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ON THE CYNOPOTAMINAE, A NEW SUBFAMILY OF CHARACIDAE (OSTEICHTHYES, OSTARIOPHYSI, CHARACOIDEI)

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INTRODUCTION

The present study deals with the systematics and evolution of the genera *Cynopotamus, Acestrocephalus* and *Galeocharax,* included by many authors in the subfamily Characinae. It is here hypothesized that these genera form a natural group and show distinct evolutionary trends.

The relationships between *Cynopotamus, Acestrocephalus* and *Galeocharax* and the remaining genera of the subfamily Characinae have never been adequately studied. The taxonomic history of *Cynopotamus* and closely related forms was summarized by Géry & Vu-Tân-Tuê (1963a; 1963b). Based on the examination of certain type-specimens, which they redescribed, they considered the species treated in this work as belonging to a single genus, *Cynopotamus. Acestrocephalus* as well as their new *Hybocharax* were included as subgenera. They considered *Galeocharax* synonymous with *Acestrocephalus.* This same arrangement was again presented by Géry (1972a:27).

In the study of *Cynopotamus* and closely related forms, a great deal of importance has been attributed to the dentition, especially to the presence or absence of a short inner row of teeth on the lower jaw. This character, however, was never examined and compared in all forms involved; other morphological characters, which I consider of greater phylogenetic significance, have consistently been neglected. The systematic arrangement proposed by Géry (l.c.) contributed, to a certain extent, to a better understanding of the group, but as will be discussed later, his interpretation of some morphological characters and his conclusions about the arrangement of the teeth on the lower jaw do not reflect relationships based on the morphological data found in the present study. The comparative study of the morphology and of the geographic distribution of all forms involved led me to consider the so called "*Cynopotamus*-group" as composed of three genera: *Cynopotamus, Galeo-*

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charax and *Acestrocephalus.* They share some important characters apparently not found in any genus or group of the family Characidae. It is here proposed that they form a monophyletic group.

It has not been my intention in this work to present complete morphological accounts of the three genera and to establish direct comparisons between them and the remaining genera of the subfamily Characinae. Although all members of the Characinae exhibit the same generalized characid osteological pattern as described by Weitzman (1962), some morphological characters that have not received attention appear to have great adaptive value and are correlated with distinct evolutionary trends within the group.

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MATERIAL AND METHODS

This study is based on the examination of 213 specimens from the localities shown in figure 1 and in the Appendix. The localities involved were identified with the help of the Map of Hispanic America, published by the American Geographical Society. The materials belong to the following institutions:

CAS	California Academy of Sciences.
CAS (IUM)	Specimens belonging to the California Academy of Sciences but formerly deposited at the Indiana Museum.
USNM	United States National Museum, now National Museum of Natural History, Washington, D.C.
NMW	Naturhistorisches Museum Wien, Austria.
ZMA	Zoölogisch Museum, Amsterdam, Netherlands.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MLP	Museo de La Plata, La Plata, Argentina.
MZUSP	Museu de Zoologia da Universidade de São Paulo, Brasil.
MNRJ	Museu Nacional, Rio de Janeiro, Brasil.

Counts, measurements and the study of geographic variation were made according to the methods used by Menezes (1969b).

During the analysis of meristic and morphometric variation, sexes were considered separately but, since no significant differences were found, males and females were grouped in the samples as presented in the text. No change in meristic values associated with growth was found, with the exception of the number of teeth in the posterior row on the dentary, which proved to vary ontogenetically and was studied by regression analysis (Fig. 55).

The following body proportions were analyzed, all regressions being linear.

Body depth x standard length
Head length x trunk length
Snout length x head length
Orbital diameter x head length
Interorbital distance x head length
Caudal peduncle depth x body depth
Predorsal distance x standard length
Preanal distance x standard length
Predorsal distance x preanal distance

The following meristic characters were studied:

Number of branched anal fin rays
Number of scales on the lateral line
Number of scales above lateral line
Number of scales below lateral line
Number of teeth on the maxillary
Number of teeth in the inner row on the dentary

The number of ventral fin rays and caudal fin rays proved to be constant for all species and the number of dorsal fin rays and gill rakers on the first gill arch showed minimal interspecific variation.

The tables and graphs containing the values of meristic and morphometric characters of the species include also, whenever feasible, data from the literature.

For the analysis of the main food types, the stomach contents of most specimens were examined.

Alizarin specimens for osteological studies were prepared according to the method of Taylor (1967). All drawings were made by myself, based on direct observation of the specimens under the stereomicroscope. Figures 21A-B, 31A-B, and 36A-B are diagrammatic, but accurate with respect to the main structures involved. The names of bones are those of Weitzman (1962). The abbreviations used in figures 2-13 are listed in page 57.

Statements about osteological characters, not documented by literature citations, are based on personal observations made for the purpose of this work.

OBSERVATIONS

CRANIUM

Cynopotamus, Galeocharax and *Acestrocephalus* have the same basic cranial structure.

In all specimens of all three genera the ethmoid ends anteriorly in a spine which extends almost to the tip of the snout, thus almost entirely preventing the contact between the premaxillaries on the midline (figs. 5, 6, 7).

The cranial fontanel (figs. 5, 6, 7) is well developed and was found at all stages of development in all individuals of the three genera.

The supraoccipital region of the cranium varies only with respect to slope and to the degree of development of the supraoccipital spine. In *Cynopotamus* (fig. 2), the occiput has a strong slope and the supraoccipital spine is extraordinarily developed. The elevation of the occipital region in this genus determines the development of a deep concavity on the median upper part of the cranium. In *Acestrocephalus* (fig. 4) the occiput is only slightly sloping, the supraoccipital spine small and the upper part of the cranium is virtually straight from the tip of the snout to the end of the supraoccipital spine. *Galeocharax* (fig. 3) can be placed in a intermediate condition. The inclination of the occipital region is certainly correlated with body shape, as will be discussed later.

The rhinosphenoid is absent but the orbitosphenoid is a well developed bone, in intimate contact with the parasphenoid in adult specimens of the three genera. The presence or absence of the rhinosphenoid and the contact of the orbitosphenoid with the parasphenoid have been subjected to various interpretations. In the diagnosis of the subfamily Characinae, Weitzman (1962:48) stated that "The orbitosphenoid is well developed, *but not directly articulated with the parasphenoid*" (italics mine). The Characinae defined by Weitzman, however, included some other groups and is not equivalent to the concept of the subfamily adopted in this study (see also p. 20). On the other hand, Roberts (1969:406) reached the conclusion that within the Characoidei the rhinosphenoid is apparently restricted to the family Cynodontidae and to the American groups of the family Characidae in which the parasphenoid lies far from the orbitosphenoid. He also emphasized that the orbitosphenoid is in contact with the parasphenoid in many groups of fishes, e.g. in the Erythrinidae, Anostomidae, Lebiasinidae, Hepsetidae and Ctenoluciidae of the Characoidei, as well as in *Salminus* of the family Characidae. According to Roberts, this condition would be an indication of primitiveness within the Characoidei; since he considered the contact between those two bones in *Salminus* to be only partial, he concluded that, with respect to this character, the genus would be intermediate between primitive Characoidei lacking the rhinosphenoid and having the orbitosphenoid connected to the parasphenoid, and some more specialized Characidae in which the rhinosphenoid is present but the parasphenoid lies far from the orbitosphenoid.

Examination of *Cynopotamus, Galeocharax* and *Acestrocephalus,* and other genera of the subfamily Characinae, revealed that the presence or absence of the rhinosphenoid and the degree of contact between the orbitosphenoid and parasphenoid are conditions which vary considerably inside natural groups and apparently are of little phylogenetic value at the levels suggested by Roberts (1969) or Weitzman (1962). In *Acestrorhynchus,* the rhinosphenoid is strongly developed and it is this bone and not the orbitosphenoid that contacts the parasphenoid (Menezes, 1969b:35). In *Moralesia,* both the rhinosphenoid and orbitosphenoid are present and the latter is only partially connected to the parasphenoid. *In Roeboides,* the rhinosphenoid is lacking in some species which have the orbitosphenoid closely attached to the parasphenoid. Other species have both the rhinosphenoid and the orbitosphenoid and the latter not connected to the parasphenoid. Furthermore, the connection between orbitosphenoid and parasphenoid depends on the stage of development of the individual. In some genera where the contact was observed in the adult, the young had only partial or even no contact at all.

