ventral process of the mesethmoid (sensu Starks, 1926:163). 0, absent; 1, present.
7. Ventral processes of the mesethmoid. 0, ventrally oriented; 1, anteriorly oriented.
8. Vomer-mesethmoid contact. 0, anterior surface of vomer without contact with posterior surface of the ventral processes of the mesethmoid; 1, anterior surface of vomer contacting posterior surface of the ventral processes of the mesethmoid.
9. Ventral diverging lamellae of the mesethmoid. 0, well developed; 1, reduced.
10. Portion of the ventral diverging lamellae of the mesethmoid that contacts the lateral

surface of the vomer. 0, covering only the upper anterior corner of the lateral surface of the vomer; 1, covering most of the lateral surface of the vomer.

11. Articular surface on the lateral wing of the mesethmoid. 0, absent; 1, present.
12. Vomer. 0, crest on its ventral surface absent; 1, crest on its ventral surface present.
13. Lateral arms of vomer. 0, continuous all the way to its anterior portion, almost proximate to articulation with the mesethmoid (vomer is an inverted "Y" in cross section along its entire extension); 1, gradually reducing anteriorly extending just until the posterior half of the extension of the bone (only the posterior portion of the vomer is an inverted "Y" in cross section).
14. Vomer-palatine contact. 0, articulation between vomer and palatine made through cartilaginous surface at other portions of these ossifications; 1, anterior portion of the palatine with a cartilaginous surface contacting a cartilaginous surface at the posterior portion of the main body of the vomer.
15. Portion in the vomer for the articulation of the maxilla. 0, not modified as described in 1; 1, Presence of a shallow depression on its anterolateral surface where the anterior tip of the maxilla abuts.
16. Ridge on lateral surface of the vomer. 0, absent; 1, present.
17. Rhinosphenoid. 0, present; 1, absent.
18. Lateral ethmoid-orbitosphenoid contact. 0, absent; 1, present.
19. Parasphenoid and main portion of orbitosphenoid. 0, well separated; 1, close to each other.
20. Dilatator fossa. 0, not extending anteriorly on the dorsal surface of the frontal or if

so, only to dorsoposterior edge of the orbit; 1, highly developed, extending anteriorly on the dorsal surface of the frontal beyond dorsoposterior edge of the orbit.

21. Frontal shelf at the posterodorsal edge of the orbit. 0, well developed; 1, reduced; 2, absent.
22. Dorsal portion of the sphenotic spine. 0, contacting ventrolateral margin of frontal; 1, not in contact with ventrolateral margin of frontal.
23. 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.
24. Third posttemporal fossa bordered by the epioccipital and exoccipital. 0, absent; 1, present.
25. Dorsal posttemporal fossa. 0, present; 1, absent.
26. Neurocranium-first vertebra joint. 0, portion of the basioccipital at the neurocranium-vertebral joint not flared posteriorly; 1, portion of the basioccipital at the neurocranium-vertebral joint flared posteriorly and forming a receptacle for the first vertebra.
27. Hyomandibula. 0, shaft of bone contacting the preopercle without a process; 1, with a process, separate from main body of hyomandibula.
28. Symplectic. 0, without posterior process contacting the hyomandibula or if such a process contacts the hyomandibula, it does not fit into a roofed over groove; 1, posterior portion extending dorsally to distinctly fit into a roofed over groove in

the medial face of the lower arm of the hyomandibula.

29. Metapterygoid teeth. 0, Absent; 1, Present.

30. Mesopterygoid teeth. 0, Absent; 1, Present.

31. Ectopterygoid teeth. 0, absent or not as in 1; 1, very small, arranged in a patch covering most or all surface of ectopterygoid.

32. Ectopterygoid-metapterygoid contact. 0, absent; 1, present.

33. Ectopterygoid-mesethmoid contact. 0, absent; 1, present.

34. Branchiostegal rays. 0, three or four rays; 1, five rays.

35. Posterior ceratohyal. 0, with one attached branchiostegal ray; 1, with two attached branchiostegal rays.

36. Lower jaw. 0, dentary with no developed canines or if canines developed not with one canine conspicuously more developed than the others; 1, dentary with one canine of moderate to large size relatively more developed than remaining teeth; 2, dentary with a highly developed canine.

37. Foramen in anterior portion of the snout for the dentary canine. 0, not as in 1; 1, delimited anteriorly and laterally by the premaxilla, posteriorly and posteromedially by the ascending process of the maxilla and anteromedially by the vomer-mesethmoid, with the ascending process of the maxilla passing posterior to the dentary canine.

38. Replacement tooth trenches. 0, not as in 1; 1, shallow, open replacement trenches with the teeth in the mandibular replacement trench horizontally aligned with the tip of the replacement teeth projecting posteriorly.

39. 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.

40. 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 the surface, in some cases one or more spines are further enlarged, and prominent.

41. Anterior portion of first hypobranchial. 0, unelaborated; 1, anteroventrally prolonged, into a prong-shaped process extending from the ventrolateral margin of its main body.

42. Anterior portion of first ceratobranchial. 0, straight, not forming an angle relative to the longitudinal axis of the remaining portion of that ossification; 1, slightly dorsally directed, forming an angle relative to the longitudinal axis of the remaining portion of that ossification; 2, Dorsally directed portion of first ceratobranchial relatively longer than in 1 above, and angle relative to the longitudinal axis of the remaining portion of that ossification more pronounced.

43. Ventral processes on first centrum. 0, absent; 1, present.

44. Contact between neural complex of Weberian apparatus and posterior margin of neurocranium. 0, absent; 1, present.

45. Transverse process of second vertebra. 0, absent; 1, very developed, with a bifurcation distally.

46. Lateral process of second centrum. 0, single structure extending laterally; 1,

dorsoventrally expanded with articular surface at its distal end with two short processes; 2, dorsoventrally flat, with articular surface at its distal with no processes as in 1; 3, triangular-shaped flat sheet of bone, from a dorsal view, extending laterally and posteriorly under the tripus.

47. Lateral process of third centrum. 0, absent; 1, originating ventral to the portion of the transverse process of the second vertebra that is in contact with the transverse process of the third neural arch; 2, originating posterior to the portion of the transverse process of the second vertebra that is in contact with the transverse process of the third neural arch.
48. Blade-like portion of tripus. 0, not elongate; 1, anteriorly elongate.
49. 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 an enlarged rectangular bony plate.
50. Fourth pleural rib + parapophysis. 0, plate-like lateral process; 1, with an greatly enlarged distal end forming a basal plate.
51. Process on posteroventral portion of fourth centrum attached by ligament to process on anterior portion of fifth centrum. 0, absent; 1, present.
52. Process on anteroventral portion of fifth vertebra. 0, absent; 1, present; 2, greatly developed.
53. Fifth pleural rib. 0, not as in 1; 1, relatively very short, with flattened proximal portion bearing two processes, one medially and the other posteriorly directed, distal portion very slender.

54. Parapophysis of precaudal vertebrae. 0, not articulating with vertebra anterior to it; 1, articulating with vertebra anterior to it.

55. Baudelot's ligament. 0, not connected to lateral process of the second vertebra; 1, connected to lateral process of the second vertebra.

56. Second postcleithrum. 0, present; 1, absent.

57. Third postcleithrum. 0, present; 1, absent.

58. Posterodorsal foramen in the coracoid. 0, absent or if present not enlarged as in 1; 1, very enlarged.

59. Coracoids. 0, not expanded; 1, expanded.

60. Coracoids. 0, not fused or corrugated; 1, fused and having a corrugated pattern.

61. Mesocoracoid. 0, small, its dorsal tip reaching the midlength of vertical portion of the cleithrum; 1, enlarged, with broad articular surfaces with cleithrum and coracoid, its dorsal tip reaching the midlength of vertical portion of the cleithrum.

62. Articulation of scapula with medial surface of cleithrum. 0, not shifted posteriorly with scapular foramen covered by cleithrum and vertical through the base of the unbranched pectoral-fin ray is situated anterior to a vertical through the posteriormost margin of the cleithrum; 1, shifted posteriorly so that the scapular foramen is exposed in lateral view and a vertical through the base of the unbranched pectoral-fin ray is situated posterior to a vertical through the posteriormost margin of the cleithrum.

63. Anterior portion of cleithrum articulating with anterior margin of coracoid. 0, not ending in a distinct process; 1, in the form of a vertically elongate process with its

anterodorsal tip pointed; 2, in the form of a vertically elongate process with its anterodorsal portion not pointed but forming a continuous curve.

64. Pelvic-fin insertion. 0, inserted at the ventral profile of the abdomen; 1, inserted dorsally, far from the ventral profile of the abdomen.

65. Branched anal-fin rays. 0, 60 or less; 1, more than 60.

66. 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.

67. Anteromedial branch of one of the anterior epineurals. 0, not contacting the neural complex of the Weberian apparatus; 1, contacting the neural complex of the Weberian apparatus.

68. Myorhabdoi. 0, absent; 1, present.

69. Scales. 0, cycloid; 1, with serrations on their exposed portion.

70. Fringe-like appendices along the lateral surface of posterior chamber of gasbladder. 0, absent; 1, present.

Table 2. Number of specimens of various *Hydrolycus* species with cited neural-spine number posterior to which the first dorsal-fin pterygiophore inserts.

Species	17	18	19	20
Hydrolycus scomberoides	13	28	1	-
Hydrolycus armatus	-	4	13	-
Hydrolycus n. sp. 1	2	41	2	
Hydrolycus n. sp. 2	-	-	8	26

Table 3. Number of specimens of various *Hydrolycus* species with cited hemal-spine number posterior to which the first anal-fin pterygiophore inserts.

Species	25	26	27	28	29	30
Hydrolycus scomberoides	-	27	15	-	-	-
Hydrolycus armatus	-	-	10	3	1	-
Hydrolycus n. sp. 1	-	-	-	4	15	6
Hydrolycus n. sp. 2	23	22	-	-	-	-

Table 4. Morphometrics of (A) holotype of Hydrocynus scomberoides MNHN A 8659 (dry specimen); (B) holotype of Cynodon pectoralis BMNH 1866.2.15.22; (C) all other specimens of Hydrolycus scomberoides from which measurements were taken; (D) holotype MZUSP 00000; (E) paratypes MZUSP 00000; and (F) all other specimens of Hydrolycus n. sp. 1 from which measurements were taken. Dashes indicate proportions that could not be determined because of the condition of the specimen.

Character	A	B	C	D	E	F
Standard length	211.0	145.5	45.0-284.0	286.0	224.0-288.0	70.5-335.0
Body depth at pelvic-fin origin	21.0	29.6	21.6-33.4	31.5	29.1-32.8	27.0-35.3
Body depth at dorsal-fin origin	18.7	24.2	19.1-33.7	30.3	28.0-31.4	24.9-33.2
Snout to dorsal-fin origin	54.2	59.7	52.2-59.5	55.9	54.8-57.3	55.0-58.3
Snout to pectoral-fin origin	22.4	26.6	25.1-31.6	26.7	25.9-27.1	26.0-29.8
Snout to pelvic-fin origin	45.8	44.1	44.0-49.6	47.3	46.3-49.3	45.3-50.0
Snout to anal-fin origin	68.5	67.2	65.6-74.4	67.1	66.0-68.9	63.3-71.8
Eye to dorsal-fin origin	47.4	50.0	42.7-52.9	47.9	46.5-48.0	44.5-49.8
Dorsal-fin origin to caudal-fin origin	45.4	44.9	41.3-46.2	46.8	45.9-47.9	43.4-48.4
Dorsal-fin origin to adipose fin origin	33.4	32.8	30.0-35.3	33.3	32.9-35.2	30.7-35.1
Pectoral-fin origin to anal-fin origin	52.7	41.5	37.6-52.9	42.7	40.3-44.1	37.6-48.5
Caudal-peduncle length	8.1	7.6	6.3-8.0	8.1	7.8-9.4	7.1-9.4
Caudal-peduncle depth	4.9	7.7	6.4-7.9	7.1	6.5-7.8	6.2-7.9
Head-length	19.4	21.9	19.8-26.4	21.7	21.4-22.4	21.1-24.8
Snout length	24.5	22.3	22..0-25.9	23.7	23.0-25.7	22.6-27.6

Table 4. (continued)

Character	A	B	C	D	E	F
Orbital diameter	30.6	31.7	29.5-35.7	36.4	35.7-37.5	35.4-43.0
Inter-orbital width	27.6	27.3	21.8-30.5	22.7	22.8-24.6	20.1-25.4
Pos-orbital length	47.9	48.3	43.2-50.2	41.2	39.0-41.5	33.2-43.7
Dorsal-fin base	5.1	5.2	5.9-7.6	8.0	7.6-8.6	7.1-9.1
Dorsal-fin length	-	17.1	15.7-20.8	-	20.6-21.7	19.5-23.1
Anal-fin base	26.5	28.2	25.4-29.1	29.8	28.4-31.3	27.5-31.3
Pectoral-fin length	-	32.8	30.9-37.1	31.3	29.1-32.7	29.4-33.4
Pelvic-fin length	-	12.7	8.7-15.1	15.4	13.8-15.7	13.5-17.0
Upper jaw length	85.1	81.8	79.0-89.2	77.8	77.5-80.0	73.2-81.6
Dentary canine length	25.4	21.0	14.6-25.4	13.4	13.3-15.7	11.6-17.3

Table 5. Meristics of (A) holotype of Hydrocynus scomberoides, MNHN A 8659 (dry specimen); (B) holotype of Cynodon pectoralis, BMNH 1866.2.15.22; (C) all other specimens of Hydrolycus scomberoides from which counts were taken; (D) holotype MZUSP 00000; (E) paratypes MZUSP 00000; and (F) all other specimens of Hydrolycus n. sp. 1 from which counts were taken. Dashes indicate counts that could not be determined because of the condition of the specimen.

Character	A	B	C	D	E	F
Scales along lateral-line series	-	100	93-106	95	89-95	89-99
Scale rows above lateral line	-	22	17-23	19	16-19	17-21
Scale rows below lateral line	-	15	16-25	15	12-15	12-18
Scale rows around caudal peduncle	-	31	27-32	25	25-28	24-28
Branched anal-fin rays	-	44	39-47	42	38-42	36-43
Branched pectoral-fin rays	17	18	15-19	16	16-17	16-18
Branched pelvic-fin rays	8	8	7-9	8	7-8	7-9
Gill rakers on first ceratobranchial	-	18	13-20	15	14-18	15-20

Table 6. Morphometrics (A) all specimens of Hydrolycus armatus from which measurements were taken; (B) holotype, MZUSP 00000; (C) paratypes MZUSP 00000; and (D) all other specimens of Hydrolycus n. sp. 2 from which measurements were taken.

Character	A	B	C	D
Standard length	132.1-656.0	268	244.0-445.0	136.0-430.0
Body depth at pelvic-fin origin	23.4-32.9	28.9	24.6-28.2	22.0-31.5
Body depth ar dorsal-fin origin	22.5-31.	27.9	24.9-27.8	21.3-30.7
Snout to dorsal-fin origin	54.4-61.1	58.6	57.3-59.8	54.5-59.6
Snout to pectoral-fin origin	25.7-30.7	26.8	26.0-27.8	24.9-29.7
Snout to pelvic-fin origin	43.1-49.8	46.2	44.4-49.0	43.9-48.4
Snout to anal-fin origin	66.3-74.2	69.8	67.9-72.0	67.2-74.4
Eye to dorsal-fin origin	44.5-51.3	48.4	47.4-50.2	44.5-50.7
Dorsal-fin origin to caudal-fin origin	42.7-49.9	44.2	42.6-48.3	43.5-48.2
Dorsal-fin origin to adipose fin origin	28.8-35.9	31.6	30.4-34.0	29.9-34.5
Pectoral-fin origin to anal-fin origin	39.8-50.0	44.0	40.2-45.2	41.1-51.6
Caudal-peduncle length	8.4-11.2	9.0	8.1-9.4	8.2-10.3
Caudal-peduncle depth	6.4-8.4	6.7	6.3-7.0	5.9-7.8
Head-length	22.5-25.9	22.4	21.8-23.3	20.2-24.4
Snout length	22.2-26.0	24.7	22.7-25.4	22.0-24.9

Table 6. (continued)

Character	A	B	C	D
Orbital diameter	20.8-35.0	32.3	28.6-33.7	27.8-38.9
Inter-orbital width	23.8-29.9	25.8	24.4-25.8	21.2-27.5
Pos-orbital length	44.5-57.1	44.7	44.9-48.0	40.5-50.8
Dorsal-fin base	22.3-28.5	7.8	8.1-8.6	7.0-8.9
Dorsal-fin length	16.4-24.4	18.4	18.4-21.7	17.3-20.9
Anal-fin base	22.3-28.5	25.5	24.0-27.3	21.8-27.0
Pectoral-fin length	24.5-32.6	27.2	26.9-28.4	25.8-31.5
Pelvic-fin length	12.9-18.9	15.9	13.1-16.0	13.3-18.1
Upper jaw length	80.0-88.0	87.5	80.8-86.6	81.6-88.6
Dentary canine length	20.5-26.9	22.2	18.3-21.2	18.2-29.1

Table 7. Meristics of (A) all specimens of Hydrolycus armatus from which counts were taken; (B) holotype, MZUSP 00000; (C) paratypes MZUSP 00000; and (D) all other specimens of Hydrolycus n. sp. 2 from which counts were taken.

Character	A	B	C	D
Scales along lateral-line series	121-154	109	106-112	102-119
Scale rows above lateral line	30-42	24	20-26	20-29
Scale rows below lateral line	24-38	19	15-19	14-22
Scale rows around caudal peduncle	32-41	29	28-33	25-33
Branched anal-fin rays	27-35	35	32-36	29-37
Branched pectoral-fin rays	14-17	16	15-17	15-17
Branched pelvic-fin rays	7-9	8	8	7-9
Gill rakers on first ceratobranchial	15-21	-	15-18	12-20

Table 8. Frequency distribution of number of vertebrae of Hydrolycus species. Vertebrae incorporated into fused $PU_1 + U_1$ counted as a single element and vertebrae of Weberian apparatus counted as four elements.

Species	44	45	46	47	48	49	50	51	52	53
Hydrolycus somberoides	-	-	-	-	-	16	23	3	-	-
Hydrolycus armatus	1	5	12	-	-	3	4	2	-	-
Hydrolycus n. sp. 1	-	-	-	-	-	-	9	34	2	
Hydrolycus n. sp. 2	-	-	-	-	-	-	1	14	19	1

Table 9. Frequency distribution of pelvic-fin rays in Cynodon species.

Species	6	7	8
Cynodon gibbus	-	3	58
Cynodon n. sp. 1	1	44	3

Table 10. Morphometrics of (A) all specimens of *Cynodon gibbus* from which measurements were taken; (B) holotype MZUSP 00000; (D) paratypes MZUSP 00000 of *Cynodon* n. sp. 1; and (D) all other specimens of *Cynodon* n. sp. 1 from which measurements were taken.

Character	A	B	C	D
Standard length	77.0-280.0	238.0	202.0-238.0	94.5-312.0
Body depth at pelvic-fin origin	21.5-31.0	28.8	24.9-26.3	22.4-28.9
Body depth ar dorsal-fin origin	19.8-25.9	26.3	22.4-24.3	20.5-26.4
Snout to dorsal-fin origin	52.9-59.0	56.8	54.9-55.8	52.6-57.1
Snout to pectoral-fin origin	24.8-28.9	26.3	24.6-25.9	24.4-27.9
Snout to pelvic-fin origin	43.3-49.3	45.8	44.1-46.2	43.2-47.9
Snout to anal-fin origin	50.2-58.0	53.7	52.4-54.9	49.7-55.9
Eye to dorsal-fin origin	45.1-52.3	49.4	48.7-49.6	45.5-51.0
Dorsal-fin origin to caudal-fin origin	43.8-48.5	46.1	45.2-46.9	44.7-48.4
Dorsal-fin origin to adipose fin origin	31.3-36.5	35.3	32.6-35.1	32.4-35.8
Pectoral-fin origin to anal-fin origin	26.3-33.1	29.9	27.3-33.1	26.3-32.3
Caudal-peduncle length	5.5-7.6	5.7	5.9-6.7	5.1-8.3
Caudal-peduncle depth	5.6-7.5	7.8	6.5-7.1	6.1-7.8
Head-length	19.0-22.1	21.1	19.6-20.3	18.8-21.8
Snout length	23.5-29.4	24.5	24.2-26.0	23.4-27.8

Table 10. (Continued)

Character	A	B	C	D
Orbital diameter	24.9-33.8	30.4	30.7-32.1	30.1-34.4
Inter-orbital width	26.1-36.6	29.2	27.7-29.2	23.5-30.9
Pos-orbital length	43.3-54.7	48.9	48.4-49.6	42.7-48.7
Dorsal-fin base	4.5-6.5	6.6	5.6-6.4	5.0-6.6
Dorsal-fin length	13.1-17.0	15.9	14-15.1	13.3-15.9
Anal-fin base	41.5-49.0	45.3	45.4-46.7	42.0-48.1
Pectoral-fin length	28.9-34.0	33.1	30.8-30.9	27.4-33.0
Pelvic-fin length	6.9-10.5	6.9	7.3-8.0	7.4-9.1
Upper jaw length	75.5-84.6	75.3	76.0-80.0	75.7-84.6
Dentary canine length	11.6-16.9	10.9	11.3-12.7	9.6-16.1

Table 11. Meristics of (A) all specimens of *Cynodon gibbus* from which counts were taken; (B) holotype MZUSP 00000; (C) paratypes, MZUSP 00000, of *Cynodon* n. sp. 1; and (D) all other specimens of *Cynodon* n. sp. 1 from which counts were taken. See "Remarks" under *Cynodon* species accounts for details about number of branched pelvic-fin rays, indicated by stars in the table below.