A firm attachment of the orbitosphenoid to the parasphenoid in *Cynopotamus, Galeocharax* and *Acestrocephalus* and in most genera of the subfamily Characinae suggests that this condition has possibly been attained in connection with predatory habits. These forms, feeding on large prey, apparently need a firm connection between the parasphenoid and the bones of the cranial roof. In *Acestrorhynchus* this condition would have been attained through the rhinosphenoid. In *Brycon* (Weitzman, 1962) and the remaining generalized characids a firm connection is apparently not needed, since they usually feed on small organisms and in consequence the orbitosphenoid is generally separated from the parasphenoid.

The parasphenoid in *Cynopotamus* (fig. 2) is slightly curved along its median portion, apparently correlated with the steep dorsal cranial profile; in *Galeocharax* and *Acestrocephalus* (figs. 3, 4) it is virtually straight. The magnitude of the ventral median curvature of the parasphenoid is a character which also varies within the Characinae and apparently does not have the phylogenetic value suggested by Roberts (1969:406). Forms such as *Charax* and *Roeboides, Paroligosarcus* (Menezes, 1969b), *Roestes* (Menezes, 1974) and *Cynopotamus,* which have the posterior part of the head and the anterior dorsal part of the body elevated, also tend to have the median part of the parasphenoid decurved. Forms with the head less elevated posteriorly and the body elongate and not deep anteriorly, for example, *Acestrorhynchus* (Menezes, 1969b) and *Acestrocephalus,* have the parasphenoid nearly straight.

The lateral posterior part of the cranial roof, which involves the frontal and the sphenotic bones and where the dilator groove is found, presents some interesting peculiarities. In *Cynopotamus,* the dilator groove (fig. 5) is extraordinarily long and developed, extending dorsally beyond the middle of the orbit. The sphenotic spine (figs. 5, 8) is not well differentiated and, as a result, the lateral margin of the cranium, formed by the sphenotic and frontal bones, is almost straight. The sixth infraorbital is laterally in contact with the frontal but its dorsal part does not overlay the groove (fig. 5). In this respect, *Cynopotamus* differs considerably from *Galeocharax* and *Acestrocephalus,* and also from other Characinae examined. In *Galeocharax* and *Acestrocephalus* (figs. 6, 7) the dilator groove is relatively small, reaching at most a point roughly corresponding to the middle of the orbit. The sphenotic spine (figs. 6, 7, 9, 10) is differentiated and developed in such a way that the lateral end of the sphenotic bone extends far beyond the lateral margin of the frontal. In *Galeocharax* (fig. 6) the dilator groove is only partially roofed by the upper part of the sixth infraorbital and the anterior end of this bone is not in contact with the frontal. In *Acestrocephalus* (fig. 7), the sixth infraorbital overlays the dilator groove almost entirely and is anteriorly and posteriorly in contact with the frontal.

JAWS

Cynopotamus, Galeocharax and *Acestrocephalus* have elongante jaws, and the gape is consequently long.

The maxillary (figs. 2, 3, 4) is a fairly elongate bone with a row of conical teeth along its ventral edge; its posterior part reaches beyond the posterior border of the second infraorbital and is excluded from the gape. More anteriorly, the maxillary is partially overlain by the first infraorbital. Close examination of the maxillary revealed the presence of a canal, and special attention was paid to this structure because there seems to be no reference to it in the literature. The maxillary in characoids has been described as a plain and compact bone (Weitzman, 1962). In *Cynopotamus, Galeocharax* and *Acestrocephalus* (figs. 2, 3, 4, 15B, 16B, 17B) and other members of the Characinae examined, such as *Charax, Roeboides, Moralesia, Roestes, Gnathocharax,* and *Heterocharax,* there is a small hole on the distal third of the external surface of the bone. This hole corresponds to the posterior opening of a canal, which extends from this region to the anterior part of the maxillary, runs through the ascending process of this bone, at the tip of which it ends in one or more openings. Smaller branches of the main canal open at the surface of the maxillary through very small holes, which are irregularly distributed along the bone. In the Acestrorhynchini (Menezes, 1969b) this structure had been identified as a laterosensory canal, but recent observations made by Weitzman (personal communication) indicate that the maxillary canal is present in other characids and, although very short, it is structurally different from a true laterosensory canal. According to him, in *Moenkhausia oligolepis* (a tetragonopterine), histological sections of the short canal revealed that through it run nerves and blood vessels that feed the roots of the maxillary teeth as well as the lateral surface of the posterior shaft of the maxillary; one of the nerves is a branch of the maxillary ramus of the fifth nerve. Thus, it seems that the maxillary canal is a feature common to many characids. As described above, in *Cynopotamus, Galeocharax* and *Acestrocephalus,* and other Characinae, this canal extends to the distal third of the maxillary and this seems to represent a very specialized condition, as in other characid groups it is apparently very reduced.

The premaxillary (figs. 15A, 16A, 17A) bears one external row of conical teeth, of which the first and the last are canines, and two conical teeth located more internally. Such an arrangement of the teeth on the premaxillary is constant for all the species in the three genera, and not found in any other member of group of the Characinae. The arrangement of the teeth on the dentary, however, varies within the group. In all the species of the genus *Cynopotamus* there is one external row of teeth, anteriorly formed by 4 spaced conical teeth, of which the first, second and third are strongly developed and can be considered as canines. The third canine is notably more developed than the others. Following the canines, there is one row of small conical teeth, slightly curved posteriorly. One to 3 small conical teeth are usually found near the symphysis of the lower jaw, next to the first mandibular canines and consequently in a position slightly more internal than the teeth of the external row. These teeth represent a rudimentary inner row, very variable in number, and sometimes absent. Among the specimens of *Cynopotamus argenteus* examined, only one proved to have one small conical tooth near the symphysis of the lower jaw; in *Cynopotamus caliurus* no tooth was observed. In the remaining species of the genus, 1, 2 or 3 teeth are always present. In *Galeocharax* (fig. 16C) the teeth forming the external row on the lower jaw are arranged in the same fashion as in *Cynopotamus,* but in addition to the external row there is a well differentiated inner row, formed by 7 to 11 small conical teeth. An identical inner tooth row represented by 9 to 11 teeth is also present in *Acestrocephalus* (fig. 17C). The external tooth row in this genus is identical to those of the other two genera, but, in the great majority of the specimens, there are only 3 instead of 4 large conical teeth on the anteriormost part of the lower jaw.

Considering the arrangement of the teeth on the lower jaw, it is evident that *Galeocharax* and *Acestrocephalus* are much more closely related to each other than to *Cynopotamus.*

SUSPENSORIUM AND PALATINE ARCH

The palatine arch and the suspensorium have the same basic structure in *Cynopotamus, Galeocharax* and *Acestrocephalus,* but there are some differences, mainly in the shapes of the bones. The ectopterygoid, in characids, is normally a thin laminar bone (Weitzman, 1962; Roberts, 1969; Menezes, 1969b) but in the three present genera there is a deep concavity on its dorsal surface (figs. 11, 12, 13) in such a way that the continuity of the surface formed by the mesopterygoid and ectopterygoid is interrupted by the depression in the latter. In *Cynopotamus* and *Acestrocephalus* there is, along the median ventral part of the ectopterygoid, a blade-like bony crest, which extends from the anterior part of the bone to about two thirds of its length (figs. 8, 10, 11, 13, 14). This bony blade was observed in *Acestrocephalus* by Eigenmann (1912:21), who described the palatines (=ectopterygoids) as not having teeth but "with a sharp ridge". The bony crest is absent in *Galeocharax,* and in this regard it differs from the other two genera. The presence of a bony crest on the ectopterygoid is uncommon, since in characoids in general the ventral surface of this bone is smooth or, in some cases, provided with teeth, as for example in *Acestrorhynchus* (Menezes, 1969b), *Hoplias, Serrasalmus* and *Boulengerella* (Roberts, 1969). In other Characinae examined, the ventral surface of the ectopterygoid is smooth. However, the presence of a bony crest does not appear to be restricted to *Cynopotamus* and *Acestrocephalus;* a similar structrure exists in *Salminus* (Roberts, 1969:469, fig. 31). The development of a bony crest on the palatal region is possibly related to predatory habits, but the function of this structure seems to be different from that of the ectopterygoid teeth, which are primarily used for holding prey within the mouth cavity.

The hyomandibular in *Acestrocephalus* (fig. 13) has a prominent process extending dorsal to the posterior dorsal portion of the metapterygoid, but is strongly inclined in relation to the metapterygoid and to the quadrate, and consequently does not contact the posterior part of the mesopterygoid. In *Cynopotamus* and *Galeocharax* (figs. 11, 12) the process of the hyomandibular is much less prominent and the hyomandibular is vertically aligned with the posterior parts of the metapterygoid and quadrate, making possible the contact between mesopterygoid and hyomandibular. These differences are all part of a character complex correlated with body shape and depth and configuration of the posterior part of the cranium in the three genera, as will be shown below.

FACIAL BONES

The nasal bone in *Cynopotamus* and *Acestrocephalus* (figs. 2, 4, 5, 7) is tubular and largely consists of the canal which represents the cephalic laterosensory system in this region. In *Galeocharax* (figs. 3, 6), however, the nasal is laminar and, in addition to the canal, there is a bony projection which makes the nasal a laterally expanded bone in close contact with the ethmoid. Within the family Characidae, besides *Galeocharax,* apparently only *Acestrorhynchus* has a laminar nasal bone (Menezes, 1969b:35) but this is also found in other Characoidei, as demonstrated by Roberts (1969:419). He suggested the presence of a laminar nasal bone in some genera of the suborder Characoidei to be primitive and considered the characteristics of the nasal bone in *Salminus* and *Alestes* to be an indication that these two genera were intermediate between forms with a laminar nasal bone and forms having the nasal bone reduced to a canal. It seems to me that the evidence points to an independent development of a laminar nasal bone in different characoid groups, but the situation should be adequately investigated in all groups for a proper evaluation of the phylogenetic value of the character.

Cynopotamus, Galeocharax and *Acestrocephalus* have an incomplete series of circumorbital bones. The supraorbital is absent and the sixth infraorbital reduced, so that the frontal is a major component of the upper part of the orbit. In *Cynopotamus* (fig. 2) the first infraorbital is long and narrow and its anterior end slightly contacts the ventral tip of the antorbital. In *Acestrocephalus* (fig. 4) the first infraorbital is somewhat broad and short and the ventral tip of the antorbital just touches its anteriormost part. In *Galeocharax* (fig. 3), on the other hand, the first infraorbital is fairly well developed, especially broad on its median part, and remarkably long, almost as long as the second infraorbital. As a result of this enlargement, the anterior end of the first infraorbital is on top of a small portion of the posterior part of the premaxillary and its internal upper surface is lateral to the ventral tip of the antorbital, leading to a more intimate contact between the two bones. This condition is completely different from those described for the other two genera and from those found in any other characins examined.

The opercular bones of *Cynopotamus, Galeocharax* and *Acestrocephalus* correspond to the description presented by Weitzman (1962:32) for *Brycon* in shape, number and arrangement. In the three genera, however, there is a distinct bone bearing part of the laterosensory canal of the preopercle, and dorsally situated in relation to this bone (figs. 2, 3, 4, 11, 12, 13). Weitzman (l.c.) noticed this condition in *Acestrocephalus* and named the bone "supraopercle". This name was used by Menezes (1969b), when describing the structure in *Paroligosarcus* and *Oligosarcus.* Dr. S. Weitzman told me that the name, as it appears in his paper (p. 32) is a *lapsus calami:* he intended "suprapreopercle", following Stensiö (1947:168). "Supraopercle", instead is a lamellar bony structure which is present in the Hepsetidae and Erythrinidae as observed first by Weitzman (1964:135) and later by Roberts (1969:42).

Sometimes the suprapreopercle appears as an isolated bone above the preopercle, but in some cases they are fused; this condition varies in characoids and particularly within the Characinae. In *Acestrorhynchus* (Menezes, 1969b), *Roestes* (Menezes, 1974), *Gnathocharax, Heterocharax,* and *Hoplocharax* it is fused but in other genera such as *Charax, Roeboides,* and *Moralesia* it remains isolated from the preopercle. The latter condition, however, is constant within the genera involved in the present study and, with respect to this character, they can be considered as a homogeneous and well defined group.

GILL ARCHES

The gill arches of *Cynopotamus*, *Galeocharax* and *Acestrocephalus* are structurally identical with those found in many characoid groups. The gill rakers, however, show some variation among the three genera. In the first gill arch (figs. 21B, 31B, 36B) one or two anterior rakers on the upper arm and five or six on the lower arm are elongate, but the posteriormost ones are transformed into small spiny bony plates. The change from the elongate pattern on the median part to the laminar one towards both ends of the gill arch is clearly gradual. In the remaining gill arches the difference is more conspicuous, since the rakers on the median part of the arches are less elongate than the corresponding ones on the first gill arch, and have a decidedly more laminar aspect.

Most characoids have elongate gill rakers, which tend to become gradually reduced in size towards the ends of the gill arches: *Brycon* (Weitzman, 1962), *Astyanax* (personal observation), *Paroligosarcus* and *Oligosarcus* (Menezes, 1969b), and many other genera. In *Acestrorhynchus,* all the rakers are modified into small spiny bony lamellae (Menezes, 1969b; Roberts, 1969). These structures are also found in *Hoplias* and *Raphiodon* (Roberts, 1969) among the Characoidei, and some other groups not related to the Ostariophysi. All these fishes have in common the predatory habit, feeding mostly on other fishes and this fact strongly suggests that spiny lamellar rakers are structures adapted to help holding prey within the mouth cavity and the gill chamber. As far as these characters are concerned, *Cynopotamus, Galeocharax* and *Acestrocephalus* do not differ among themselves but, since they exhibit only partial modification of the gill rakers, the group can be considered as intermediate between *Acestrorhynchus* and the remaining members of the Characinae with normal gill rakers.

SCALES

All species of *Cynopotamus, Galeocharax* and *Acestrocephalus* have ctenoid scales; this is a unique feature, as all other Characinae have cycloid scales. The scales of *Cynopotamus* and closely related forms were described by Géry & Vu-Tân-Tuê (1963a, 1963b) as cyclo-ctenoid, but a detailed examination of these structures revealed they have all the characteristics of a true ctenoid scale (figs. 21A, 31A, 36A). The structures which appear on the surface of the free edge of each scale are true spines and must not be confused with the ciliary structures found in other groups of fishes. They are present in all stages of development of all species and occupy a considerable portion of the distal end of the scale. They are arranged in slightly irregular series, starting near the focus, where there is one series represented by one or two cteni. The number of cteni in each series gradually increases towards the upper margin of the scales. The circuli are disposed around the focus but do not reach the region of the cteni.

In all species the scales are regularly imbricate and cover practically all the body with exception of the head. The scales on the dorsal region, and especially those anterior to the dorsal fin, are smaller than the remainder. The axial scale above the base of the ventral fin is longer than the adjacent ones and bears fewer cteni, in a single incomplete row on the uppermost part of the margin.