Character	A	B	C	D
Scales along lateral-line series	96-109	100	104-106	100-109
Scale rows above lateral line	17-23	19	16-19	15-21
Scale rows below lateral line	18-23	19	16-18	13-20
Scale rows around caudal peduncle	27-33	28	26-29	24-30
Branched anal-fin rays	65-80	69	69-76	61-77
Branched pectoral-fin rays	14-17	16	15-16	15-17
Branched pelvic-fin rays	7-8*	7	6-7	7-8*
Gill rakers on first ceratobranchial	16-20	19	19-20	15-21

Table 12. Frequency distribution of branched anal-fin rays in Cynodon species.

Species	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Cynodon gibbus	-	-	-	-	2	-	-	3	4	6	7	5	6	5	6	5	5	11	2	2
Cynodon n. sp. 1	1	-	1	2	2	3	3	5	7	4	4	3	4	3	5	1	1	-	-	-

Table 13. Frequency distribution of branched anal-fin rays in *Rhaphiodon vulpinus*. Three specimens (MZUSP 32808) from Rio Xingu, Brazil have 50 anal-fin rays.

38	39	40	41	42	43	44	45	46	47	48	49	50
1	2	5	7	10	8	7	6	6	2	-	-	3

Table 14. Frequency distribution of lateral-line scales in *Rhaphiodon vulpinus*. Three specimens (MZUSP 32808) from Rio Xingu, Brazil have 142, 150 and 152 lateral-line scales.

122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137
1	1	1	-	4	7	4	6	5	6	4	7	6	4	1	-

138	139	140	141	142	143	144	145	146	147	148	149	150	151	152
1	-	-	-	1	-	-	-	-	-	-	-	1	-	1

Table 15. **Morphometrics of (A) holotype of Rhaphiodon vulpinus, MHNN 822; (B) holotype of Hydropardus rapax, ZMC 183; and (C) all other specimens of Rhaphiodon vulpinus (including specimens from upper Rio Xingu, Brazil, MZUSP 32808) from which measurements were taken. Dashes indicate proportions that could not be determined because of the condition of the specimen.**

Character	A	B	C
Standard length	303.0	623.0	68.9-604.0
Body depth at pelvic-fin origin	12.9	-	13.3-19.9
Body depth ar dorsal-fin origin	13.3	14.8	12.7-19.6
Body depth at pectoral-fin origin	15.1	18.1	16.0-21.2
Snout to dorsal-fin origin	72.9	69.8	69.3-74.4
Snout to pectoral-fin origin	23.1	22.0	20.9-25.4
Snout to pelvic-fin origin	60.4	-	57.4-63.3
Snout to anal-fin origin	70.0	68.4	67.4-73.2
Eye to dorsal-fin origin	65.3	62.4	61.0-68.0
Dorsal-fin origin to caudal-fin origin	28.2	28.9	26.5-32.8
Dorsal-fin origin to adipose fin origin	17.0	18.6	15.3-19.8
Pectoral-fin origin to anal-fin origin	48.2	48.8	36.6-54.7
Caudal-peduncle length	6.7	7.1	6.2-8.3
Caudal-peduncle depth	5.5	5.8	5.3-7.3
Head-length	19.3	18.5	17.2-22.5
Snout length	26.4	28.4	25.2-29.3

Table 15. (continued)

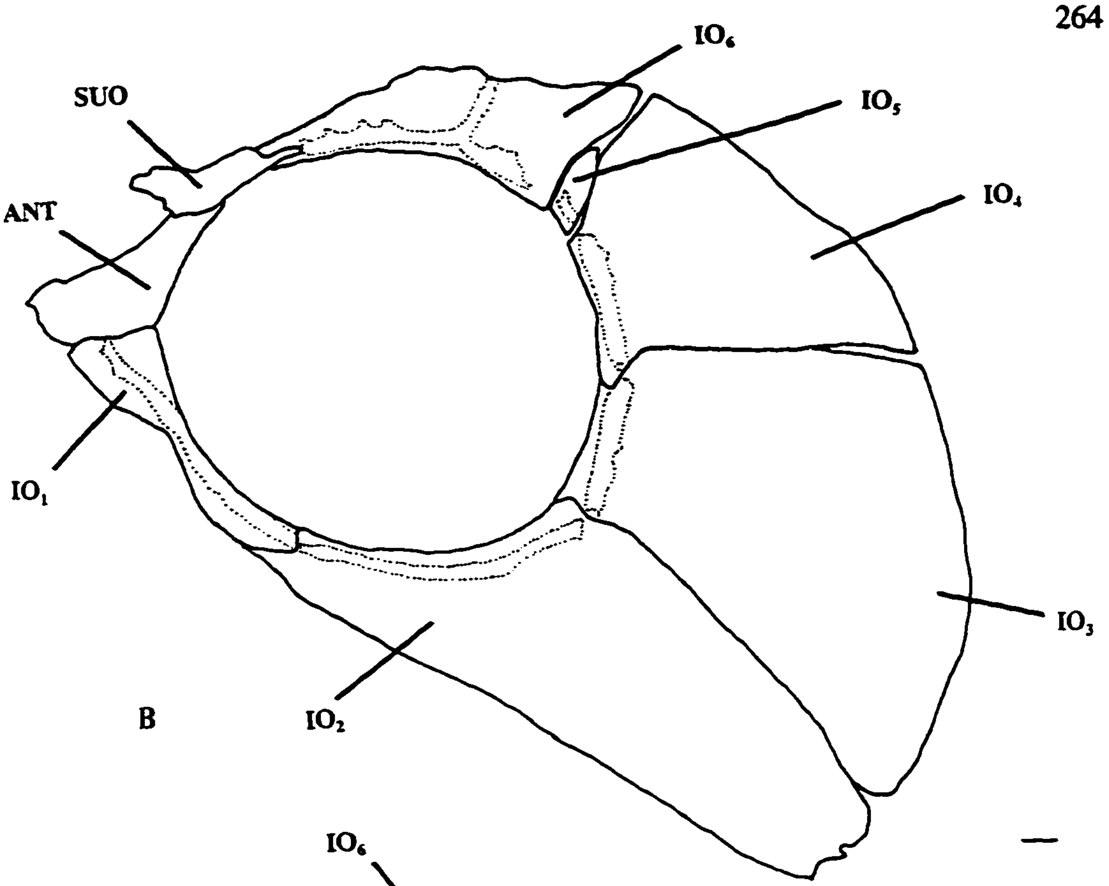
Character	A	B	C
Orbital diameter	20.0	17.8	17.5-26.6
Inter-orbital width	16.8	20.7	14.7-19.4
Pos-orbital length	55.0	55.9	46.5-58.9
Dorsal-fin base	5.3	5.5	4.4-6.5
Dorsal-fin length	-	9.4	8.6-12.2
Anal-fin base	25.9	24.1	23.6-28.4
Anal-fin length	-	-	8.3-13.4
Pectoral-fin length	-	-	20.9-29.2
Pelvic-fin length	-	-	4.4-6.6
Upper jaw length	69.3	69.7	67.1-76.1
Dentary canine length	17.6	19.3	12.1-17.9

Table 16. Meristics of (A) holotype of Rhaphiodon vulpinus MHNN 822; (B) holotype of Hydropardus rapax, ZMC 183; and (C) all other specimens of Rhaphiodon vulpinus (including specimens from upper Rio Xingu, Brazil, MZUSP 32808. See tables 13 and 14 for details on counts indicated below by a star) from wich counts were taken. Dashes indicate counts that could not be determined because of the condition of the specimen.

Character	A	B	C
Scales along lateral-line series	135	121	122-152*
Scale rows above lateral line	29	-	22-33
Scale rows below lateral line	16	-	15-22
Scale rows around caudal peduncle	37	27	30-39
Branched anal-fin rays	45	37	38-50*
Branched pectoral-fin rays	16	15	12-17
Branched pelvic-fin rays	7	-	6-7
Gill rakers on first ceratobranchial	17	18	15-21

Figure 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.

Figure 2. Infraorbital series, supraorbital and antorbital of (A) Hydrolycus n. sp. 1, MZUSP 32638; and (B) Hydrolycus armatus, MZUSP 32607; left side, lateral view, anterior to left.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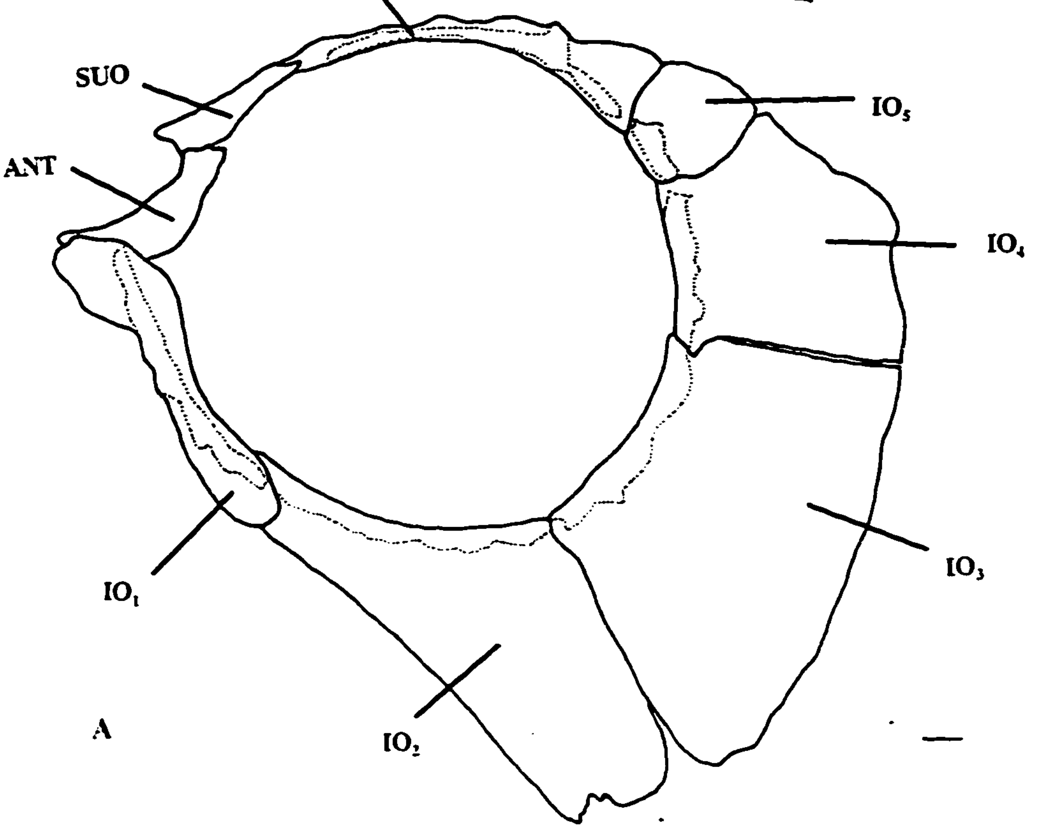
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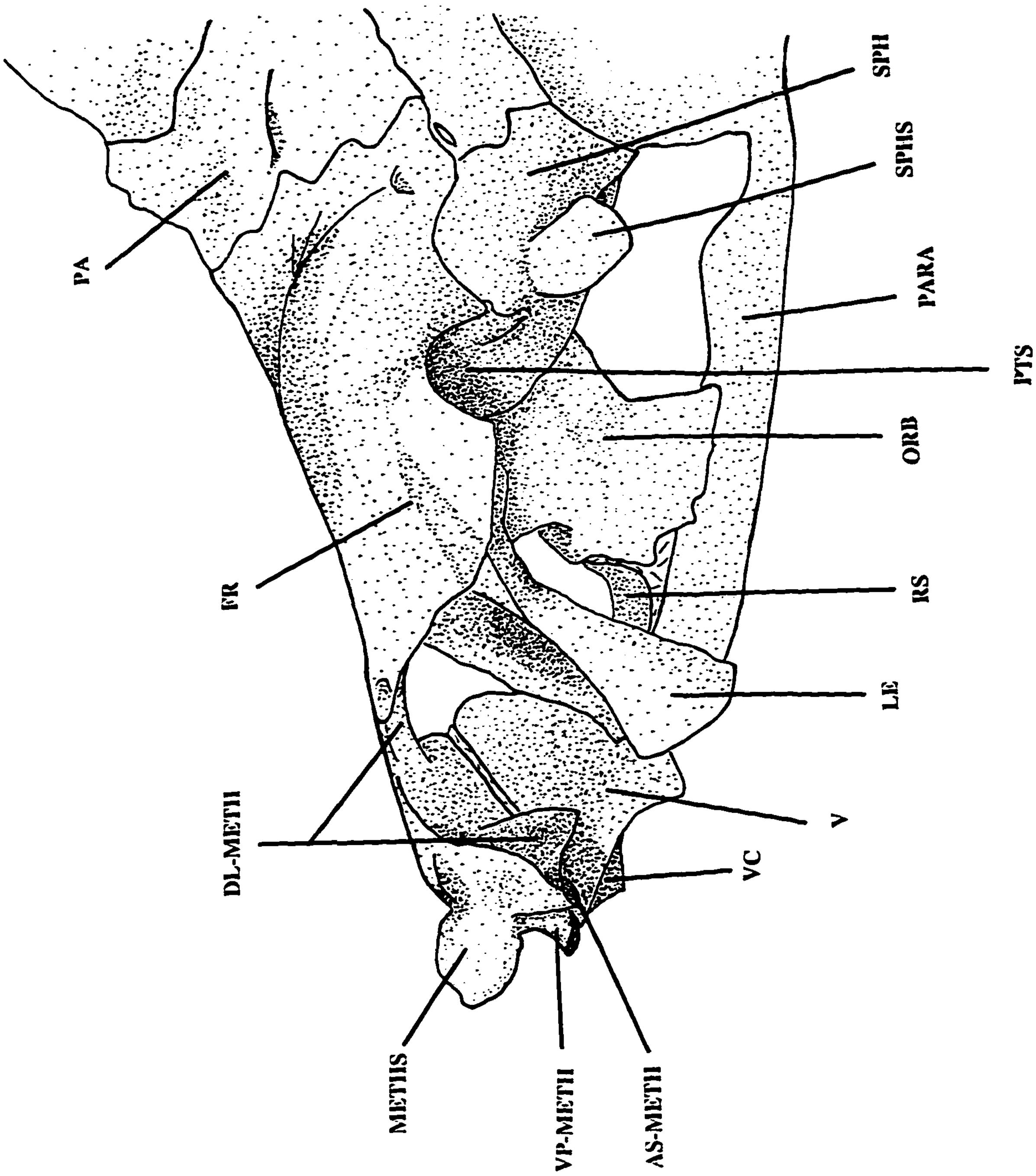
Figure 3. Anterior and orbital regions of neurocranium of Hydrolycus scomberoides, MZUSP 32093; left side, lateral view, anterior to left.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PA

Figure 4. Anterior and orbital regions of neurocranium of Hydrolycus n. sp. 1, MZUSP 32638; left side, lateral view, anterior to left.

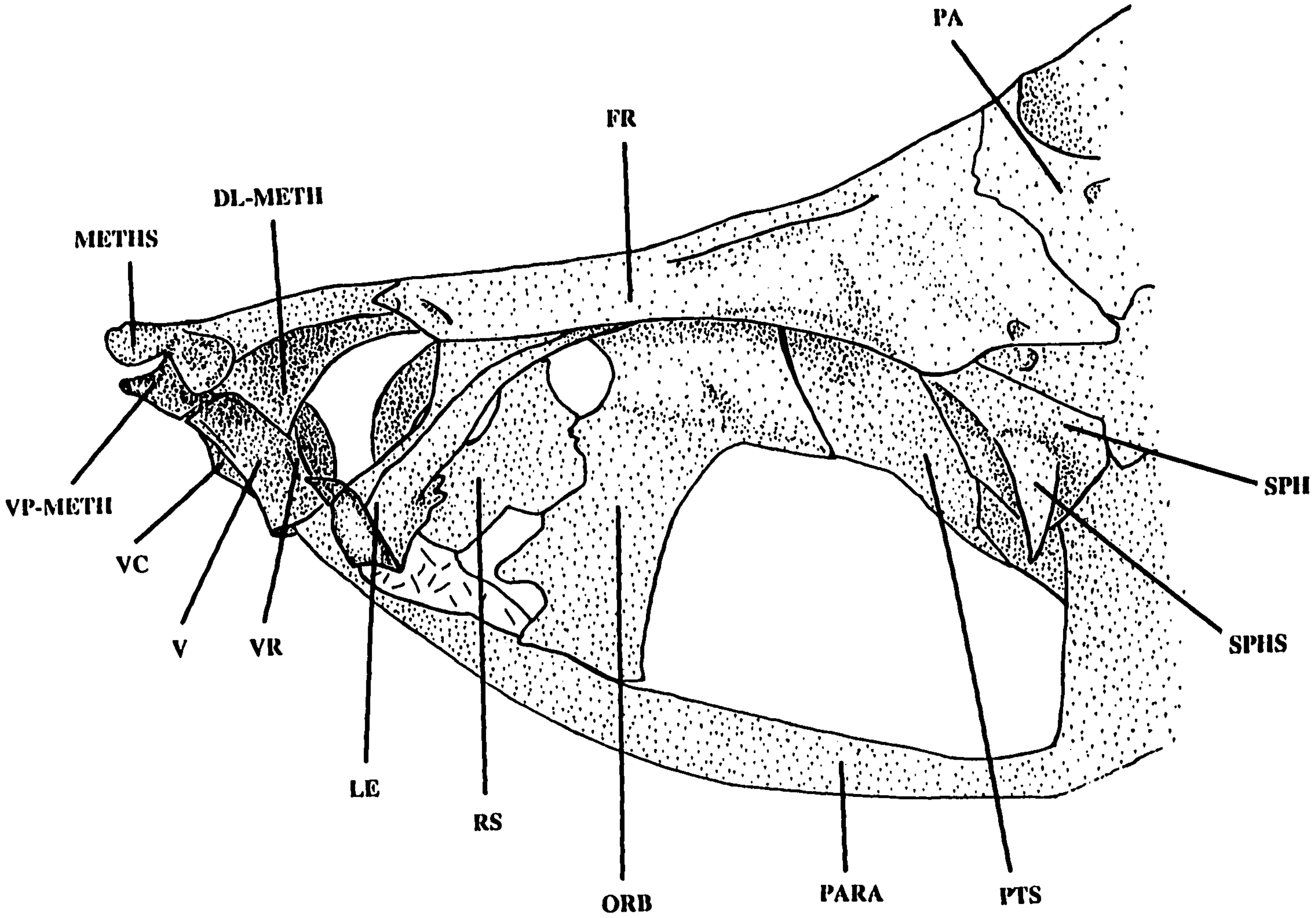
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Figure 5. Anterior and orbital regions of neurocranium of *Hydrolycus armatus*, MZUSP 32607; left side, lateral view, anterior to left.