Thus, the presence of ctenoid scales is a character which separates *Cynopotamus, Galeocharax* and *Acestrocephalus* from any other genus of the subfamily Characinae, and as such is of utmost importance to the definition of the group.

With respect to number of scale rows, *Acestrocephalus* differs from *Cynopotamus* and *Galeocharax* in having fewer scales on the lateral line, above and below the lateral line (table 3). *Galeocharax* (table 4) has in general fewer scales than *Cynopotamus,* but the counts for *C. amazonus* and *C. essequibensis* (table 2) are very close to the value obtained for the species of *Galeocharax.* In general, however, we can say that *Acestrocephalus* and *Cynopotamus* have extreme values and *Galeocharax* intermediate ones.

FINS

In *Cynopotamus, Galeocharax* and *Acestrocephalus* the fins and the bony structures associated with them have the same basic organization and the same elements found in characoids in general, and particularly in Brycon (Weitzman, 1962). However, there are differences in the number of rays of some fins, in the relative position and length of the anal fin, and in the shape of the cleithrum.

There is little variation in the number of dorsal fin rays, most species having 11 (ii+9) rays. *Cynopotamus argenteus, C. caliurus* and *C. kincaidi* are the only species that have 12 (ii+10) rays, this number being constant in all specimens examined. Géry & Vu-Tân-Tuê (1963b: 241) defined groups of species in *Cynopotamus* with basis on this difference. *C. argenteus* was considered a southern superspecies, *C. amazonus* an Amazonian species or superspecies, and *C. atratoensis* a northern polytypic species. Although the one ray difference in the dorsal fin can be used to separate two species groups within the genus *Cynopotamus,* the criterium does not reflect evolutionary trends, as discussed below.

In *Galeocharax,* dorsal fin rays vary from 10 to 11 but some specimens of *G. knerii* have 12. All the *Acestrocephalus* examined have 11 dorsal fin rays.

In the three genera the dorsal fin is situated approximately on the middle of the body, its origin being almost equidistant from the tip of the snout and the base of the caudal fin.

The range of pectoral fin rays is broader (12-17), but there is considerable overlap when we compare the values of the three genera (tables 2, 3, 4), so that the total number of pectoral fin rays cannot be used to separate them.

In the pectoral girdle, however, some differences can be detected. In all species of *Cynopotamus* the cleithrum has a prominent notch on its inferior border (fig. 2), whereas in *Galeocharax* and *Acestrocephalus* the lower border of the cleithrum is just slightly sinuous. This is a sizable difference between *Cynopotamus* and the two other genera.

The presence of a notch on the inferior border of the cleithrum is not an exclusive characteristic of *Cynopotamus.* It is also present and more conspicuous in *Charax, Asiphonichthys, Moralesia, Roeboides* and, less conspicuous but distinctly visible, in *Roestes* (Menezes, 1974), *Gnathocharax,* and *Hoplocharax.* All these forms have, like *Cynopotamus,* the body anteriorly elevated, the mouth partially or decidedly directed upwards, an the pectoral fins very long, with bases fitting the notch of the cleithrum. Thus, in those forms which have similar body shapes and apparently similar habits, there seems to exist a relationship between the presence of the notch and the shape of the body, and it seems as if the inferior border of the cleithrum is modified to accomodate the base of the pectoral fin. In *Galeocharax* and *Acestrocephalus* and other genera, such as *Paroligosarcus* and *Acestrorhynchus* (Menezes, 1969b), *Heterocharax* and *Lonchogenys,* which do not have the characters described above, the base of the pectoral fin is not deeply inserted into the cleithrum, but placed just below its inferior border.

The pelvic fin has 8 rays, a number characteristic of most groups of Characidae.

The number of caudal fin rays was also found to be constant for the group, all specimens having 19 (i+17+i) principal caudal rays.

The number of anal fin rays is highly variable in the group and is useful in species recognition (tables 2, 3, 4). The range of the number of anal fin rays shows that *Cynopotamus, Galeocharax* and *Acestrocephalus* differ in length and relative position of the anal fin. In *Cynopotamus* anal fin rays range from 42 to 53, the fin is quite long, and has its origin below the first dorsal fin rays. However, once more *C. amazonus, C. essequibensis* and, in this case, also *C. kincaidi,* do not fit exactly the main pattern, for the variation in number of anal fin rays of these species (36-43) is within the range of *Galeocharax.* The species of *Acestrocephalus* have a short anal fin, with fewer rays (29-35). In this genus the origin of the anal fin is under the last dorsal fin rays. In *Galeocharax,* the number of anal fin rays ranges from 36 to 45, intermediate between *Cynopotamus* and *Acestrocephalus;* the origin of the anal fin is approximately below the median dorsal fin rays. Thus the anal fin has an intermediate length to those of the former genera.

The differences in position and length of the anal fin in the three genera are possibly related to the shape of the body, as discussed below.

BODY SHAPE

Some of the characters discussed in previous sections in order to evaluate the degree of morphological distinction among *Cynopotamus, Galeocharax* and *Acestrocephalus,* are related to the peculiar shape of the body of the species which compose these genera. In *Acestrocephalus* (figs. 31, 33) the body is typically elongate, like in *Acestrorhynchus,* an unusual feature within the Characinae. The anterior dorsal region is not greatly elevated, which gives the dorsal profile, from the tip of the snout to the origin of the dorsal fin, a continuous but not prominent curvature. The mouth is directed forward, on the main longitudinal axis of the body. In *Galeocharax* (figs. 34, 35, 36) the body is also elongate, but different from *Acestrocephalus,* because the anterior dorsal region is higher. The profile from the tip of the snout to the origin of the dorsal fin is not smooth but interrupted at the median upper part of the cranium by a slight depression caused by the more pronounced elevation of the anterior dorsal part of the body. This region shows a distinct inflection, but not the gibbosity of *Cynopotamus.* The mouth is just slightly inclined upwards. The shape of the body of *Cynopotamus* (figs. 21, 23, 30) is considerably different and this is largely due to the extraordinary depth of the anterior dorsal region of the body. All the species of the genus have a typical gibbosity, which definitely influences certain structures of the head. The development of such a structure is the result of changes in the arrangement of the muscles of the region, and it is not to be confused with the temporary swellings, linked to the reproductive state, which appear in the anterior dorsal region of the body of the males of some groups of fishes. In *Cynopotamus* the remarkable development of the anterior dorsal musculature is correlated with the extraordinary development of the supraoccipital spine, that must afford a firm insertion to the epaxial muscles, as already observed in other characoids (Alexander, 1964:176; Roberts, 1969:411). For this reason *Cynopotamus* has the supraoccipital region of the cranium decidedly more inclined and the supraoccipital spine notably more elongate than *Galeocharax* and, especially, *Acestrocephalus.* Another consequence of the raised profile of the anterior dorsal region of the body and of the posterior part of the cranium is the development, in *Cynopotamus,* of a conspicuous depression on the median upper region of the cranium, with a general uplift of the anterior part of the head. Thus, in this genus the mouth is more visibly upturned and not along the main axis of the body. All these adaptations affect the arrangement of the suspensorium of *Cynopotamus,* as described above. There are also repercussions in the arrangement of some facial bones. The opercle and the upper portion of the preopercle in *Cynopotamus* are clearly inclined forward (figs. 2, 11), whereas in *Acestrocephalus* (figs. 4, 13) these bones are almost vertical.

The general body shape and the modifications described above for *Cynopotamus* are characteristic of all the species of the genus, but in *C. amazonus, C. kincaidi,* and *C. essequibensis* (figs. 24, 25, 26) the gibbosity is more prominent, the snout shorter, and the maxillary more elongate. Such features give a slightly different aspect to the body shape of these species, especially in the anterior region. These are the same species that have the scale counts and anal fin rays slightly off the range of most species in the genus. It seems that *C. amazonus, C. kincaidi,* and *C. essequibensis* form a specialized group of species, but one that still possesses the basic characteristics of the genus.

As far as the shape of the body is concerned, it seems clear that the species of *Acestrocephalus* have the body long and low; the species of *Cynopotamus* are deep-bodied, and those of *Galeocharax* of intermediate body depth. Since the anal fin is short in *Acestrocephalus,* long in *Cynopotamus,* and of intermediate length in *Galeocharax,* there seems to be a strong correlation between elongation of this fin and depth of body. Géry (1972b), based mainly on the lenght of the anal fin, divided the suborder Characoidei into two broad groups and stated that in some genera (among others *Charax* and *Cynopotamus*) the correlation was quite evident. Among the Characinae, the relationship between anal fin length and body depth seems to be a general rule. Fishes such as *Charax, Roeboides, Moralesia* and *Roestes,* which have a typical gibbosity like *Cynopotamus,* and therefore a very deep body, also have a very elongate anal fin. On the other hand, *Acestrocephalus* and some other less deep-bodied genera have a shorter anal fin. It is evident that the development of a gibbosity and the consequent increase in the body depth tend to alter hydrostatic balance. The correlated elongation of the anal fin may well be a compensatory mechanism. The correlation, however, is not perfect: *Cynopotamus, Galeocharax* and *Acestrocephalus* show an almost perfect gradation, but, as pointed out earlier, *Cynopotamus amazonus, C. kincaidi,* and *C. essequibensis,* that have more pronounced gibbosity and consequently a deeper body than the remaining species of the genus, have a relatively short anal fin. Since these species have a body shape somewhat different from the generalized pattern which characterizes most species of the genus, it is reasonable to assume that elongation of the anal fin is not an exclusive function of body depth, but that it depends on the integration of several factors, which on the whole determine the shape of the body of the individuals.

COLOR PATTERN

The species of *Cynopotamus, Galeocharax* and *Acestrocephalus* have a definite color pattern, characterized by a narrow silvery stripe on the sides of the body, a dark blotch on the humeral region and another one on the caudal base. There are slight variations in size und shape of the humeral and caudal blotches, and in the degree of contrast of the lateral stripe. In fresh specimens the silvery color of the lateral stripe is masked to a large extent by dark pigment, which disappears in preserved specimens.

A marked variation of the general pattern of coloration exists only in *Cynopotamus caliurus* which, in addition to the characters described above, has distinct dark blotches on certain parts of the body and fins (fig. 23). This species can be easily recognized by its peculiar coloration.

Many characid fishes have color patterns very similar to that described for the species of *Cynopotamus, Galeocharax* and *Acestrocephalus.* However, the constancy of the basic elements of the pattern in all species adds strength to the hypothesis of the homogeneity of the group.

FOOD HABITS

All MZUSP specimens, and some others that are here cited by their original institution numbers, but which were subsequently exchanged with us, have been examined for stomach contents. A considerable number of specimens had empty stomachs; among those containing food, fishes prevailed over other items.

The fishes found in the stomach of all species of the 3 genera were in a highly unusual, and to my knowledge, undescribed situation. It is usual to find the prey of carnivore fishes lying straight in the digestive tract, having been swallowed head first. All prew examined in the stomach of *Cynopotamus, Galeocharax* and *Acestrocephalus* were found folded, head and tail extending anteriorly (see also below).

As to food items in *Acestrocephalus,* only specimens of *A. sardina* were examined, and in only one was found a small unidentified fish, partially digested in the stomach. Among *Cynopotamus,* food, largely fishes, was found in the stomach of *C. argenteus, C. amazonus,* and *C. essequibensis.* Crustaceans (shrimps) occurred in the stomach of one specimen of *C. amazonus* and of one specimen of *C. essequibensis.* Most fishes found in the stomach of the three species of *Cynopotamus* were identified as tetragonopterines, a group of small schooling characids which generally live near the surface of the water. They were in very poor condition, unidentifiable below subfamily level; however, at least in one case it was possible to identify specimens taken out of the stomach of *C. argenteus* as belonging to the genus *Astyanax.*

The species of *Galeocharax* seem to have a more varied diet. In the stomach of 7 *G. humeralis,* fishes, mostly in an advanced stage of digestion, were the only food. Only from the stomach of one specimen was a small catfish (*Pimelolus* sp.) taken in very good condition.

The stomach contents of *G. gulo* revealed insects, adults and larvae, shrimps and fishes. In most stomachs fishes were the main component of the diet. It was possible to determine the presence of a loricariid

(*Loricaria* sp.) in the stomach of MZUSP 10432; parts of the pelvic girdle of a loricariid in the stomach of MZUSP 10438; one trichomycterid in the stomach of MZUSP 10436; and one curimatid in the stomach of MZUSP 10449. In *G. knerii* all stomachs examined contained fishes, with exception of MZUSP 10484, in which a small shrimp was found. In the stomach of *G. knerii* were tetragonopterines (MZUSP 10455 and 10483), *Bryconamericus stramineus* (MZUSP 10482), and *Characidium* sp. (MZUSP 10488, 10491, 10494, 10496 and 10500). Thus, the diet of the species of *Galeocharax* includes fishes that live near the surface of the water (tetragonopterines and *Bryconamericus stramineus*), fishes that live on the bottom of the rivers (*Pimelolus* sp., *Characidium* sp., curimatids, and loricariids), and invertebrates (insects, insect larvae and shrimps) that live on the surface or close to the surface of the water.

The data on food preferences are not sufficient to give a complete and definite picture of the overall differences in food habits of the three genera. It has not been possible to examine large series of all species, especially of *Cynopotamus* and *Acestrocephalus,* but these preliminary data interpreted in connection with the peculiar body shape of the three genera, provide useful informations about their general habits. The orientation of the mouth and the aspect of the anterior part of the body of all species of *Cynopotamus* indicate they are potentially adapted to feed on the surface. Therefore, it is not surprising to have found in the stomach of three species of this genus fishes which live near the surface of the water. This finding supports the idea that probably all the species of *Cynopotamus* primarily feed on the surface or near the surface of the water. Very little can be said of *Acestrocephalus,* beyond that, having the body typically elongate, in strong contrast with the body shape of *Cynopotamus*, this genus almost certainly explores another type of prey. If we consider that *Galeocharax* has a body shape intermediate between those of *Cynopotamus* and *Acestrocephalus,* it is reasonable to assume that it is potentially adapted to explore a greater variety of environments. As a matter of fact, the analysis of stomach contents of the species of *Galeocharax* corroborate this assumption, for in the stomach of these species were found both surface-living fish and invertebrates, and bottom dwellers.

As stated, practically all the fish prey found in the stomachs of this group were characteristically folded. A definite explanation will depend on experimental studies, but some speculations can be made. I think it highly improbable that the folding process takes place after the prey is in the predator's stomach; it is much more reasonable to admit that it occurs during capture, and this assumes manipulation before ingestion. *Cynopotamus, Galeocharax* and *Acestrocephalus* must have a unique procedure of catching and ingesting prey. Other characids, with rapacious conical dentition, and also feeding on fishes (e.g. *Acestrorhynchus*) generally ingest the prey in a different way. It was seen (Menezes, 1969a) that the fishes ingested were never folded and had their heads invariably posteriorly oriented into the predator's stomach.

Examining intra-group differences in our materials, we come to the preliminary conclusion that the species of *Cynopotamus* and *Acestrocephalus* seem to explore well defined zones of the aquatic environment in order to obtain their food whereas the species of *Galeocharax* apparently obtain theirs in more diverse types of environments.

DISCUSSION

Cynopotamus, Galeocharax and *Acestrocephalus* form a homogeneous group of phylogenetically related genera. The presence of an incomplete series of circumorbital bones, the constancy of the number and arrangement of the premaxillary teeth, the absence of the rhinosphenoid, the structure of the gill rakers, the type of contact between the orbitosphenoid and the parasphenoid, the presence of a suprapreopercle, and especially the presence of ctenoid scales on the body, are the basic characters common to the three genera which make up the group. This combination of characters is not found in any other group of genera in the family Characidae.