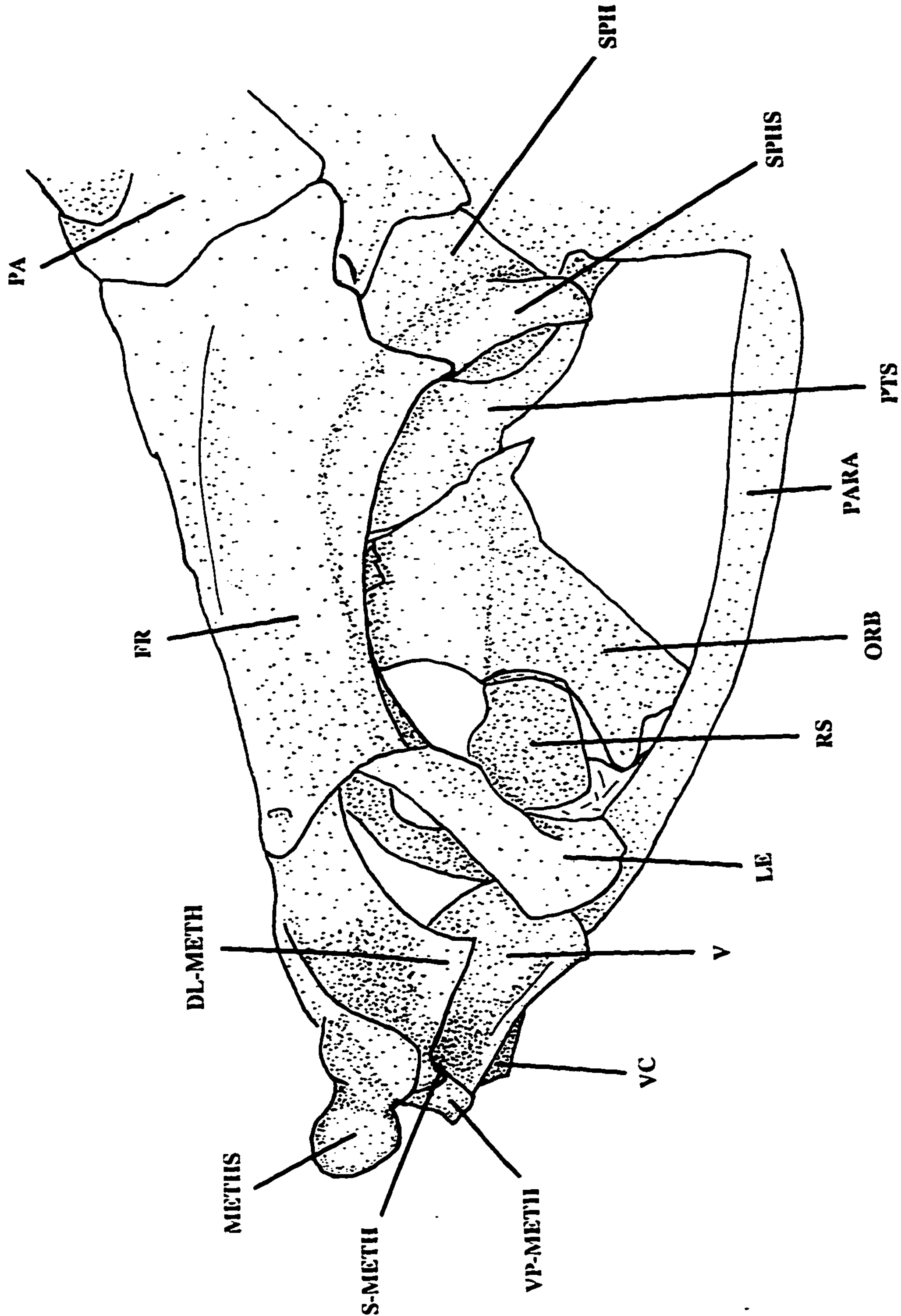
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Figure 6. Anterior and orbital regions of neurocranium of Cynodon gibbus, MZUSP 32587; left side, lateral view, anterior to left.

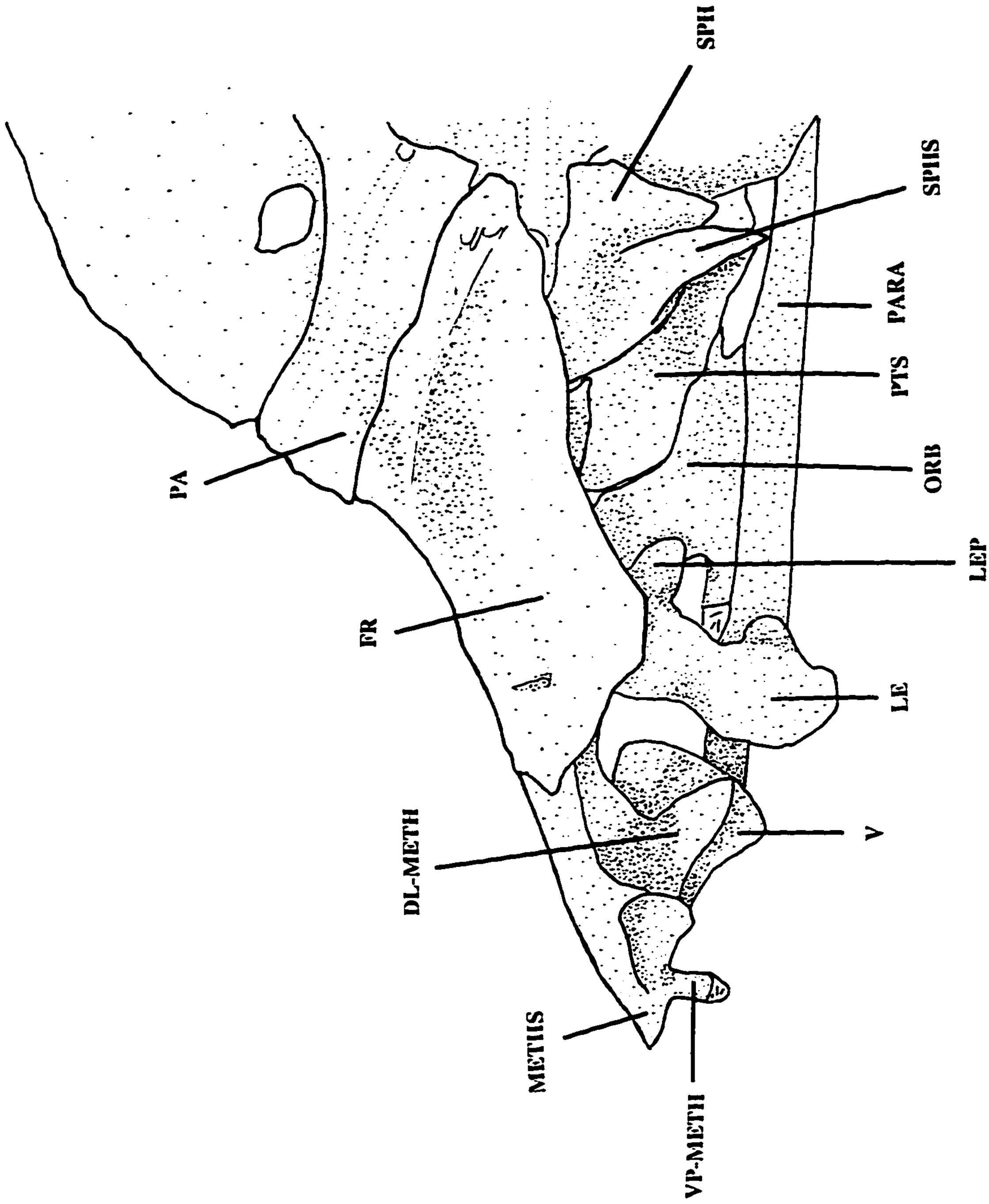
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Figure 7. Anterior and orbital regions of neurocranium of Rhaphiodon vulpinus, MZUSP 32812; left side, lateral view, anterior to left.

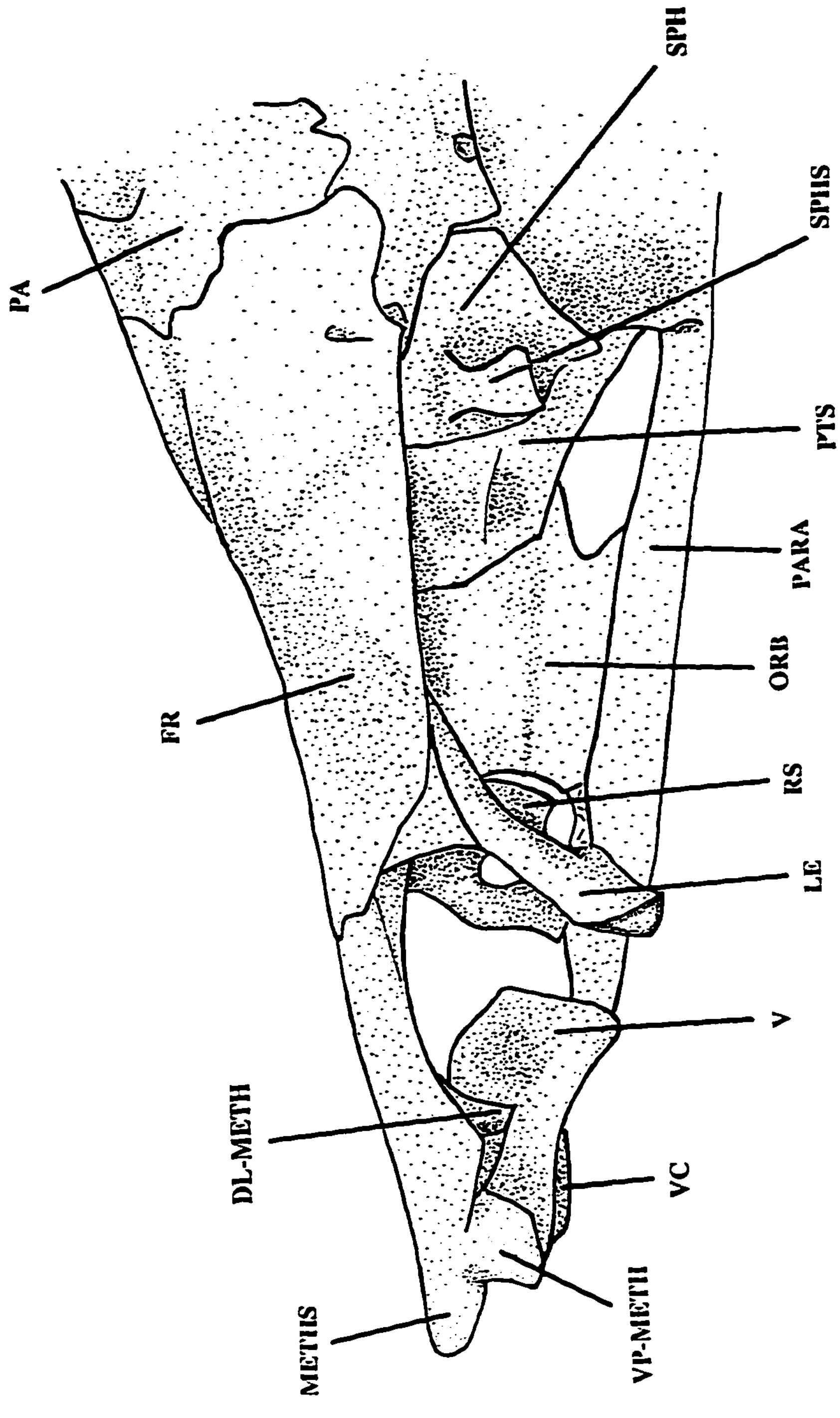
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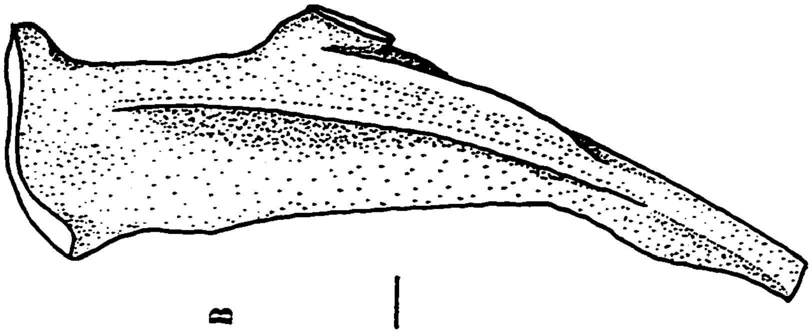
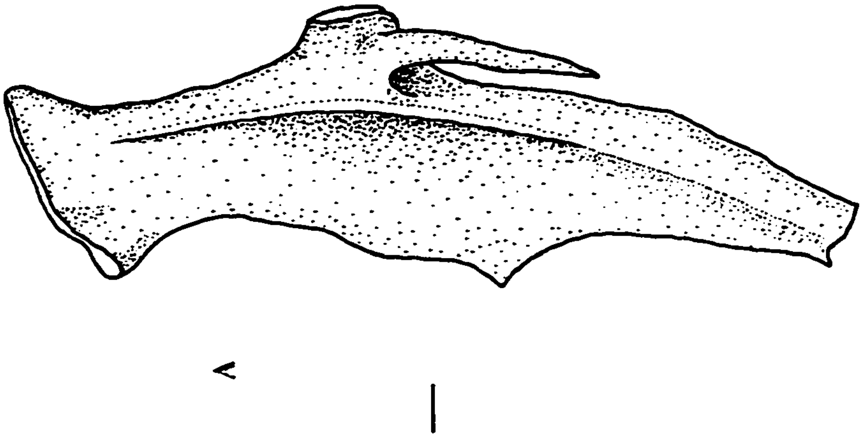
Figure 8. Hyomandibula of (A) Hydrolycus n. sp. 1, MZUSP 32638; and (B) Cynodon gibbus, MZUSP 32587; left side, lateral view, anterior to left.



B



A

Figure 9. 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.

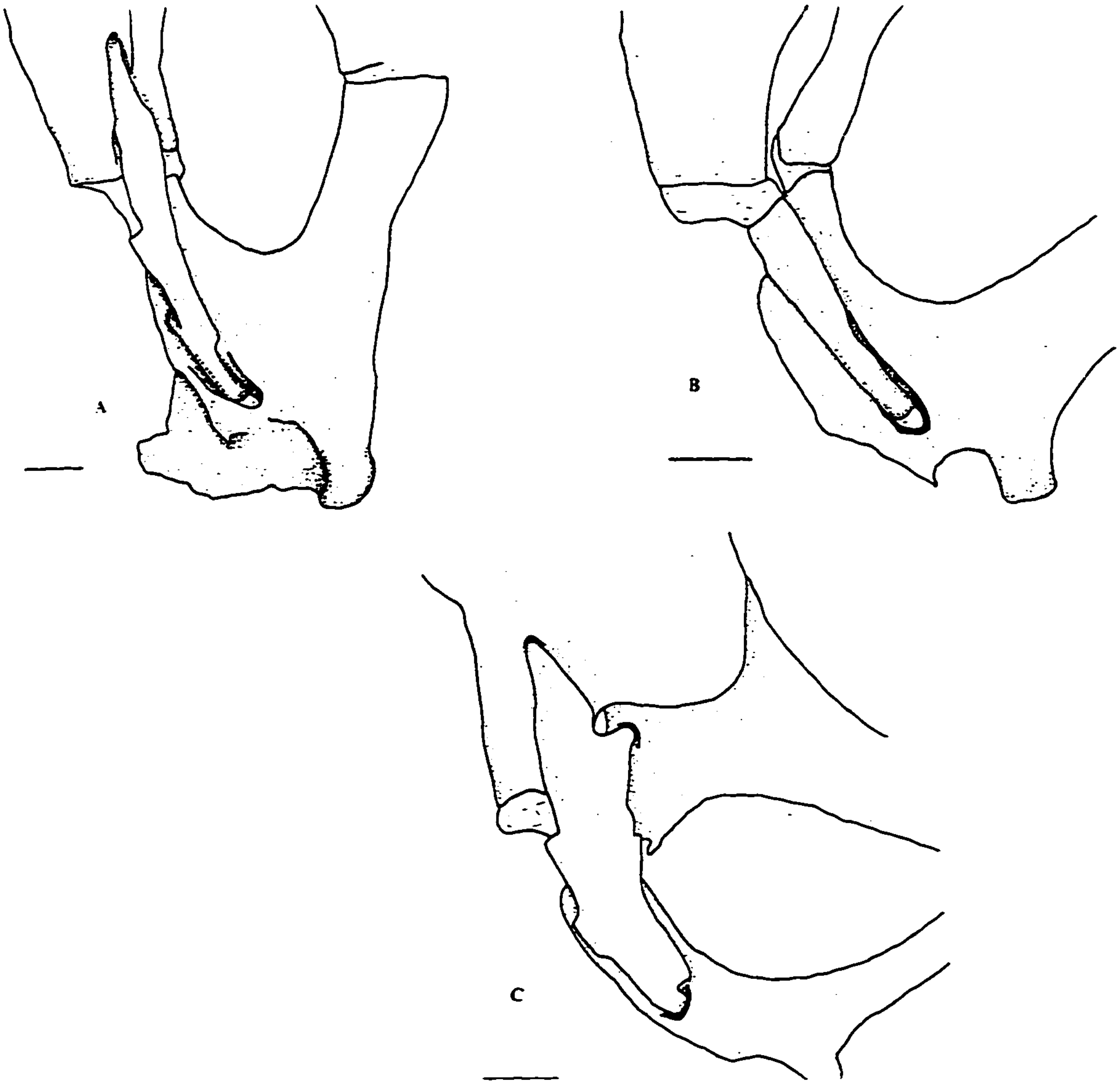

A
B
C

Figure 10. Lower jaw of (A) Hydrolycus n. sp. 1, MZUSP 32645, 226.0 mm SL, and (B) H. armatus, MZUSP 32607, 210.0 mm SL, showing the difference in the relative size of the largest dentary canine.