The presence of ctenoid scales is, perhaps, the most obvious diagnostic feature of the group; the genera of the Characinae that have always been considered as closely related to *Cynopotamus, Galeocharax* and *Acestrocephalus* (as well as the great majority of Characoid genera) have cycloid scales. Very little attention has been paid to the existence of ctenoid scales in members of the suborder Characoidei. Hubbs (1950) mentioned the possibility that all lower teleostens (i.e. the non Acanthopterygians) with cycloid scales have evolved from ancestors with ctenoid scales and noted that the Xenodexiinae, the only group of the Cyprinodontoidei to possess ctenoid scales, "may have regained a very specialized structure that was long lost in the phylogeny of the group". Discounting the word "regaining", that might stay or be substituted by "conserving", it is reasonable to believe that in the Characoidei a similar phenomenon may have occurred.

To the best of my knowledge, *Cynopotamus, Galeocharax* and *Acestrocephalus* form the only characoid group in which all the species bear ctenoid scales; but these structures also appear sporadically in some isolated forms, such as *Ctenobrycon* and *Psellogrammus* among the tetragonopterines (Eigenmann, 1927, and personal observation), and *Curimatus* and *Prochilodus*. It seems reasonable to assume then, as Hubbs (l.c.) suggested for the Cyprinodontoidei, that members of the suborder Characoidei evolved from ancestors with ctenoid scales and that during the evolution of the group the phenotypic expression of the character has been lost in most of the members.

The recognition of *Cynopotamus, Galeocharax* and *Acestrocephalus* as distinct genera is in disagreement with the conclusions reached by Géry & Vu-Tân-Tuê (1963b), who published the most recent revision of the group. As mentioned in the introduction to this study, these authors considered the group as composed of three subgenera: *Cynopotamus,* *Hybocharax,* and *Acestrocephalus. Hybocharax* was considered intermediate between *Cynopotamus* and *Acestrocephalus,* based on the characteristics of *Cynopotamus bipunctatus,* type-species of the subgenus. According to Géry & Vu-Tân-Tuê (1963a), the prominent gibbosity would characterize *bipunctatus* as a *Cynopotamus,* but the presence of three small teeth behind the mandibular canines and the position of the dorsal fin, slightly ahead of the middle of the body, would bring the species close to *Acestrocephalus.* The subgenus was further characterized as not having the notch on the clavicle (=cleithrum) and having the third infraorbital greatly developed. Also included in *Hybocharax* was *Cynopotamus magdalenae,* specimens of which Géry & Vu-Tân-Tuê did apparently not see.

Examination of the types of *Cynopotamus bipunctatus* and *C. magdalenae* revealed that they actually have all the characteristics of the genus *Cynopotamus.* The cleithrum of *C. bipunctatus* (fig. 18B), described by Géry & Vu-Tân-Tuê as not having a notch, can certainly be considered as much closer to the basic "notched-type" common to all the species of *Cynopotamus,* than to the "sinuous-type" found in the species of *Acestrocephalus.* The presence of two or three small teeth behind the mandibular canines (fig. 18A,C) does not represent an intermediate condition and cannot be relied upon to support the inclusion of those two species in a separate group because, as mentioned, these teeth represent a rudimentary row characteristic of most species of *Cynopotamus.* The relative position of the dorsal fin and the extent of development of the third infraorbital bone are characters that seem to have no phylogenetic meaning within the group.

The total evidence supports the conclusion that only three genera should be recognized: *Cynopotamus, Galeocharax,* and *Acestrocephalus.*

The problem that remains is to build up a hypothetical chain of relationships among these taxa. In order to gather an idea of the phylogenetic pathways of the group, the main morphological characters were assembled in table 1, on the basis of which figure 19 was made. The identification of each character state as primitive, intermediate or derived, was partly made according to its occurrence in the group (widespread or restricted), as has been recently suggested and discussed by Noonan (1973), partly by observing general evolutionary tendencies. Thus, as primitive are considered the characters common to all the genera, and those which represent a primitive condition within the group according to my own interpretation, based on what is known about the nature of the characters in related groups. Derived are considered to be the characters of restricted occurrence and those which represent a well known specialized condition. It should be understood that the concepts of "primitive" and "derived" as used here refer specifically to the cynopotamines and not to characids in general. For example, in the Characidae a complete series of circumorbital bones (8 bones) is considered a primitive condition and an incomplete series (less than 8 bones) a specialized condition. In the three present genera, the circumorbital series is incomplete (there are only 7 bones) but the character was considered primitive because it is common to all the genera and therefore reflect a generalized condition *for the group.*

In figure 19, characters 1-7, common to all the genera, indicate the homogeneity of the group, emphasized earlier. It is also evident from this figure that *Cynopotamus, Galeocharax* and *Acestrocephalus* represent three distinct stages of evolution, and that *Acestrocephalus* and *Galeocharax* are much more closely related to each other than to *Cynopotamus.* They possess some basic characters in common (8-11) but differ with regard to the remaining ones (12-17). Its seems clear then that *Cynopotamus* represents a lineage which evolved independently from a *Galeocharax-Acestrocephalus* ancestor, and that the latter split into two branches, *Acestrocephalus* and *Galeocharax* evolving separately.

That *Galeocharax* exhibit some intermediate characters does not mean it is intermediate between *Acestrocephalus* and *Cynopotamus.* It has peculiar characters (12-14) not shared with the other two genera, and can be considered as a distinct evolutionary unit within the group.

The geographic distribution of the group (fig. 20) supports the main conclusions on the phylogenetic relationships of the genera. *Cynopotamus* has a wide distribution in South America, from the Atrato, Magdalena, Orinoco, through the Maracaibo Basin, down to the rivers of Guiana, Surinam and French Guiana. It further occurs in the Amazon Basin, and to the south in the Paraguay, Paraná and Uruguay basins. It is interesting to note that the two groups of species of the genus *Cynopotamus* occupy different areas (fig. 22). *C. magdalenae, C. atratoensis, C. venezuelae, C. bipunctatus, C. argenteus,* and *C. caliurus,* the most generalized species, have a peripheral distribution in relation to the Amazon. On the other hand, the most specialized species, *C. amazonus, C. essequibensis,* and *C. kincaidi,* are essentially Amazonian. This suggests a pattern very much like that proposed by Menezes (1969b) for the acestrorhynchines. The Amazon Basin remains the place where adaptive innovations (and consequently radiations) occur. The forms generated there tend to push the older species towards the periphery where they remain, at least for a time, in marginal ecologies.

In accordance with this general pattern, *Acestrocephalus* has a more limited distribution, and two species are allopatric (fig. 32). *A. anomalus* is restricted to the Magdalena, and *A. sardina* is Amazonian, occurring in the upper course of some of the main tributaries of the Amazon, but not along the main course.

Galeocharax occurs in the Amazon and neighboring river basins (fig. 32). *G. humeralis* is confined to the Paraguay and Lower Paraná basins; *G. gulo* is widespread throughout the Amazon Basin, and extends to the Tocantins and São Francisco; *G. knerii* is restricted to the Upper Paraná. This pattern is very suggestive. *Galeocharax* is the only genus found outside the Amazon Basin, where some of the "old species" of *Cynopotamus* and *Acestrocephalus anomalus* occur.

This scheme applies also at the generic level. The older lineages (*Cynopotamus* and *Acestrocephalus*) are confined to the periphery of the general range, while the innovator, *Galeocharax,* is blossoming in the core Amazon valley.

This group of genera (*Cynopotamus, Galeocharax* and *Acestrocephalus*) has generally been considered as belonging to the subfamily Characinae. Some recent developments must be considered.

Géry (1972b) proposed a new classification of the Characoidei, and recognized two subtribes within the Characinae: Characini and Acestrorhynchini.

In my revision of the Acestrorhynchini (Menezes, 1969b), the status of tribe was attributed to the group, essentially with basis on Weitzman's (1962) concept of the Characinae: a large subfamily which included many of the previously recognized subfamilies within the Characoidei. As a result of the rearrangement of the familial classification of the characoids (Greenwood et al., 1966), the concept of characid subfamilies must change again, and therefore the Acestrorhynchini should be recognized as a distinct subfamily, on the same level as the Characinae.

It is hoped that this study has demonstrated that *Cynopotamus, Galeocharax* and *Acestrocephalus* are morphologically distinct from the forms which have been considered their nearest relatives, and form a monophyletic group. The recognition of a well defined and circumscribed group within the Characinae clearly indicates that the present status of the subfamily is not satisfactory, as it includes genera or groups of genera which apparently evolved independently from generalized ancestors of the suborder Characoidei, and therefore cannot be considered a natural group.

The degree of morphological differentiation reached by *Cynopotamus, Galeocharax* and *Acestrocephalus* seems to be enough to justify the subfamilial rank assigned to the group. The subfamily will be diagnosed and characterized in the next section.

SYSTEMATICS

Cynopotaminae, Subfam. n.

Body elongate, compressed; circumorbital series incomplete, the supraorbital absent and the sixth infraorbital reduced; first infraorbital partially overlaying the anterior dorsal region of the maxillary; third infraorbital well developed, but its distal part does not reach the preopercle, leaving this bone, the quadrate and the metapterygoid partially exposed (figs. 2, 3, 4); nasal bone tubular or laminar; mouth terminal, the lower jaw slightly shorter than upper when the mouth is fully open; premaxillary with two rows of conical teeth, the inner row represented by two slightly enlarged conical teeth, and the external row by one anterior canine, followed by a series of small conical teeth variable in number, and a posterior canine; each anterior premaxillary canine remains outside the mouth cavity, apposed to the border of the lower jaw, when the mouth is closed; maxillary elongate, narrow anteriorly and becoming gradually broader posteriorly; its posterior end always reaching beyond the posterior edge of the orbit; maxillary tooth row formed by small conical teeth; dentary with one or two rows of conical teeth; suprapreopercle present and isolated from the preopercle; cleithrum notched or just sinuous along its lower border; rhinosphenoid absent; orbitosphenoid in intimate contact with the parasphenoid; ectopterygoid with or without a ventral bony crest; nostrils close together, nearer to the eye than to the tip of the snout; gape long, always reaching beyond the anterior edge of the orbit; gill membranes separate from each other and free from the isthmus; gill rakers long and narrow on the median part of the gill arches, but modified into small spiny bony plates on both ends of the gill arches; there are always 5-7 well developed gill rakers, followed by 5-6 modified ones on the lower part of the first gill arch; laterosensory canal present on the circumorbital series, nasals, frontals, parietals, extrascapulars, posttemporals, supracleithra, cleithra, preopercles, and dentaries.

Scales ctenoid, relatively small and numerous, those of the anterior dorsal region of the body smaller than the remaining; lateral line complete, slightly curved anteriorly and extending to the beginning of the median caudal rays; adipose dorsal fin present, situated vertically above the posterior end of the anal fin; anal fin with iv-v, 29-35 rays, usually with recurved spines in male specimens; dorsal fin with ii, 9-10 rays, its origin about equidistant from the tip of the snout and the base of the caudal fin, but always situated ahead of the anal fin origin; caudal fin furcate, its upper and lower lobes having approximately the same length, or lower lobe slightly longer in some species; number of principal caudal fin rays, 10/9.

KEY TO THE GENERA OF THE SUBFAMILY CYNOPOTAMINAE

1. Lower edge of the cleithrum sinuous, not notched; anterior dorsal region not elevated or just slightly elevated; dentary with an inner row of 7-11 small conical teeth; nasal bone tubular or laminar; ectopterygoid with or without a ventral bony crest 2
   Lower edge of the cleithrum notched; anterior dorsal region elevated in a typical gibbosity; inner row of teeth on the dentary absent or represented only by 1-3 small conical teeth; nasal bone tubular; ectopterygoid with a ventral bony crest .... *Cynopotamus*

2. Anterior dorsal region not elevated; nasal bone tubular; ectopterygoid with a ventral bony crest; anal fin with iv-v, 29-35 rays; 72-77 perforated scales on the lateral lines .. *Acestrocephalus*
   Anterior dorsal region slightly elevated; nasal bone laminar; ectopterygoid without ventral bony crest; anal fin with iv-v, 36-45 rays; 80-101 perforated scales on the lateral lines *Galeocharax*

Cynopotamus Valenciennes, 1849

(Figs. 2, 5, 8, 11, 15)

Cynopotamus Valencinennes, 1849:316. Type-species: *Hydrocyon argenteum* Valenciennes, 1837 (Eigenmann, 1912:403).

Cyrtocharax Fowler, 1907:454. Type-species: *Anacyrtus limaesquamis* Cope, 1878:686.

Hybocharax Géry & Vu-Tân-Tuê, 1963b:240. Type-species: *Cynopotamus bipunctatus* Pellegrin, 1909:13.

Note: *Hydrocyon argenteum,* type-species of the genus *Cynopotamus* was described by Valenciennes in 1847 (p. 9) but the plate was published in 1837 (Sherborn & Griffin, 1934:131). Therefore, this date has priority over the date of publication of the text, according to article 16a vii of the International Code of Zoological Nomenclature (1964:15).

Description

Body moderate to large (S.L. 58-243 mm); anterior dorsal region notably elevated in a typical gibbosity; dorsal outline from the tip of the snout to the supraoccipital region, conspicuously concave, and almost evenly curved from this region to the caudal base; lower part of the antorbital in contact with the anterior end of the first infraorbital and with the anterior upper edge of the maxillary; first infraorbital narrow and elongate; nasal bone tubular; lower edge of the cleithrum deeply notched; ectopterygoid with a laminar bony crest along its median ventral portion; supraoccipital spine long; dentary with an external row of teeth anteriorly formed by 4 large conical teeth, of which the first, the fourth and especially the third are canines, and posteriorly by a row of small conical teeth, slightly curved backward; a rudimentary inner row, represented by 1-3 small recurved conical teeth is usually found near the mandibular symphysis, beside and slightly behind the first large conical tooth; scales small and numerous, 91-125 along the lateral line, 20-31 above and 17-28 below the lateral line; anal fin long, with iv-v, 36-53 rays, its origin situated on the vertical which passes anterior to the middle of the length of the dorsal fin base.

Distribution (fig. 20)

The genus *Cynopotamus* is represented in the Amazon Basin, in the Paraná, Paraguay and Uruguay, in the Atrato and Magdalena (Colombia), in the Orinoco and Maracaibo Basin (Venezuela), and in the rivers of the Guyanas (Guyana, Surinam and French Guyana).

KEY TO THE SPECIES OF *CYNOPOTAMUS*

1. Dorsal fin with ii, 10 rays 2
   Dorsal fin with ii, 9 rays 4

2. Dorsal fin with a large and conspicuous dark blotch which occupies most of the lower half of the fin; two smaller dark blotches situated respectively on the upper and lower basal portions of the caudal fin ..... *C. caliurus*
   Dorsal fin without large dark blotch; upper and lower basal portions of the caudal fin without dark blotches 3

3. Anal fin with iv-v, 42 rays ..... *C. kincaidi*
   Anal fin with iv-v, 46-56 rays ..... *C. argenteus*

4. 91-104 perforated scales on the lateral line 5
   107-125 perforated scales on the lateral line 7

5. Anal fin with iv-v, 36-43 rays 6
   Anal fin with iv-v, 49 rays ..... *C. bipunctatus*

6. 91-100 perforated scales on the lateral line; 20-30 scales above and 17-21 below the lateral line ..... *C. essequibensis*
   94-104 perforated scales on the lateral line; 23-28 scales above and 21-25 below the lateral line ..... *C. amazonus*

7. Anal fin with iv, 49-51 rays; 125 perforated scales on the lateral line ..... *C. magdalenae*
   Anal fin with iv, 40-47 rays; 107-121 perforated scales on the lateral line 8

8. Anal fin with iv, 45-47 rays, its origin situated vertically below the base of the second dorsal fin ray; 110-115 perforated scales on the lateral line ..... *C. atratoensis*
   Anal fin with iv, 40-46 rays, its origin situated vertically below the base of the fifth or sixth dorsal fin ray; 107-121 perforated scales on the lateral lines ..... *C. venezuelae*

Cynopotamus argenteus (Valenciennes, 1837)

(Figs. 2, 5, 8, 11, 15, 21)

Hydrocyon argenteum Valenciennes, 1837 (plate); (type-locality: America Meridionalis (Buenos Aires, Rio de La Plata); type not seen; topotype examined).