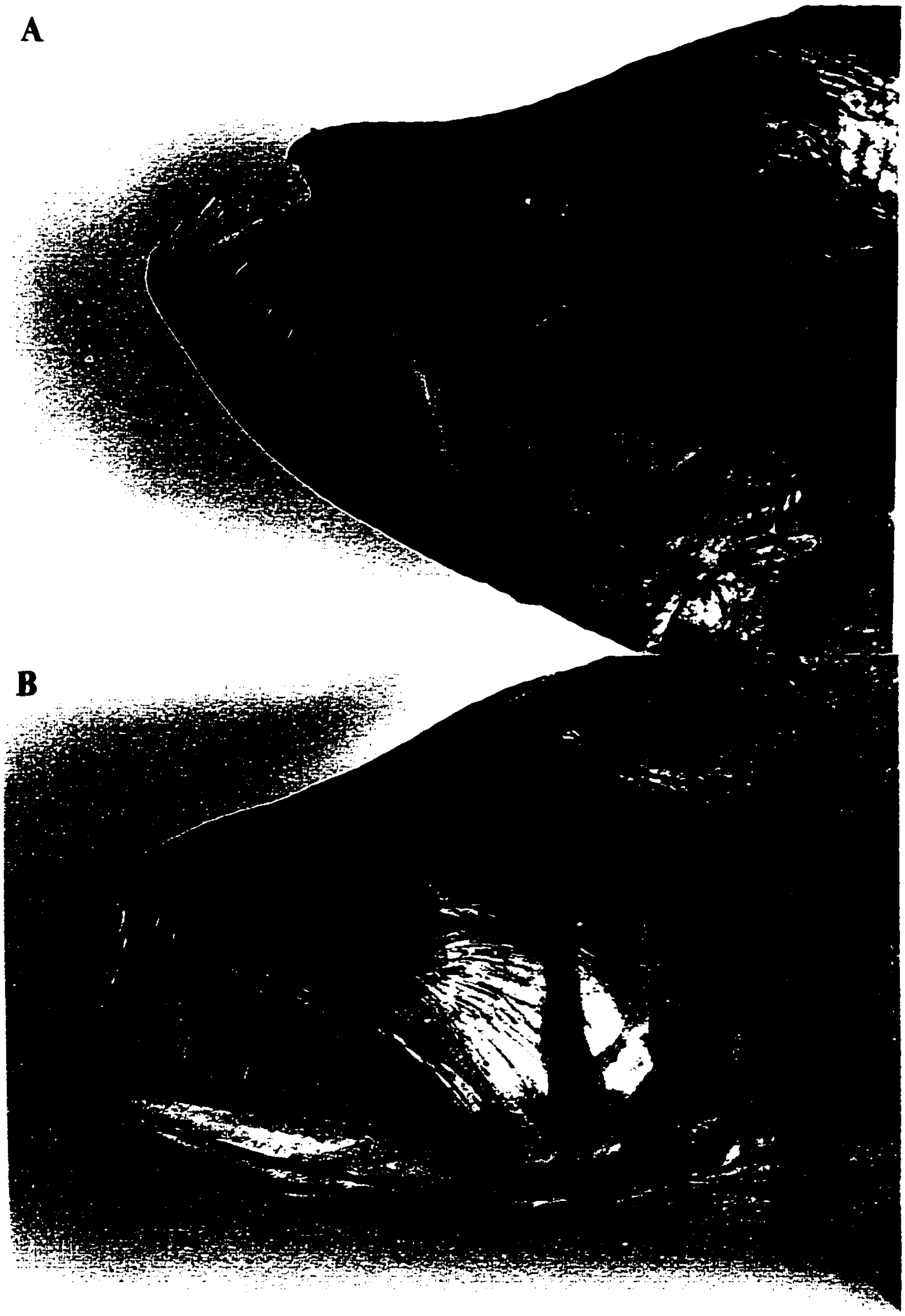

A
B

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

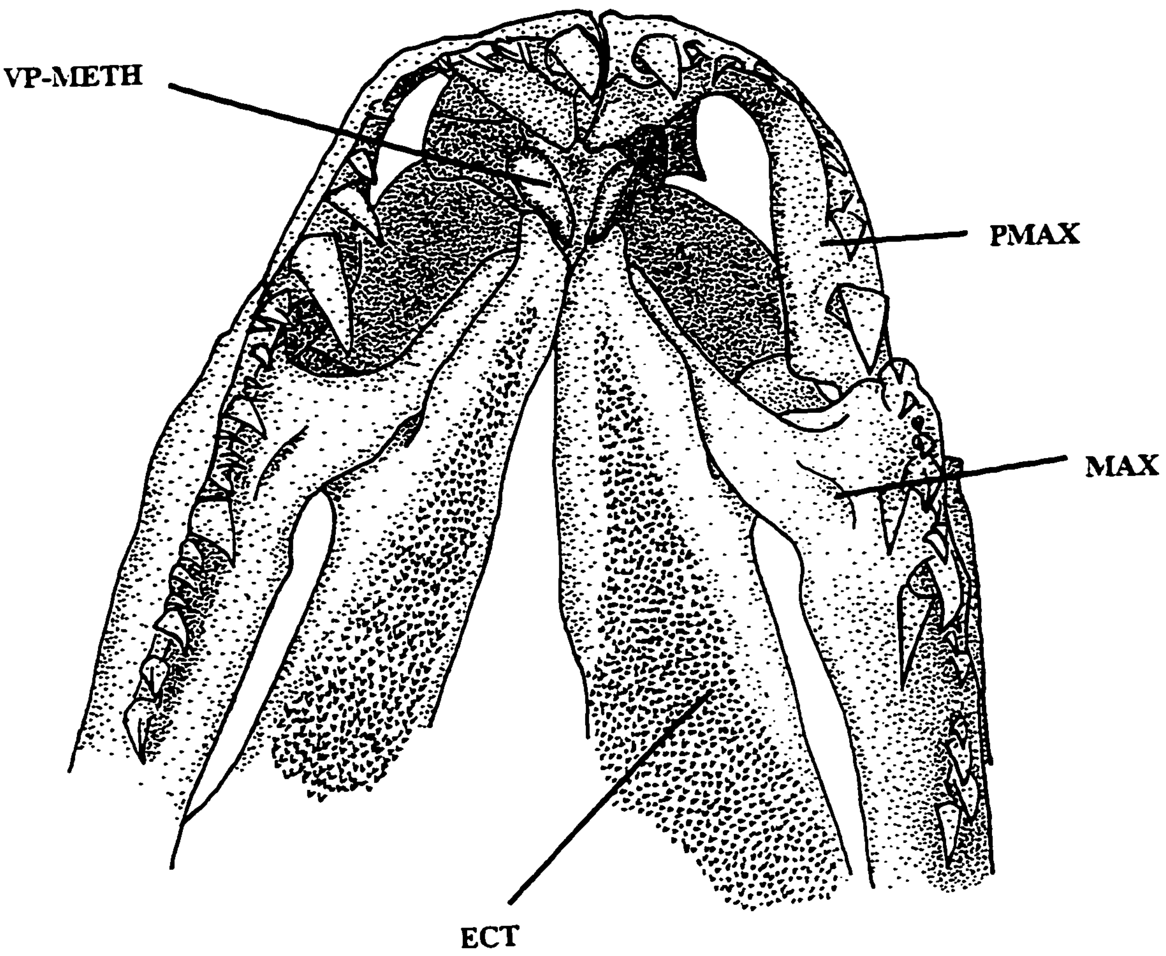
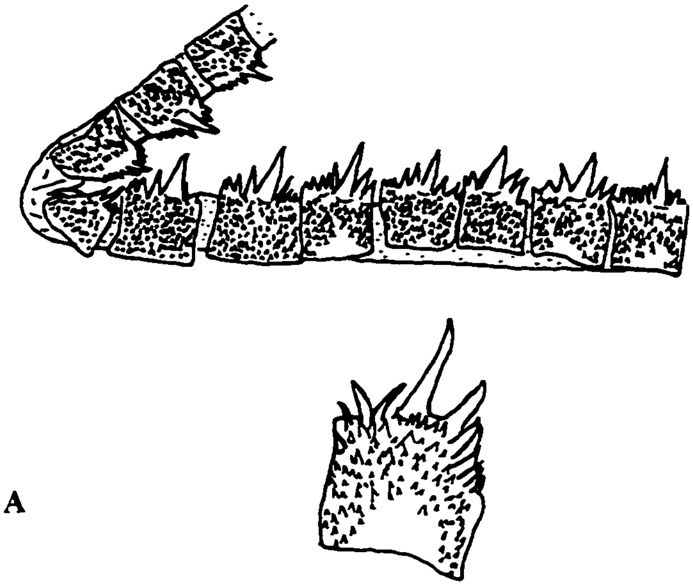
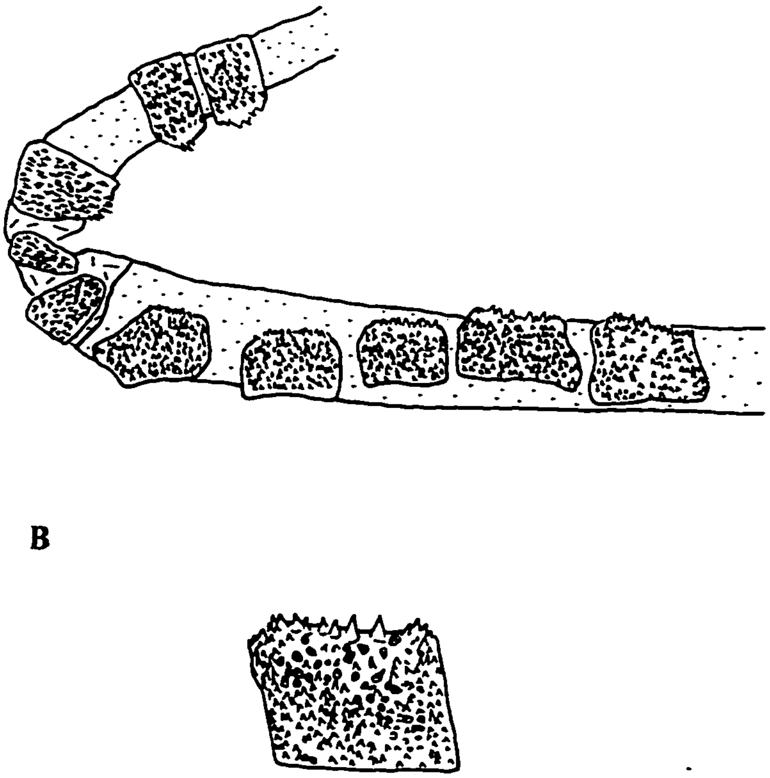

VP-METH
PMAX
MAX
ECT

Figure 12. Posterior portion of first gill arch of (A) Cynodon n. sp. 1, MZUSP 32585, and (B) Hydrolycus armatus, MZUSP 32607 with enlarged gill raker; lateral view, right side, anterior to right.



A



B

Figure 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.**

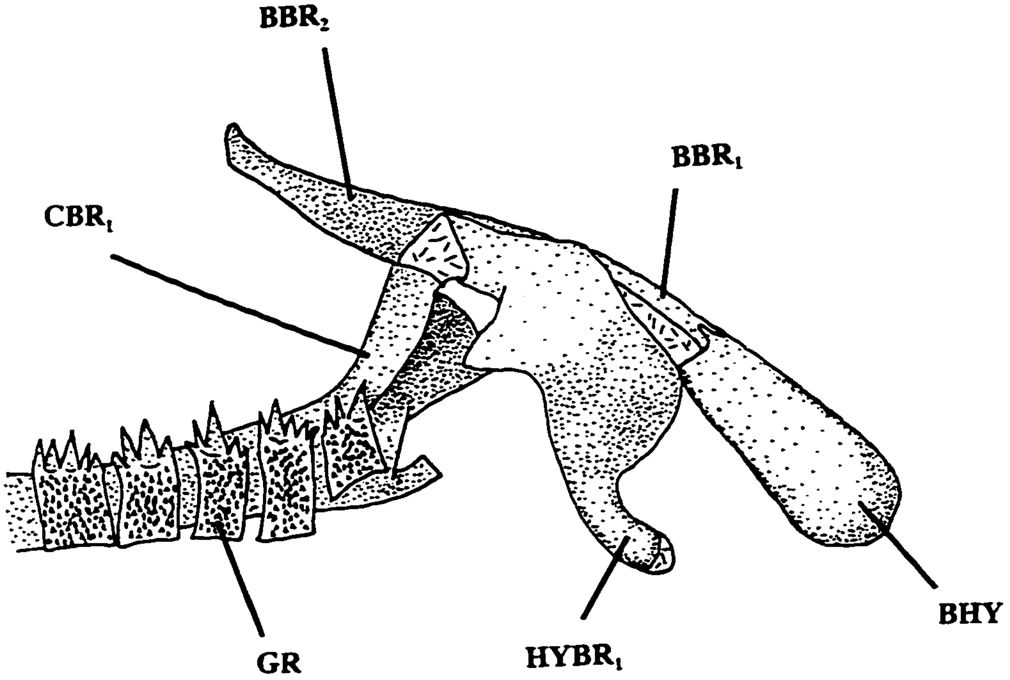

BBR₂
BBR₁
CBR₁
GR
HYBR₁
BHY

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

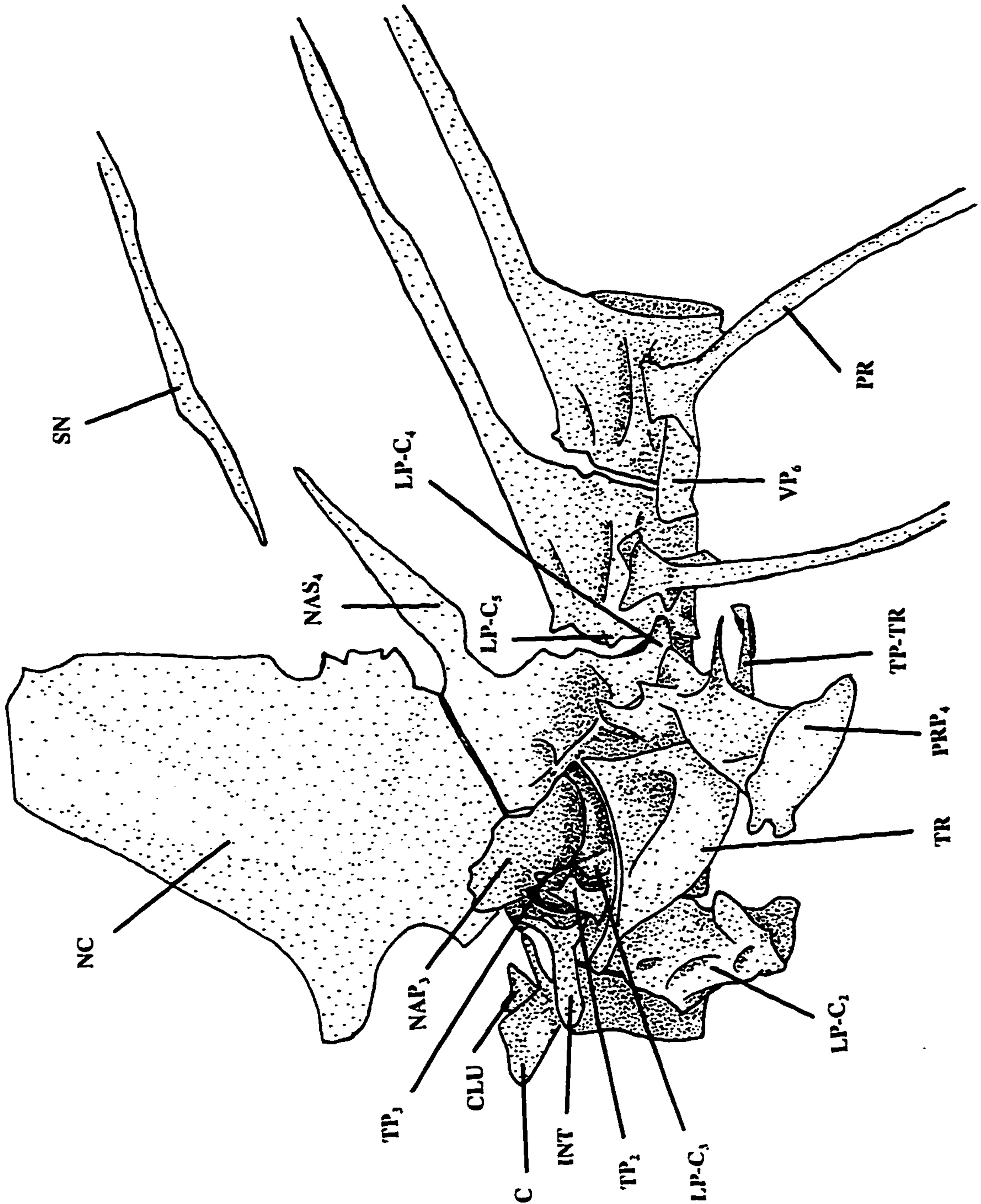

SN
LP-C$_4$
VP$_6$
PR
NAS$_4$
LP-C$_5$
TP-TR
PRP$_4$
TR
NC
NAP$_3$
TP$_3$
CLU
SC
INT
TP$_2$
LP-C$_3$
LP-C$_2$

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

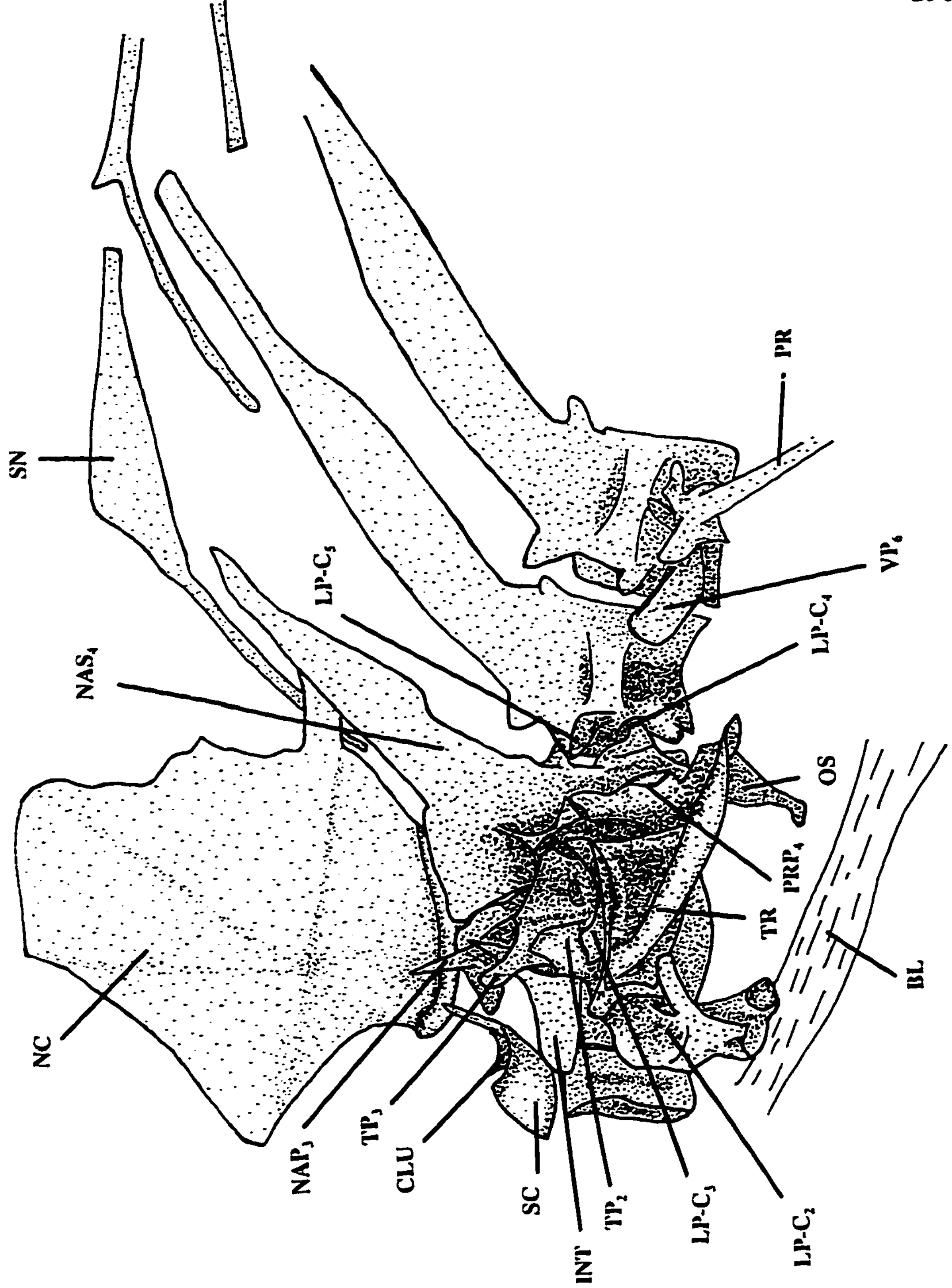

SN
NAS$_4$
LP-C$_5$
PR
VP$_6$
LP-C$_4$
OS
PRP$_4$
TR
BL
NC
NAP$_3$
TP$_3$
CLU
SC
INT
TP$_2$
LP-C$_3$
LP-C$_2$

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

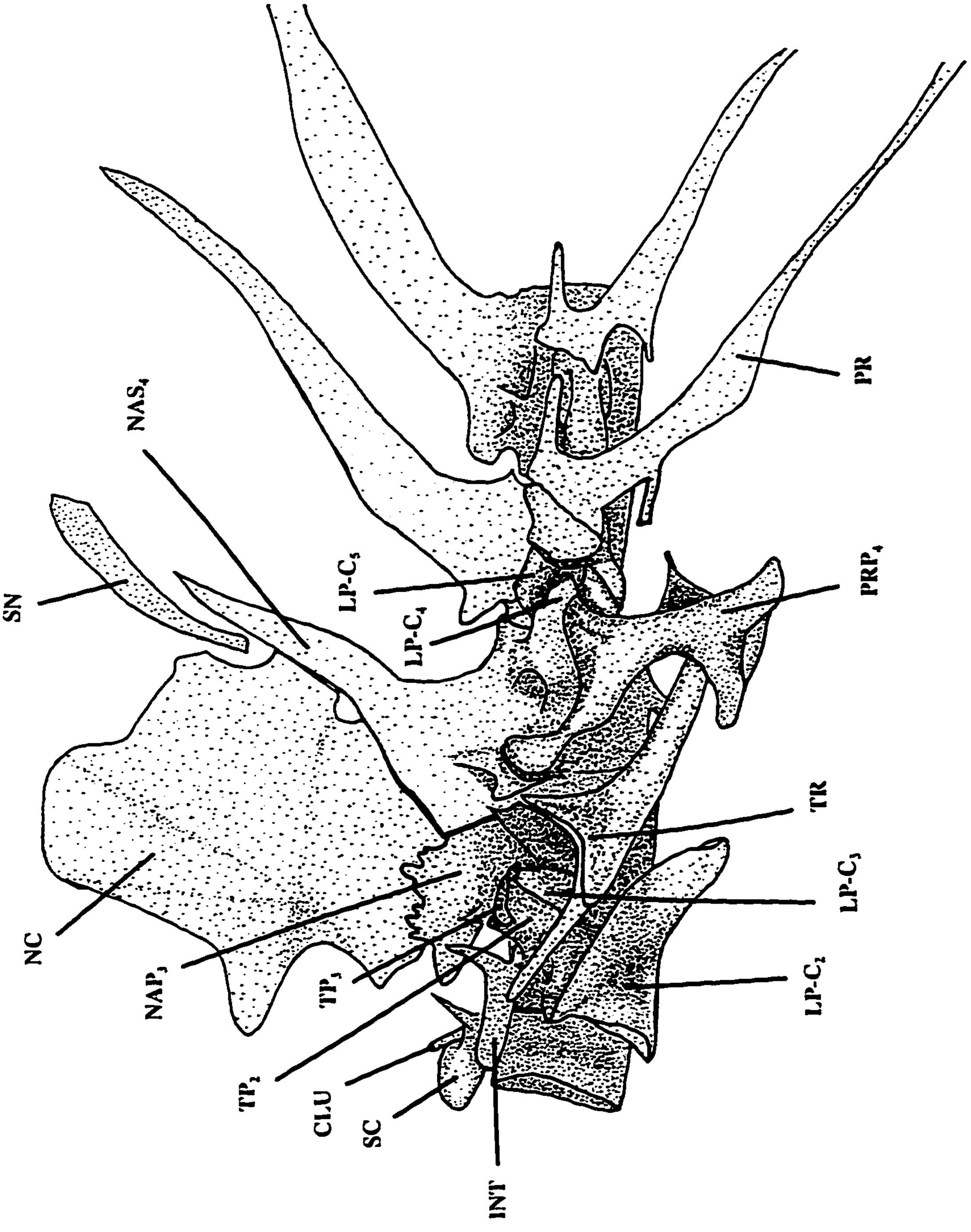

PR
PRP_4
TR
$LP\text{-}C_3$
$LP\text{-}C_2$
INT
SC
CLU
TP_2
TP_3
NAP_3
NC
SN
NAS_4
$LP\text{-}C_5$
$LP\text{-}C_4$

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

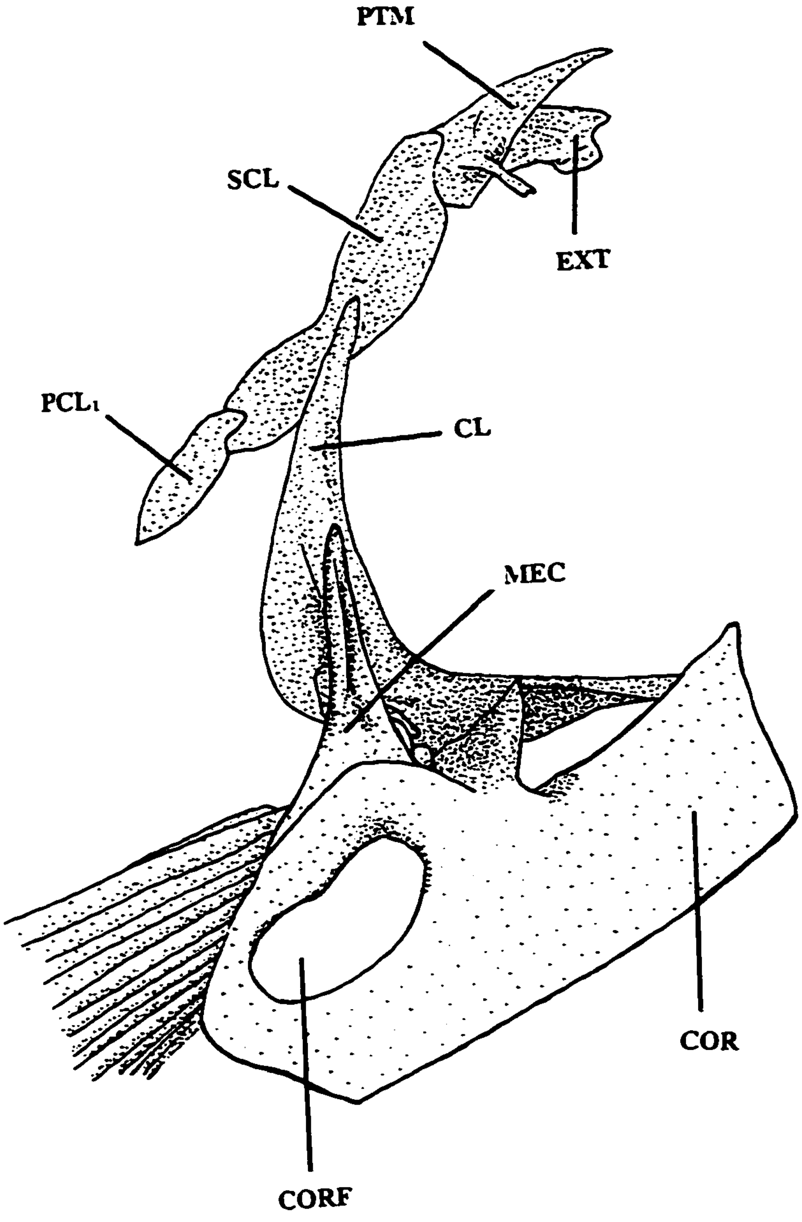

PTM
SCL
EXT
PCL1
CL
MEC
COR
CORF

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

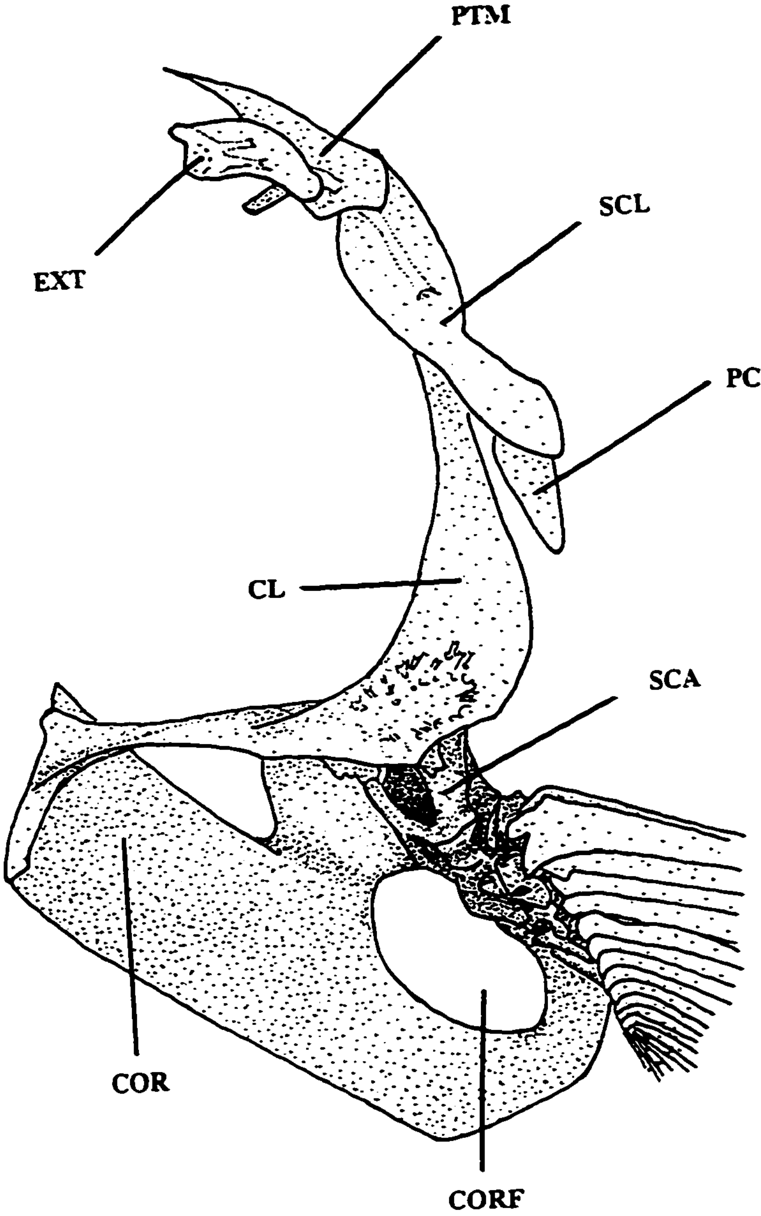

PTM
SCL
EXT
PCL₁
CL
SCA
COR
CORF

Figure 19. Left pectoral girdle of Roestes ogilvei, MZUSP 9702; medial view, anterior to right.

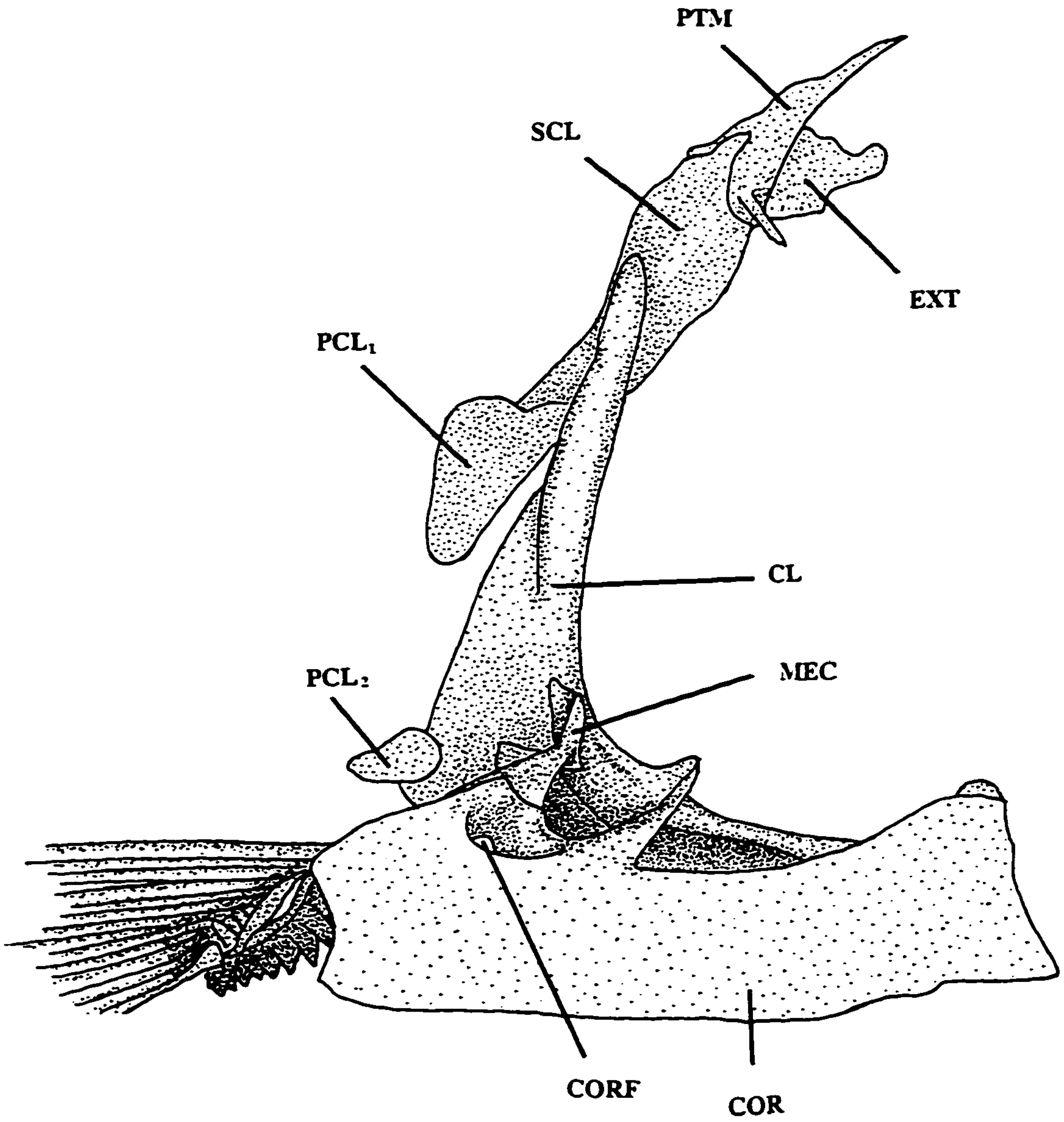

PTM
SCL
EXT
PCL₁
CL
PCL₂
MEC
CORF
COR

Figure 20. Left pectoral girdle of Roestes ogilvei, MZUSP 9702; lateral view, anterior to left.

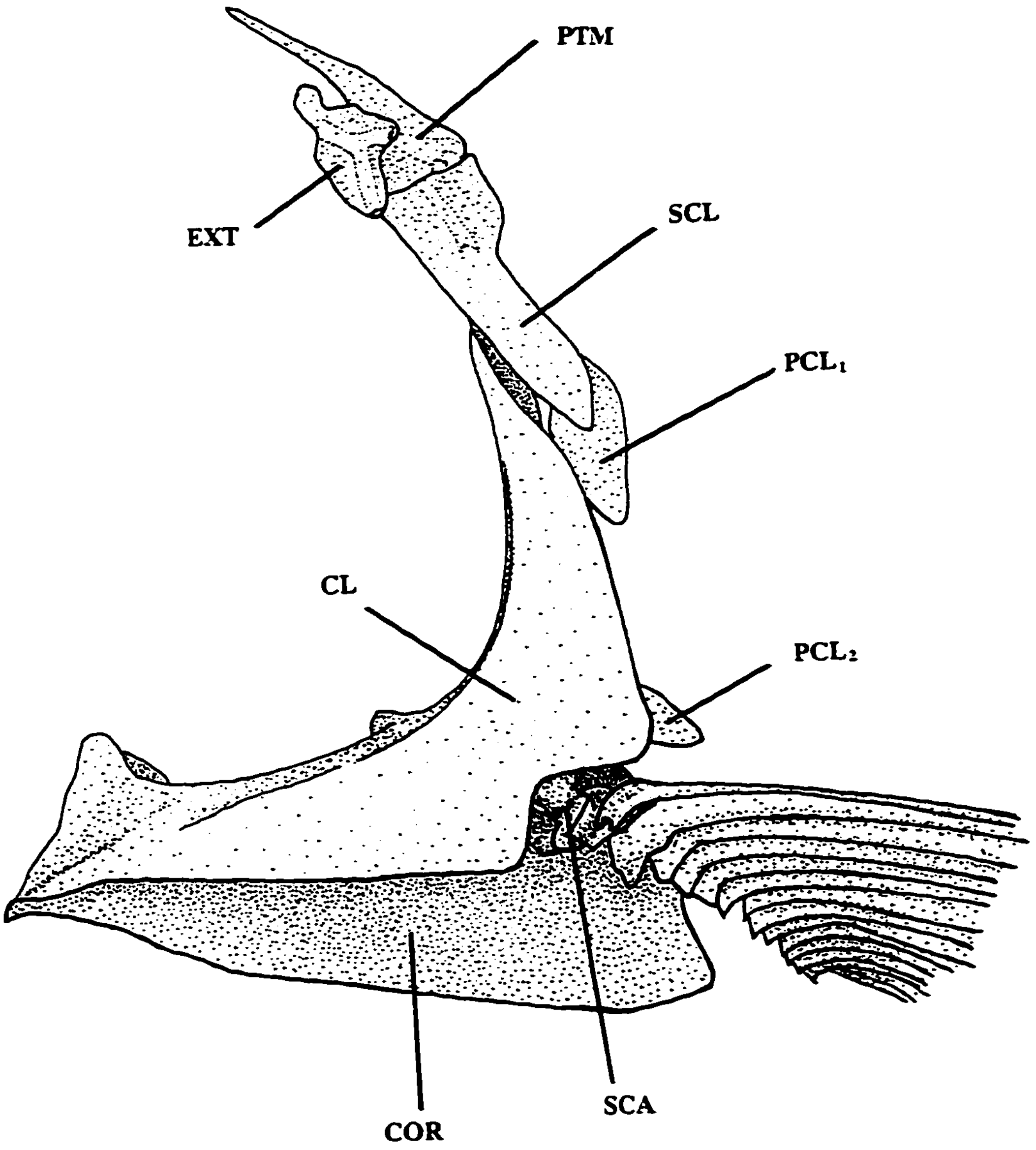

PTM
EXT
SCL
PCL₁
CL
PCL₂
COR
SCA

Figure 21. Caudal skeleton of Cynodon gibbus, MZUSP 32587; left side, lateral view, anterior to left.

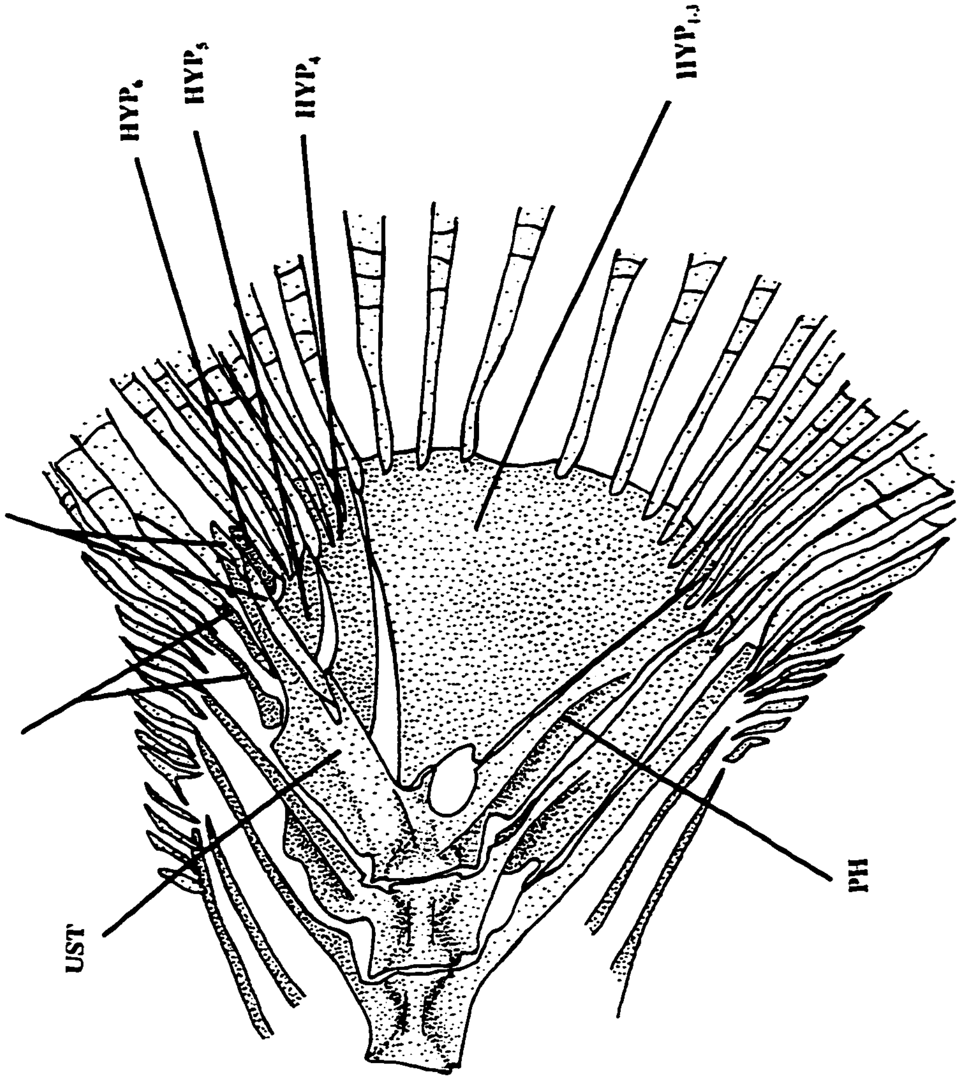

HYP6
HYP5
HYP4
HYP1-3
URO
EPU
UST
PH

Figure 22. Scale from anterior portion of midlateral surface of body of Hydrolycus scomberoides, MZUSP 47893, 222 mm SL.

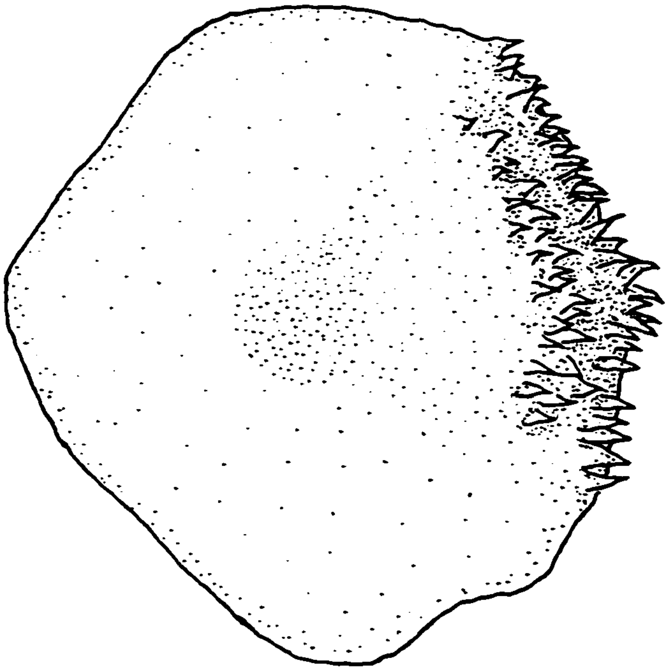


Figure 23. Cladogram 1 of the two equally most parsimonious hypotheses of relationships of cynodontine species. Unique and unreversed character states are indicated by roman numbers. Characters in which states were ambiguous are indicated by letters and subscript numbers.

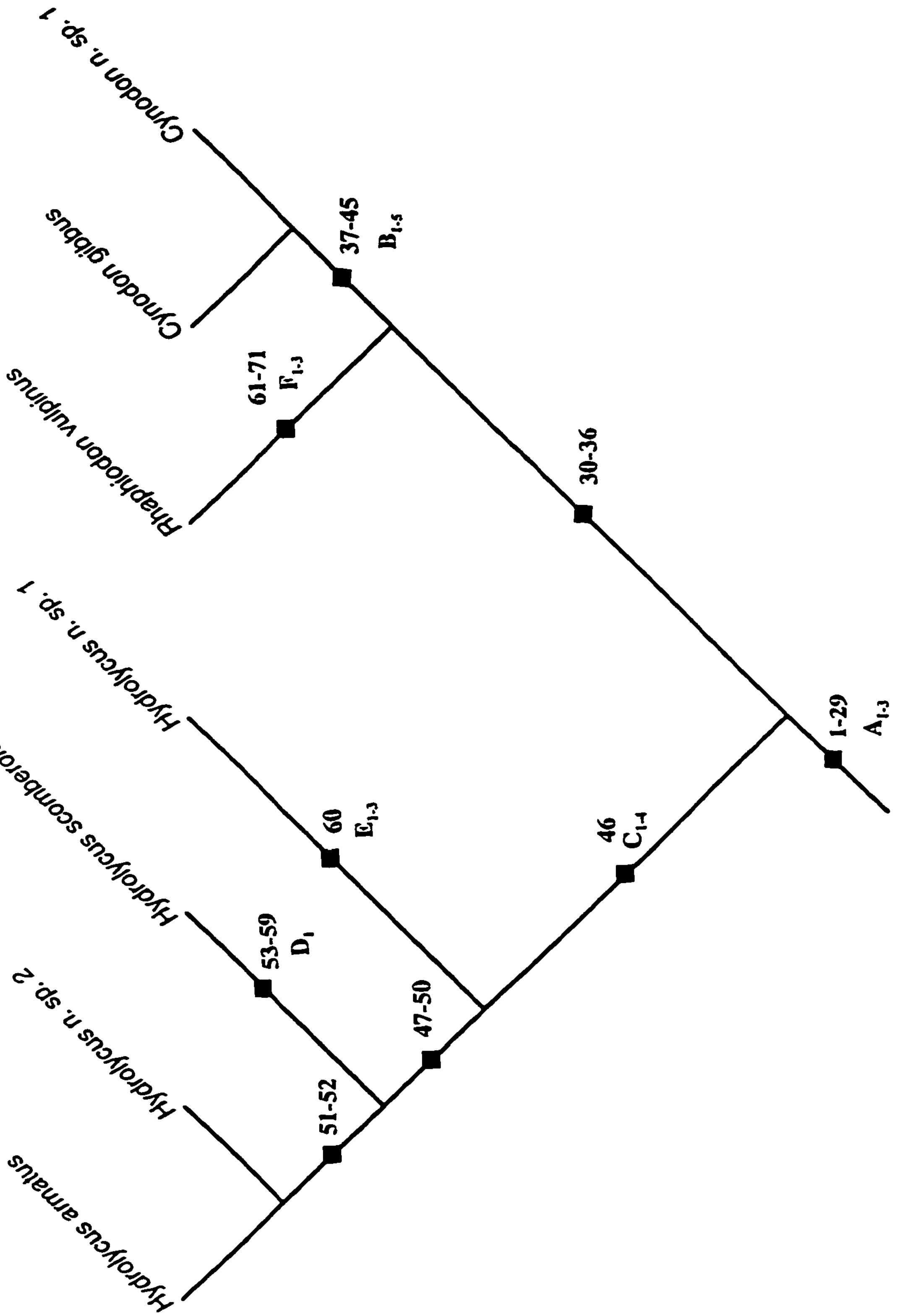

Cynodon n. sp. 1
Cynodon gibbus
Rhaphiodon vulpinus
Hydrolycus n. sp. 1
Hydrolycus scomberoides
Hydrolycus n. sp. 2
Hydrolycus armatus
37-45
B_{1-5}
61-71
F_{1-3}
30-36
1-29
A_{1-3}
60
E_{1-3}
46
C_{1-4}
53-59
D_1
47-50
51-52

Figure 24. Cladogram 2 of the two equally most parsimonious hypotheses of relationships of cynodontine species. Unique and unreversed character states are indicated by roman numbers. Characters in which states were ambiguous are indicated by letters and subscript numbers.

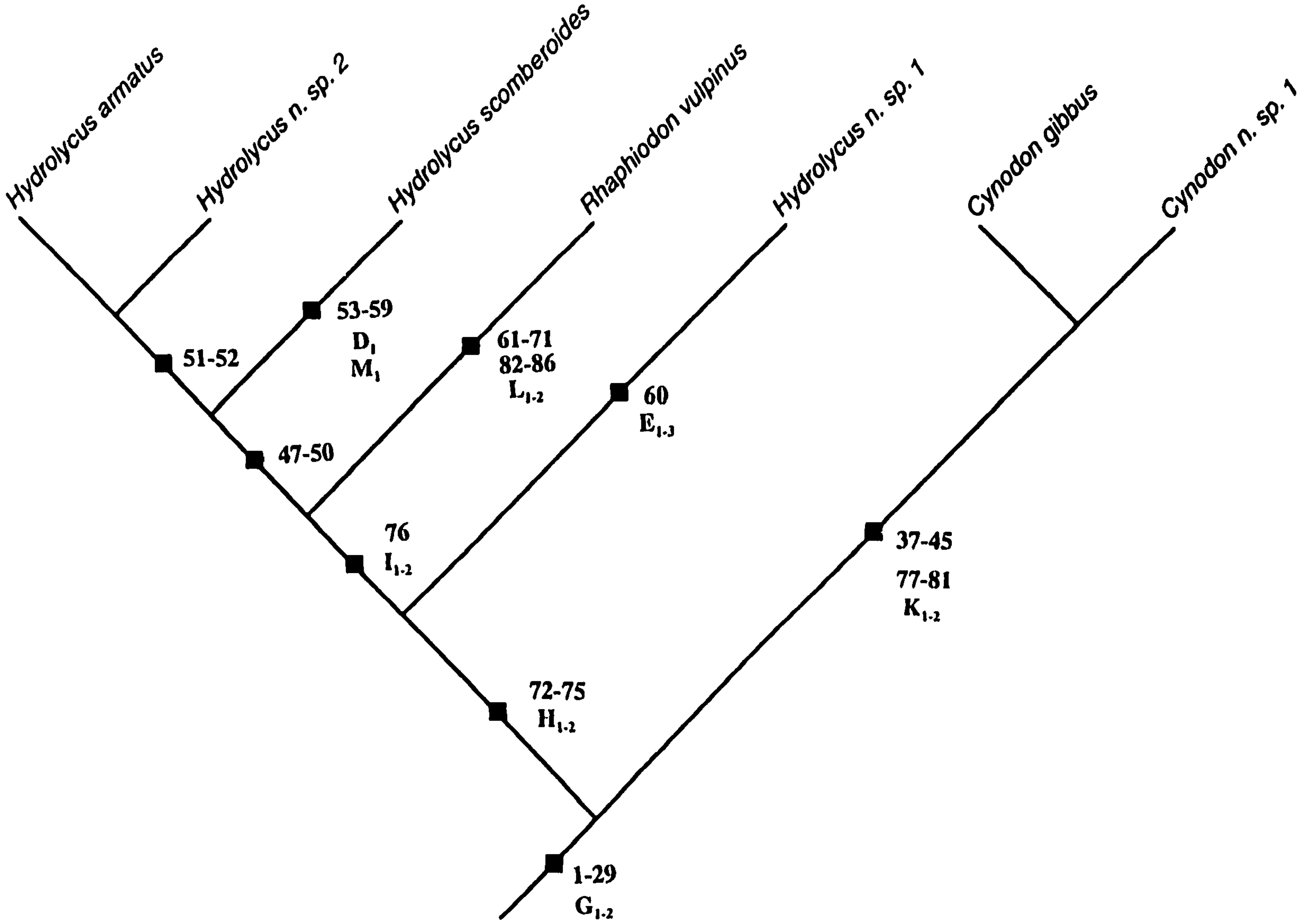

Hydrolycus armatus
Hydrolycus n. sp. 2
Hydrolycus scomberoides
Rhaphiodon vulpinus
Hydrolycus n. sp. 1
Cynodon gibbus
Cynodon n. sp. 1
51-52
53-59
D_1
M_1
47-50
61-71
82-86
L_{1-2}
76
I_{1-2}
60
E_{1-3}
72-75
H_{1-2}
37-45
77-81
K_{1-2}
1-29
G_{1-2}

Figure 25. Hydrolycus scomberoides, MZUSP 26177, 132.1 mm SL; Peru, Ucayali, Río Ucayali, Bagazán.

Figure 26. Hydrolycus scomberoides, CAS 134791, 67.8 mm SL; Peru, Loreto, Caño del Chancho, near Pebas.

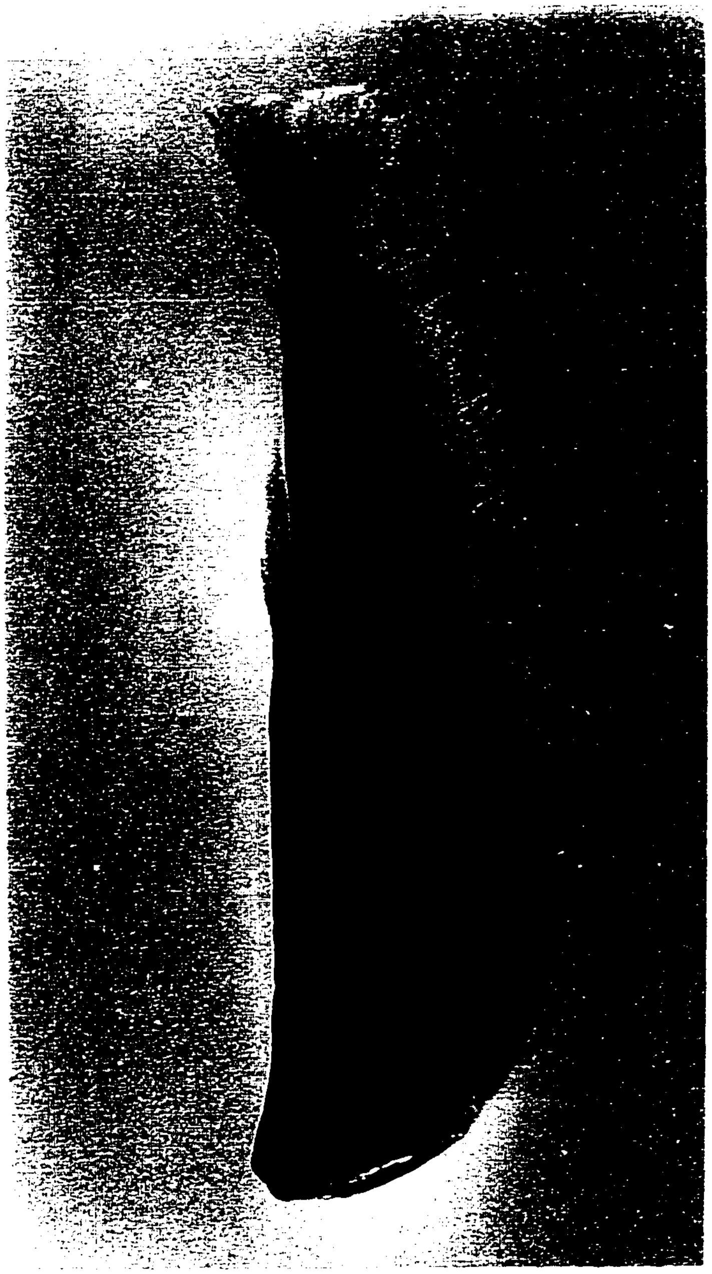


Figure 27. Hydrolycus scomberoides,, MZUSP 32093, 193.0 mm SL; Brazil, Rondônia, Rio Madeira, Calama.

Figure 28. Map of central and northern portions of South America showing geographic distribution of Hydrolycus scomberoides (type locality of Hydrocyon scomberoides and Cynodon pectoralis inexact = "Brazil", and "Upper Amazon", respectively).

Figure 29. Hydrolycus scomberoides, holotype of Hydrocyon scomberoides, MNHN A8659, 211 mm SL; Brazil.

Figure 30. Hydrolycus scomberoides, holotype of Cynodon pectoralis, BMNH 1866.2.15.22, 145.5 mm SL; upper Amazon.

Figure 31. *Hydrolycus* n. sp. 1, reproduction of the drawing presented by A. R. Wallace to the Natural History Museum, London.

Figure 32. Plot of largest dentary canine against head length, both in millimeters, for Hydrolycus n. sp. 1 (filled in circles) and remaining Hydrolycus species (open circles). Only specimens within the same size range included.

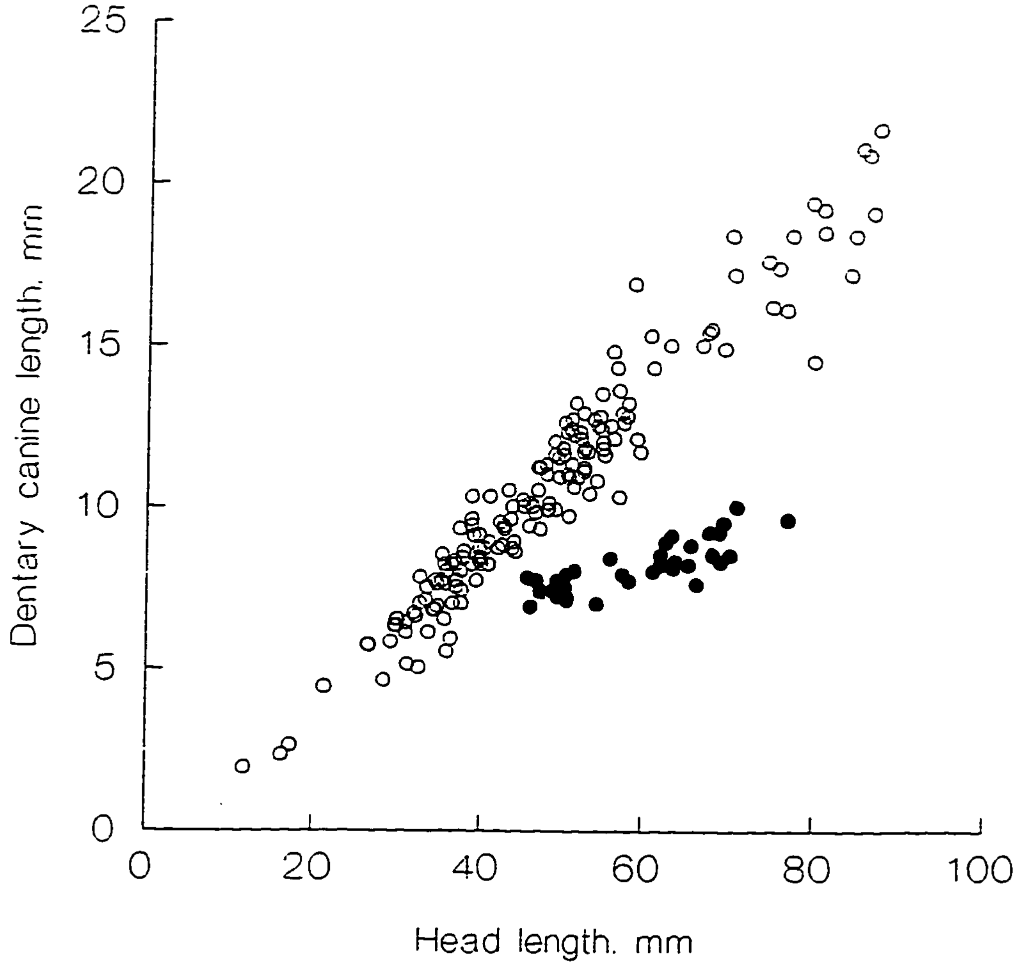

Dentary canine length, mm
0
5
10
15
20
25
Head length, mm
0
20
40
60
80
100

Figure 33. Hydrolycus n. sp. 1, MCNG, 21545, 70.5 mm SL, Venezuela, Amazonas, Río Guainia at Maroa.

Figure 34. Hydrolycus n. sp. 1, FMNH 103662, 128.9 mm SL, Venezuela, Amazonas, Río Sipapo, above mouth in Río Cuao.

Figure 35. Hydrolycus n. sp. 1, holotype, MZUSP 00000, 286 mm SL, Brazil, Amazonas, Rio Negro, Ilha de Tamaquaré.

Figure 36. Map of central and northern portions of South America showing geographic distribution of Hydrolycus n. sp. 1, (1 = type locality). Some symbols represent more than one lot of specimens or locality.


1

Figure 37. Hydrolycus armatus, MZUSP 32607, 210.0 mm SL; Brazil, Pará, Rio Xingu, Belo Monte.

Figure 38. Hydrolycus armatus, INPA POLO 405, 310 mm SL, Brazil, Rondônia, Rio Jamari, below Represa de Samuel.

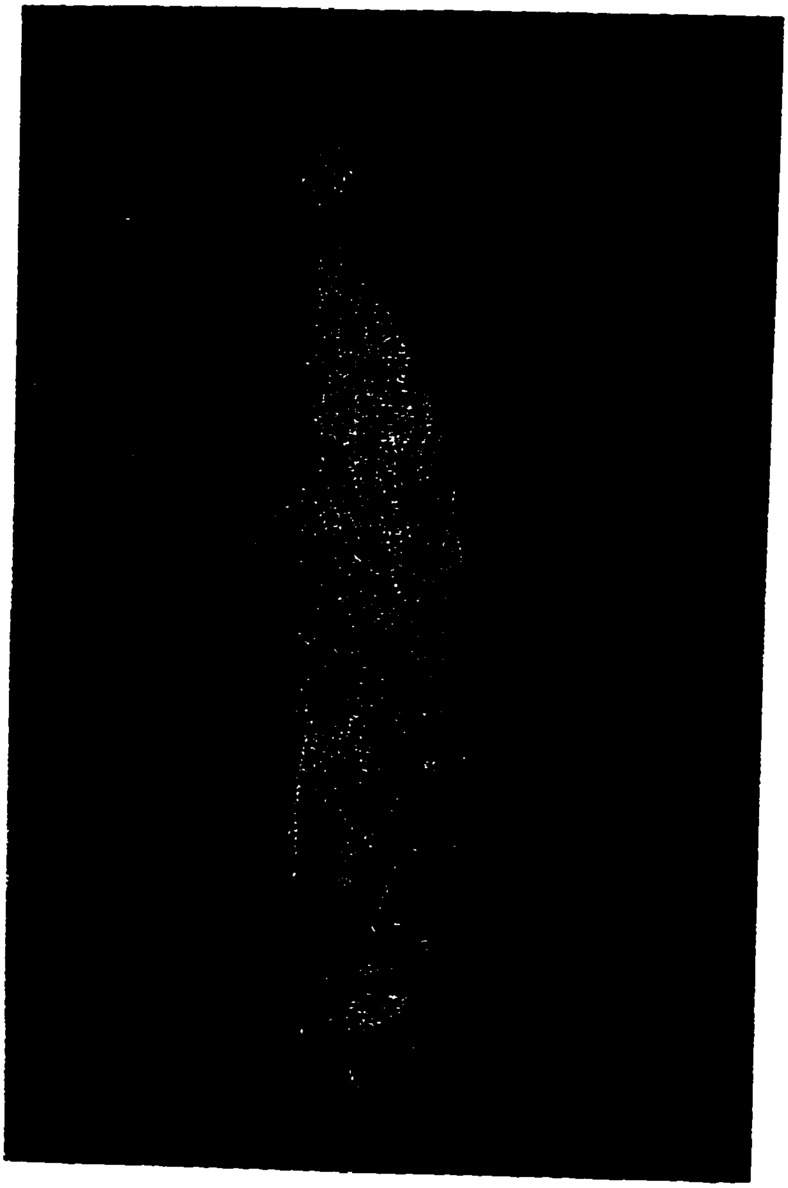


Figure 39. Map of central and northern portions of South America showing geographic distribution of Hydrolycus armatus (type locality inexact = "rivers of Guiana" [=Guyana]). Some symbols represent more than one lot of specimens or locality.

Figure 40. Hydrolycus armatus, reproduction of an anonymous drawing . "1841 - Original drawings - South American freshwater fishes. Coloured from Mr. Schomburgk's drawings" Unpublished: Natural History Museum Library, London.

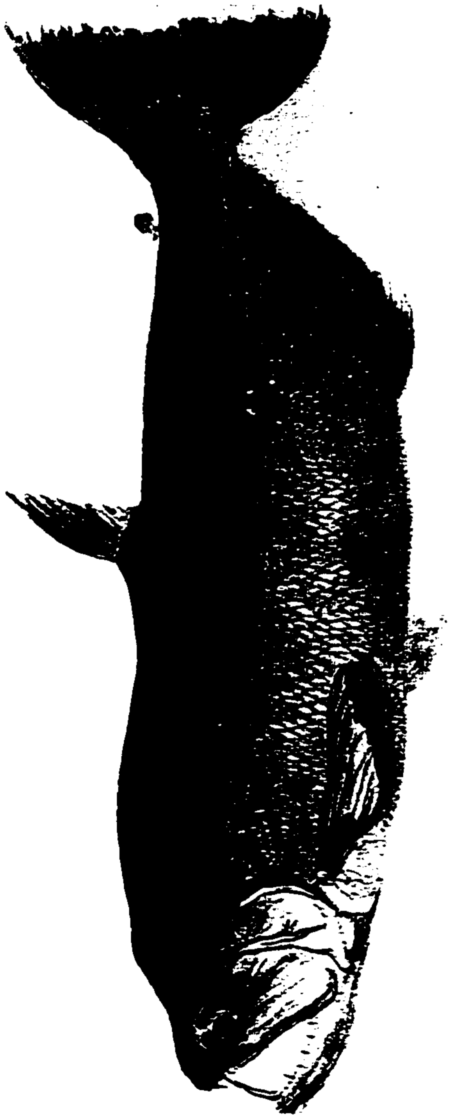


Figure 41. Hydrolycus n. sp. 2, INPA POLO 452, 290 mm SL, Brazil, Rondônia, Rio Jamari, Igarapé Japiim, above Represa de Samuel.

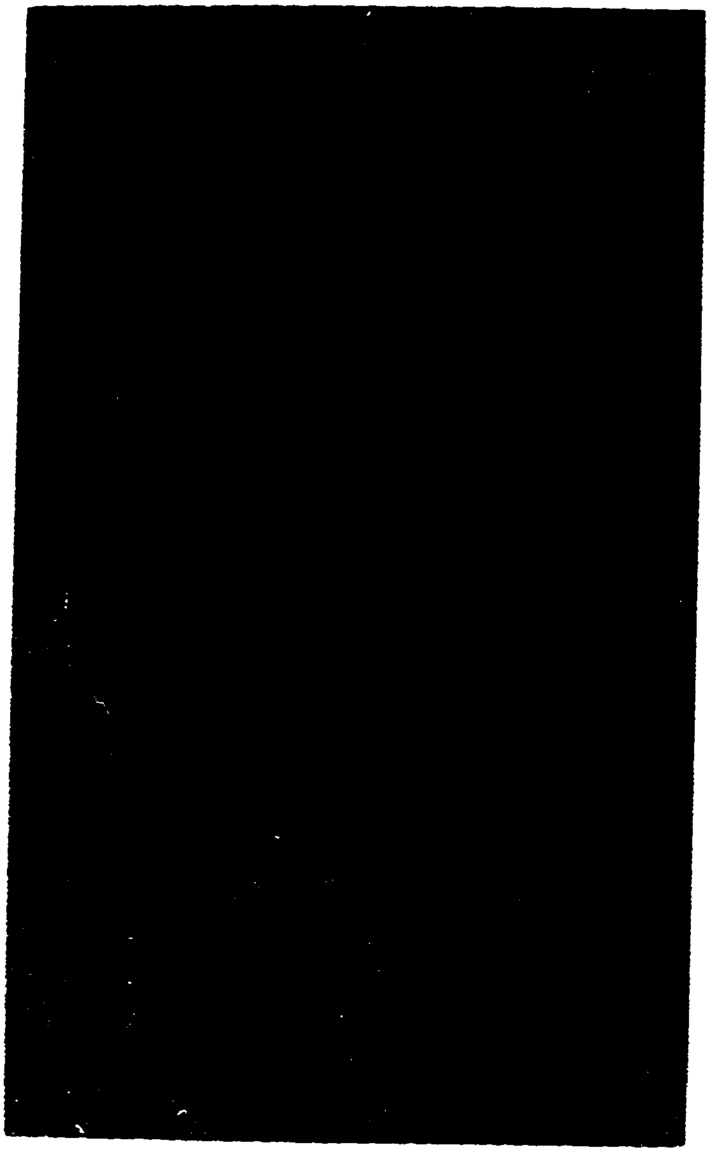


Figure 42. Hydrolycus n. sp. 2, CAS 14618, 151.0 mm SL, Venezuela, Amazonas, Río Orinoco bifurcation, TamaTama Rock.

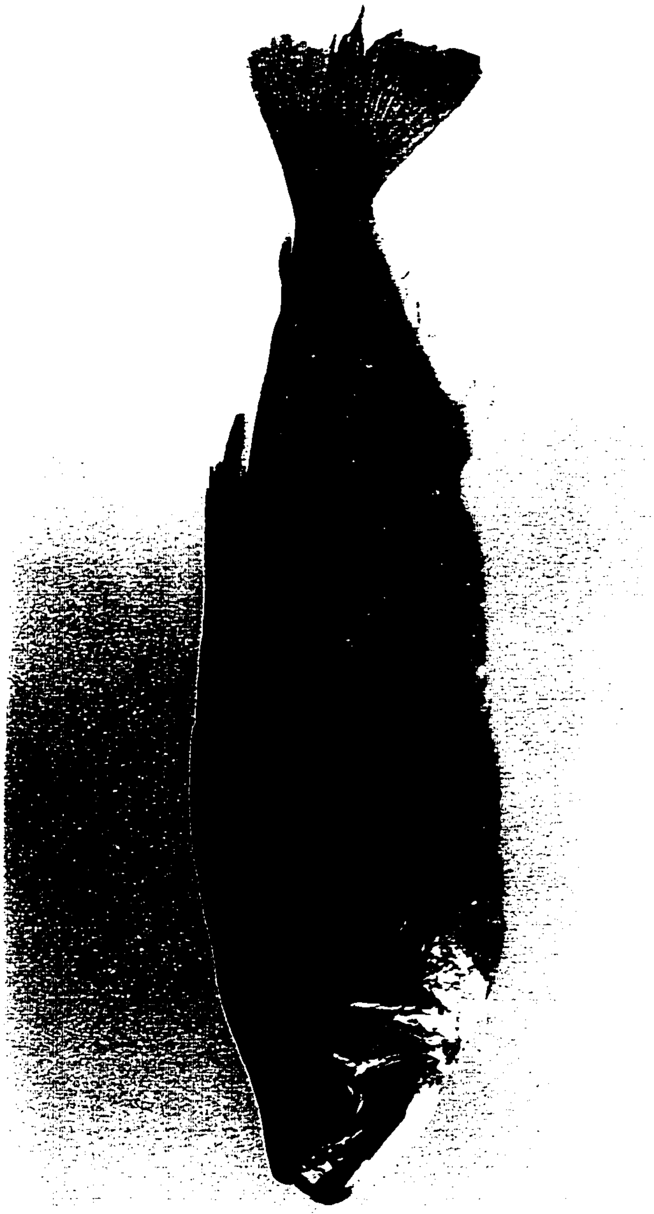


Figure 43. Hydrolycus n. sp. 2, holotype, MZUSP 00000, 268.0 mm SL, Brazil, Pará, Rio Xingu, Belo Monte.

Figure 44. Map of central and northern portions of South America showing geographic distribution of Hydrolycus n. sp. 2 (1 = type locality). Some symbols represent more than one lot of specimens or locality.

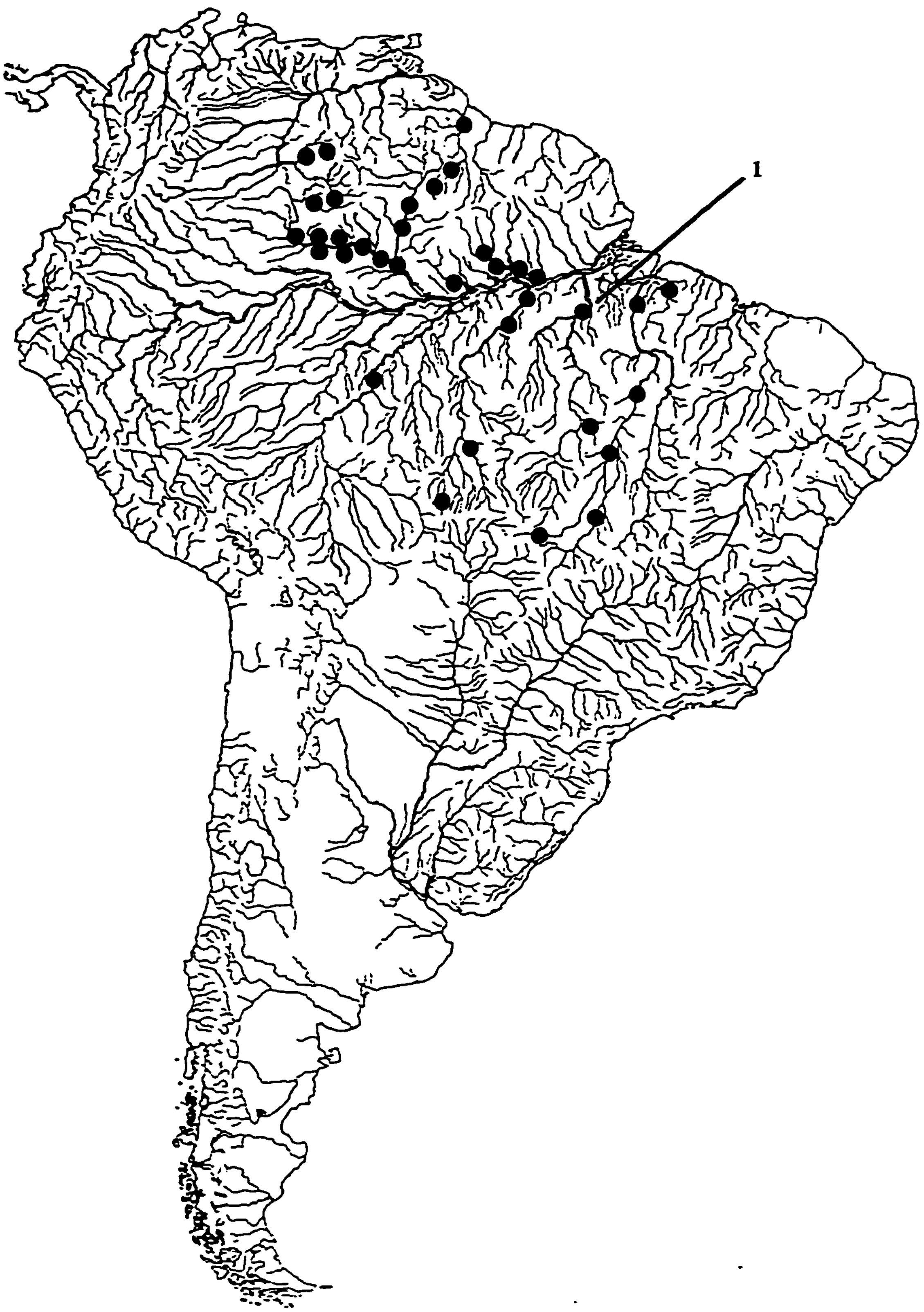

1

Figure 45. Cynodon gibbus, MZUSP 32592, 177 mm SL, Brazil, Rondônia, Rio Madeira, Calama.

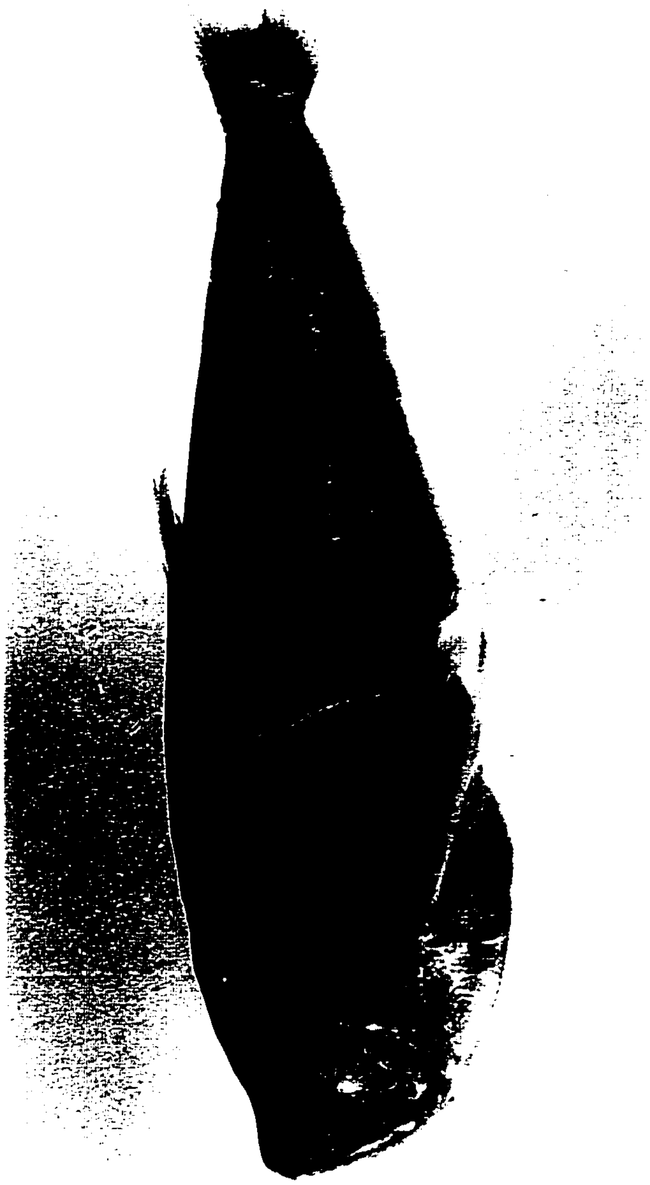


Figure 46. Cynodon gibbus, MCNG 19340, 138 mm SL, Venezuela, Portuguesa, Caño Igues.

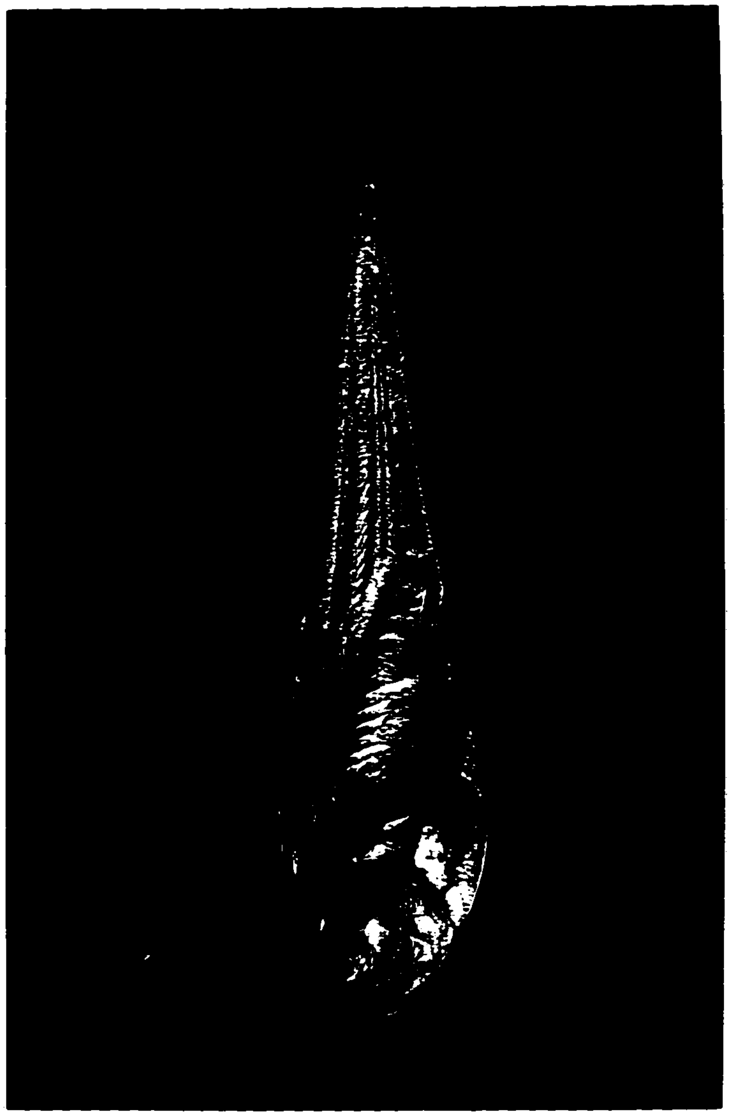


Figure 47. Plot of orbital diameter against head length, both in millimeters, for Cynodon gibbus (open circles) and Cynodon n. sp. 1 (filled in circles).

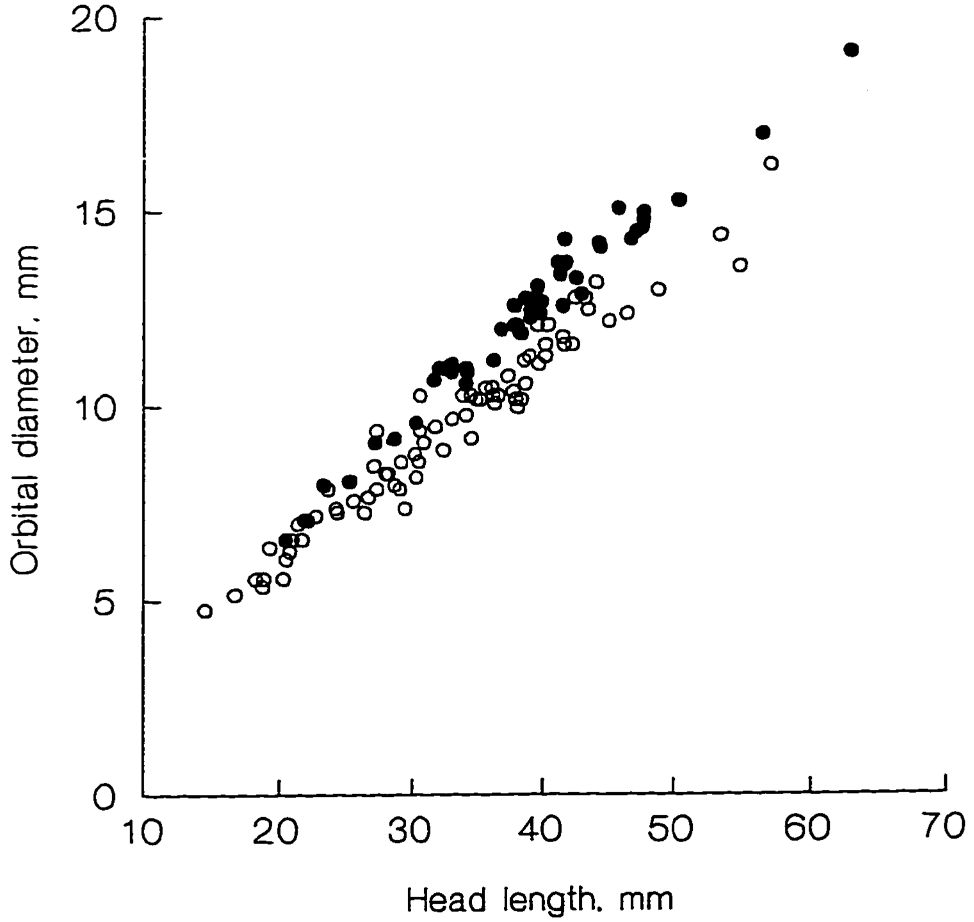

Orbital diameter, mm
20
15
10
5
0
10
20
30
40
50
60
70
Head length, mm

Figure 48. Cynodon gibbus, LACM 39857-10, 35 mm SL, Peru, Amazonas, Río Santiago at La Poza.

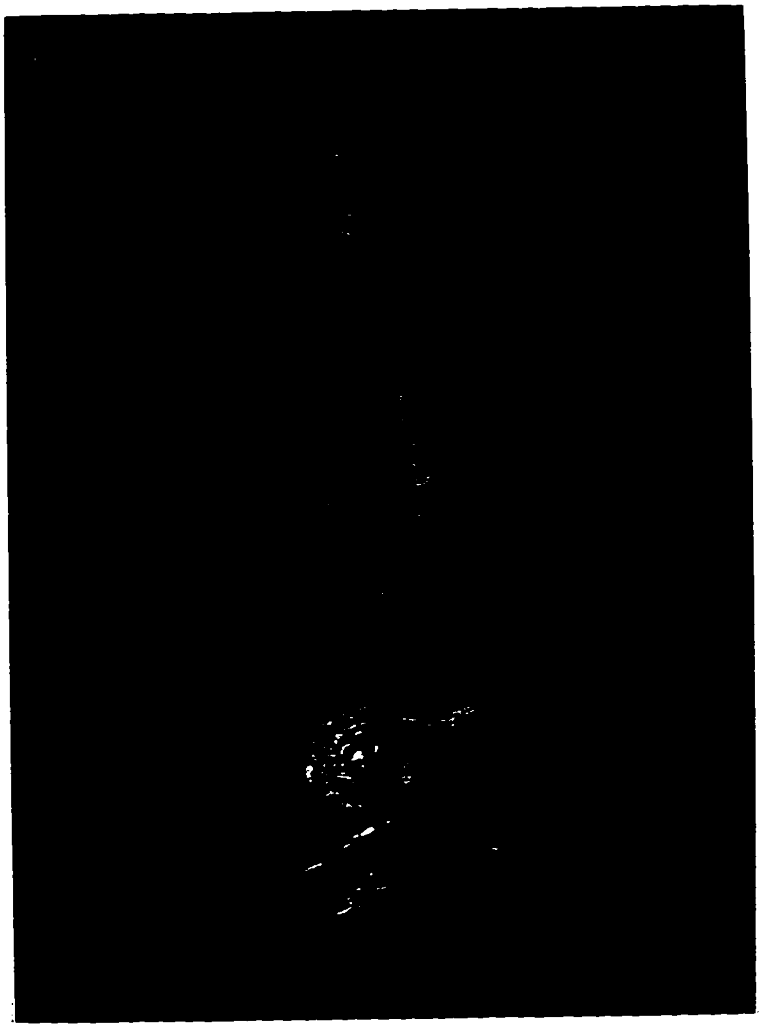


Figure 49. Map of central and northern portions of South America showing geographic distribution of Cynodon gibbus (type locality inexact = "Brasiliae fluviis" [= rivers of Brazil]). Some symbols represent more than one lot of specimens or locality.

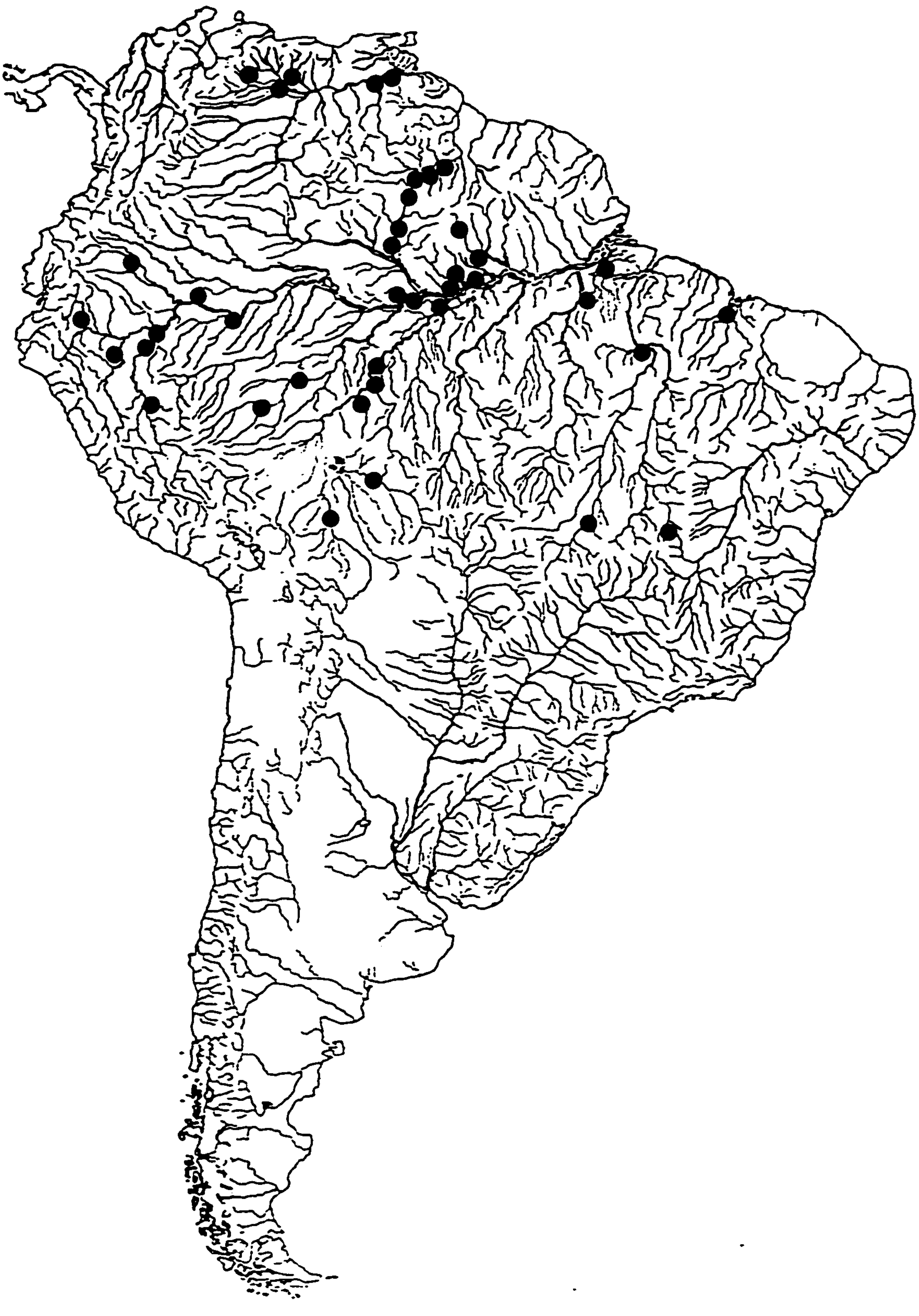


Figure 50. Cynodon n. sp. 1, holotype, MZUSP 00000, 238 mm SL, Brazil, Amazonas, Rio Tefé, Supiã-Pucu.

Figure 51. Map of central and northern portions of South America showing geographic distribution of Cynodon n. sp. 1 (1 = type locality). Some symbols represent more than one lot of specimens or locality.


1

Figure 52. Rhaphiodon vulpinus, MZUSP 32809, 305 mm SL, Brazil, Pará, Rio Xingu, Belo Monte.

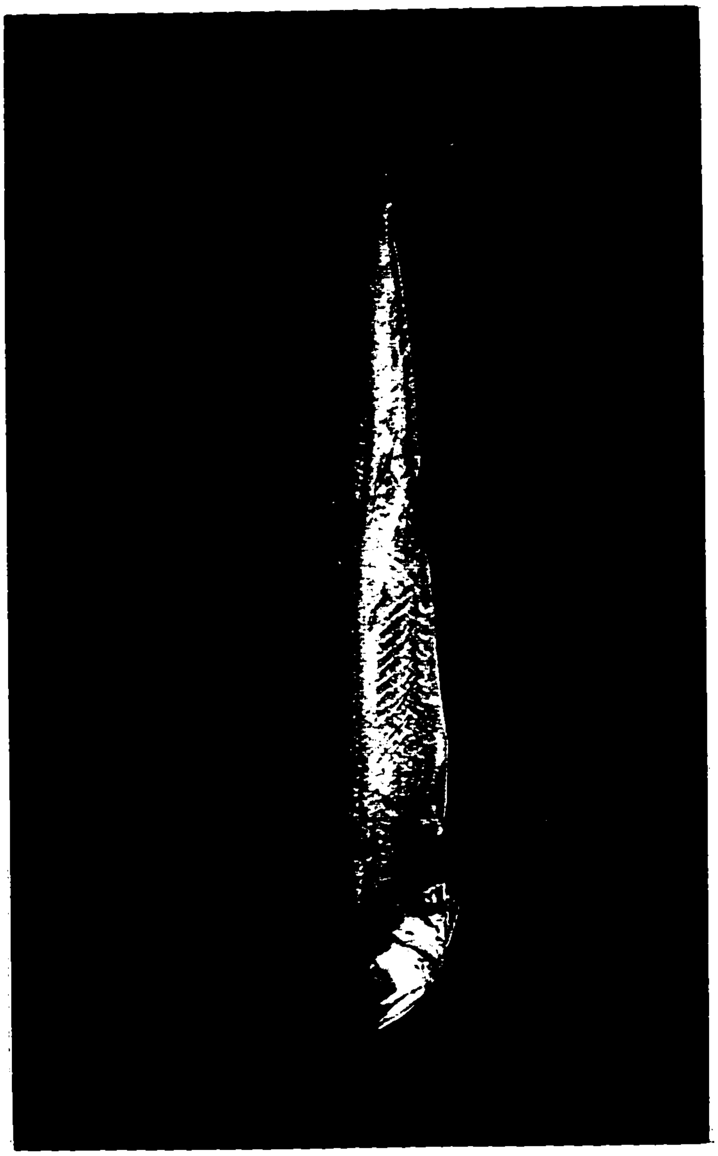


Figure 53. Rhaphiodon vulpinus, INPA 2618, 46.5 mm SL, Brazil, Amazonas, Rio Amazonas, Lago do Rei.

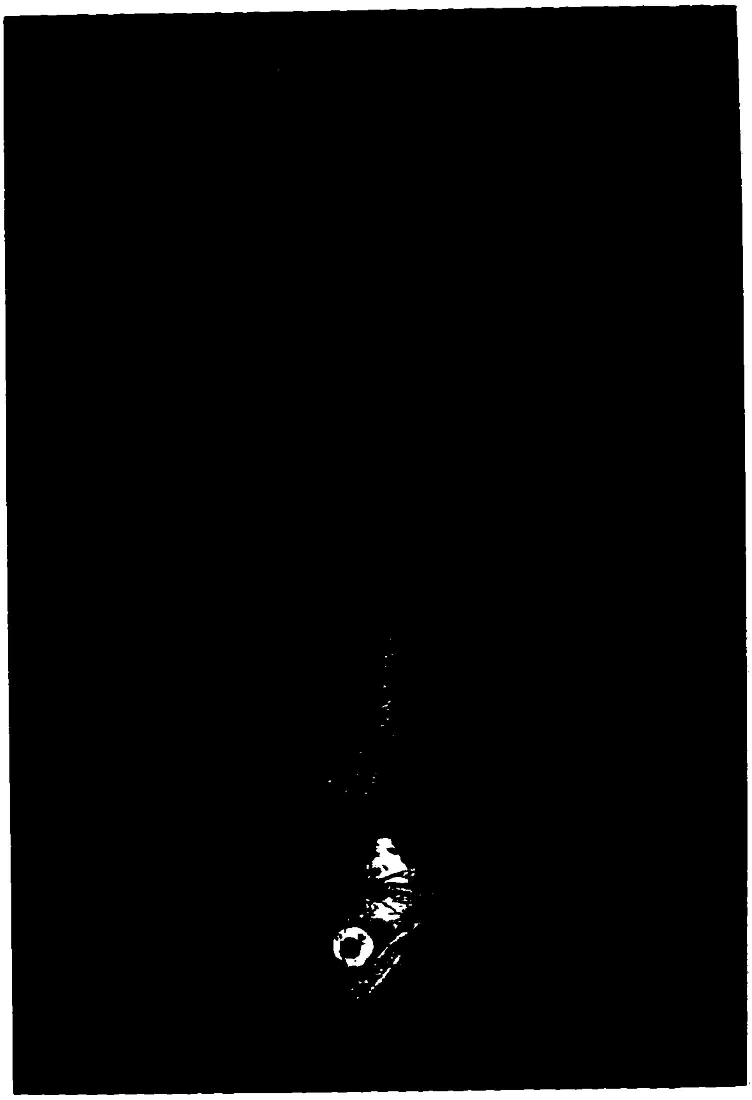


Figure 54. Rhaphiodon vulpinus, holotype, MHNN 822, 303 mm SL, Brazil.

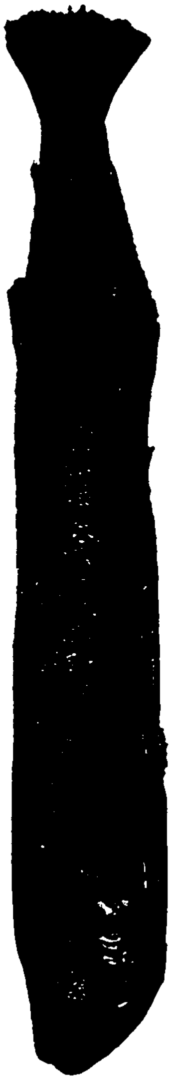


Figure 55. *Rhaphiodon vulpinus*, holotype of *Hydropardus rapax*, ZMC 183, 623 mm SL, Uruguay, Montevideo.

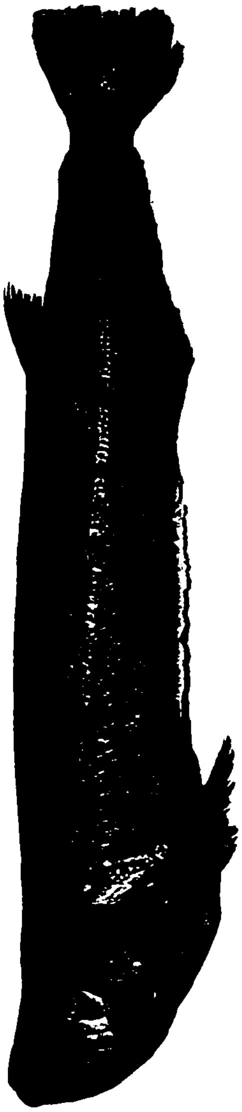
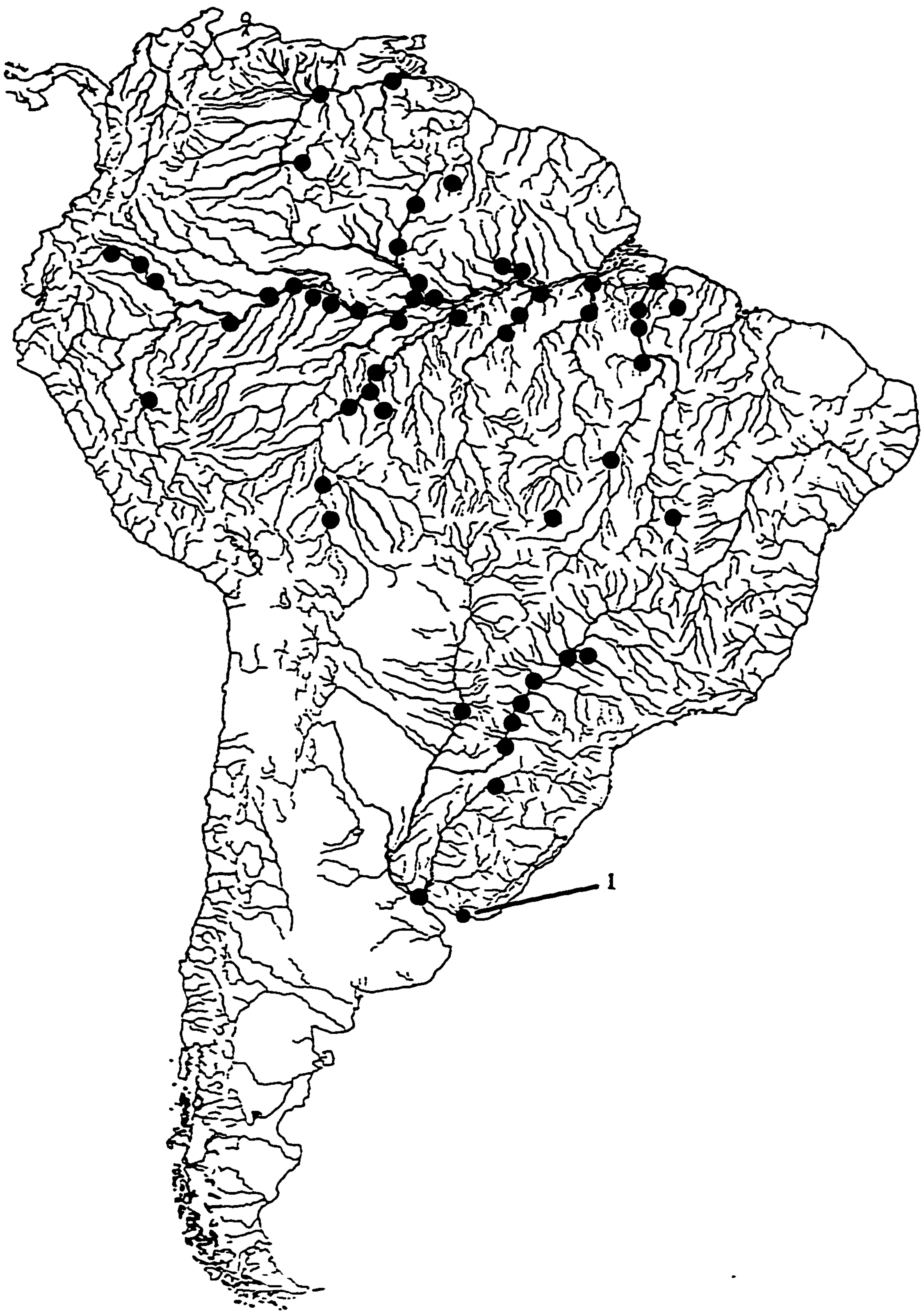


Figure 56. Map of central and northern portions of South America showing geographic distribution of Rhaphiodon vulpinus (type locality inexact = "Brasiliae fluviis" [= rivers of Brazil]; 1 = type locality of Hydropardus rapax, see comments under "Remarks" of this species account). Some symbols represent more than one lot of specimens or locality.


1

APPENDIX

PETITION REGARDING THE NOMENCLATURE OF CYNODON AND RHAPHIODON (TELEOSTEI: OSTARIOPHYSI: CHARACIFORMES)

1) Cuvier (1829:312) first introduced the genus name Cynodon in conjunction with the description of the genus Hydrocyon. Footnote number four in Cuvier (op. cit.) states [translation from the French with Cuvier's bibliographic abbreviations and punctuation not altered]: "Another species from Brazil Hydroc. scomberoides, Cuv. , Mém. Mus., V, pl. xxvii, f. 2, or Cynodon vulpinus, Spix, xxvi; - Cynodon gibbus, id., xxvii.". The plates cited in combination with the species names had not, however, been published at that time.

2) Agassiz (1829:76-78) [according to Kottelat (1988:73), Agassiz is to be considered the sole author with the correct citation being Agassiz, in Spix & Agassiz, 1829] described Rhaphiodon to include the species R. vulpinus and R. gibbus for which he also provided descriptions. The plates that accompany the descriptions are labeled Cynodon vulpinus (plate XXVI) and Cynodon gibbus (plate XXVII) with these names appearing in the text as junior synonyms attributed to Spix. Agassiz justified the creation of the name Rhaphiodon as a replacement name for Cynodon because the latter was already used in botany.

3) It has been established by Whitehead & Myers (1971) and Kottelat (1988) that Cuvier's 1829 publication predates that of Spix & Agassiz (1829).

4) Eigenmann (1910:444) designated Cynodon vulpinus as the type species of Rhaphiodon and Cynodon gibbus as the type species of Cynodon.

5) Whitehead & Myers (1971:489) reproduced Cuvier's (1829) footnote (see 1, above), the significance of which has been ignored by all authors who have addressed the Cynodon/Rhaphiodon problem (see 6, below). They also provided generalized instructions (op. cit. : 494-495) on how to solve the nomenclatural problems arising from the works of Cuvier (1829) and Agassiz (1829). Weitzman (1996) recommended that such problems be submitted to the International Comission on Zoological Nomenclature.

6) Authors, such as Campos (1945), Travassos (1946), Kottelat (1988), Eschmeyer & Bailey (1990), and Eschmeyer (1990), who have addressed the question of the validity of the names Rhaphiodon and Cynodon have arrived at different conclusions, and in some instances additional names have been created for taxa associated with those genera [e.g. Rhaphiodontichthys Campos, 1945 (p. 473) and Camposichthys Travassos, 1946 (p. 132)].

7) The species names vulpinus and gibbus have been considered congeneric by some authors and were placed either in the genus Rhaphiodon [Müller & Troschel (1844:93), Géry (1977:302), Géry & Poivre (1979), Mendes dos Santos et al. (1984:40), Galvis et al. (1989:122), Taphorn (1992:436-439)] or in Cynodon [Valenciennes (1849:329), Kner (1859:54), Günther (1864:358)]. When they are placed in different genera, the species name vulpinus is placed in Rhaphiodon and gibbus in the genus Cynodon [Fowler (1906:467; 1950:330; 1975:277), Eigenmann (1910:444), Jordan (1923:134), Eigenmann & Allen (1942:271), Schultz (1950:47), Lowe McConnell

(1964:110), Howes (1976:207), Géry (1986:63), Barriga (1991:30)]. The names Rhaphiodontichthys Campos, 1945 and Camposichthys Travassos, 1946 have seldom been adopted, see Mago Leccia (1970:30) and Machado-Allison (1987:134) for usage of Rhaphiodontichthys.

8) Our interpretation of the problem based on the evidence presented above and the International Code of Zoological Nomenclature (ICZN) of 1985, is as follows:

i) Cuvier (1829:312) considered Cynodon vulpinus the same as Hydrocyon scomberoides, as indicated by the word "or" in the footnote (see 1, above). C. gibbus was listed as an additional species to be included in the scomberoides group, as indicated by the semi-colon followed by a dash before its species name (see 1, above).

ii) The species name gibbus was not accompanied by a description or indication and consequently was a nomen nudum at that time and is, therefore, not available from Cuvier (1829).

iii) The genus name Cynodon and the species name vulpinus were first published as junior synonyms. They have been treated as available names and adopted as names of taxa by many authors prior to 1961 [Valenciennes (1849:323), Eigenmann (1910:444), Campos (1945:472), and Fowler (1950:330)] and are, therefore, available with their author and date going back to Cuvier, 1829 (ICZN: Article 11e and 50g).

iv) The species name gibbus was made available by Agassiz (1829), taking its date and authorship from that publication (ICZN: Glossary: 260).

v) From 8 iii, and 3 (above), the genus name Rhaphiodon is technically a replacement name for Cynodon [i. e., Rhaphiodon replaced the available name Cynodon, even though Cynodon became available through an act that happened subsequently, but its author and date go back to Cuvier (1829)]. As a consequence, their type species is required to be the same (ICZN: Article 67h).

vi) As the originally included species of the genus Cynodon (ICZN: Article 67l, (i)) either Hydrocyon scomberoides Cuvier, 1819 or Cynodon vulpinus Cuvier, 1829 must be chosen as the type species of Cynodon. In this context, Eigenmann's designation of type species for Cynodon and Rhaphiodon is not valid.

vii) Under Opinion 1581 of the International Commission of Zoological Nomenclature (1990:76) Hydrocyon scomberoides Cuvier, 1819 has been designated as the type species of Hydrolycus Müller & Troschel, 1844 which has been placed on the Official List of Generic Names in Zoology. In case H. scomberoides is chosen as the type species of Cynodon, the two genera (Hydrolycus and Cynodon) will be objective synonyms.

viii) If Cynodon vulpinus is chosen to be the type species of Cynodon, and the species vulpinus and gibbus are placed in different genera, Camposichthys is the available name for C. gibbus.

ix) The species name vulpinus has been widely associated with the genus Rhaphiodon, see 7 above and Nelson (1949), Nielsen (1974:45), Lesiuk & Lindsey (1978), Goulding (1980:184), Ferreira et al. (1988:344), and Goulding et al. (1988:127). Rhaphiodon, according to our interpretation, being a junior objective synonym of Cynodon, is, therefore, not a valid name.

9) The interpretation of the facts including the new evidence from Cuvier's 1829

publication, and the consequences of any of the nomenclatural acts arising from that, will in our opinion undermine the principle of stability of names because of the widespread association of Cynodon with gibbus and Rhaphiodon with vulpinus. In addition, we also understand that the facts outlined above (1 through 7) are subject to differences in interpretation. We base this observation on the widely differing responses we obtained when we solicited opinions on our interpretation (pers. comm., Bailey, Eschmeyer and Ferraris, and Kottelat). Therefore, we propose that the International Commission on Zoological Nomenclature:

(1) suppress the names Cynodon Cuvier, 1829, Cynodon vulpinus Cuvier, 1829, and Cynodon gibbus Cuvier, 1829, for nomenclatural purposes.

(2) place the name Cynodon Agassiz, in Spix & Agassiz, 1829 (gender masculine), type species Cynodon gibbus Agassiz by subsequent designation of Eigenmann (1910:444), on the Official List of Generic Names in Zoology.

(3) place the name Rhaphiodon Agassiz, in Spix & Agassiz, 1829 (gender masculine), type species Rhaphiodon vulpinus Agassiz by subsequent designation of Eigenmann (1910:444), on the Official List of Generic Names in Zoology.

(4) place the names gibbus Agassiz, 1829, as published in the binomen Rhaphiodon gibbus Agassiz, on the Official List of Specific Names in Zoology.

(5) place the names vulpinus Agassiz, 1829, as published in the binomen Rhaphiodon vulpinus Agassiz, on the Official List of Specific Names in Zoology.

(6) give priority to Cynodon over Rhaphiodon when the species names gibbus and vulpinus are considered congeneric.

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