Hydrocyon argenteus; Valenciennes, 1847:9 (text).

Xiphoramphus argenteus; Müller & Troschel, 1845:18 (listed).

Cynopotamus argenteus; Valenciennes, 1849:317 (Rio de La Plata, Buenos Aires; description); Eigenmann & Eigenmann, 1891:58 (listed). Eigenmann & Ogle, 1907:32 (Paraguay; listed); Devincenzi & Legrand, 1940 (figure); Devincenzi & Teague, 1942:72 (Rio Uruguay medio; description); Schultz, 1950:67 (listed); Fowler, 1950:308 (synonymy; distribution); Ringuelet & Aramburu, 1961:32 (listed); Géry & Vu-Tân-Tuê, 1963b:241 (diagnosis in key); Ringuelet, Aramburu & Aramburu, 1967:141 (description; distribution).

Anacyrtus argenteus; Günther, 1864:348 (description).

Anacyrtus (Cynopotamus) argenteus; Steindachner, 1879:21 (description).

Charax argentea; Bertoni, 1914:13 (listed); 1939:56 (listed).

Charax argenteus; Pozzi, 1945:257 (Rio de La Plata, Rio Paraná, Rio Paraguay); Achenbach & Bonetto, 1957:7 (Paraná medio).

Characinus squamosus Eigenmann & Kennedy, 1903:525 (type-locality: Pasito Laguna, Paraguay; type examined).

Charax squamosus; Eigenmann & Ogle, 1907:33 (listed); Eigenmann, McAtee & Ward, 1907:143 (Bahia Negra, Paraguay); Eigenmann, 1910:445 (listed).

Charax squamosa; Bertoni, 1914:13 (listed); 1939:36 (listed).

Cyrtocharax squamosus; Schultz, 1950:60 (diagnosis), Fowler, 1950:312 (synonymy; distribution); Aramburu, 1957:87 (Buenos Aires; diagnosis); Ringuelet & Aramburu, 1961:32 (listed); Bonetto, Pignalberri & Cordiviola, 1965:143 (listed); Ringuelet, Aramburu & Aramburu, 1967:144 (description).

Eucynopotamus magdalenae (not of Steindachner, 1878) Bertoni, 1939:56 (Paraguay; listed).

Specimens studied (12): MLP — Rio de La Plata, Argentina (7); Rio Paraná, Argentina (2); MZUSP — Rio Uruguay, Rio Grande do Sul (2); CAS(IUM) — Rio Paraguay, Paraguay (1).

Diagnosis

D. ii, 10; A. iv-v, 46-53; P. i, 13-15; V. i, 7; 106-112 perforated scales on the lateral line; 24-26 scales above and 22-25 below the lateral line; 45-55 teeth on the maxillary. This species is sympatric with *C. caliurus* and *C. kincaidi* in the Paraguay Basin.

Description

Body large (S.L. 58-210 mm) and deep; ventral outline of the trunk considerably more curved than dorsal. Snout conical, always longer than orbital diameter. Maxillary with 45-55 teeth. Premaxillary with 6-9 conical teeth between the two canines of the external row. Dentary usually with a single row of teeth, rarely with one small anterior conical tooth slightly internal to the first canine; posterior row on the dentary with a highly variable number of teeth (23-28).

Scales numerous, 106-112 along the lateral line; 24-26 scales from the origin of the dorsal fin to the lateral line, 22-25 from the origin of the anal fin to the lateral line; a thick sheath of scales along the anal fin base, formed by about 10 rows of scales on the anterior region, 5 rows on the median region, and 2 rows on the posterior region of the fin; caudal fin lobes covered with small scales to about 2/3 of their length.

Anal fin with iv-v, 46-53 rays; anal fin origin situated vertically below the base of the fourth or fifth dorsal fin ray. Ventral fins reaching the anterior border of the anus. Pectorals longer than ventrals, their tips reaching beyond the insertion of these fins. Lower caudal lobe longer than upper in large specimens.

Color in alcohol, dark brown above, lighter below; a narrow silvery stripe from behind the upper part of the opercle to the base of the caudal fin; a nearly round dark blotch on the caudal fin base; there are vestiges of dark pigmentation at the humeral region. Some specimens have a small dark blotch at the tip of the lower jaw, and a nearly round dark dot on the base of the first dorsal fin ray.

The regression data are in figures 37-45 and Appendix table 1.

Distribution

Lower Paraná, Paraguay, and Uruguay basins.

Geographic variation

The samples from the different river basins did not show significant differences in both meristic and morphometric characters.

Cynopotamus caliurus (Eigenmann, McAtee & Ward, 1907)

(Fig. 23)

Characinus squamosus Eigenmann & Kennedy, 1903:525 (part; only the specimen No. 9969; erroneous identification).

Charax caliurus Eigenmann, McAtee & Ward, 1907:142 (type-locality: Pasito Laguna, Paraguay; type examined).

Charax caliura; Eigenmann, 1910:445 (listed); Bertoni, 1914:13 (listed); 1939:56 (listed).

Cyrtocharax calliurus; Schultz, 1950:60 (diagnosis); Fowler, 1950:311 (synonymy, distribution).

Cynopotamus (Cynopotamus) calliurus; Géry & Vu-Tân-Tuê, 1963b:241 (diagnosis in key).

Specimens studied (1): CAS(IUM) — Rio Paraguay, Paraguay.

Diagnosis

D. ii, 10; A. iv, 50; P. i, 13; V. i, 7; 115 perforated scales on the lateral lines; 25 scales above and 23 below the lateral line; 45 teeth on the maxillary; a large dark blotch present on most of the lower half of the dorsal fin; two small dark blotches situated respectively on the upper and lower basal portions of the caudal fin; a dark dot on the base of the first dorsal fin ray. This species is sympatric with *C. argenteus* and *C. kincaidi* in the Paraguay basin.

Description

Body moderate (S.L. 84 mm) and relatively deep; dorsal and ventral outlines of the trunk almost evenly curved. Maxillary with 45 teeth. Premaxillary with 8 conical teeth between the two canines of the external tooth row. Dentary with a single row of teeth; posterior row with 24 small conical teeth.

Scales very numerous, 115 on the lateral line, 25 from the lateral line to the origin of the dorsal fin and 23 from the lateral line to the origin of the anal fin; scale sheath along anal fin base anteriorly formed by 4 or 5 rows of scales, and posteriorly by 2 rows only; small scales on the caudal fin extending at least to about 2/3 of its length.

Dorsal fin high, its anteriormost rays much longer than the posterior ones. Anal fin with iv, 50 rays, truncate, its anterior rays notably longer than the posterior ones, its origin situated vertically below the base of the fourth dorsal fin ray. Pectorals long, much longer than ventrals, their tips reaching beyond the middle of the latter. Ventrals just reaching the origin of the anus.

General ground color in alcohol as in *C. argenteus;* a conspicuous and large dark blotch on the lower half of the dorsal fin, involving the first nine rays but separated from the dorsum by a narrow pale stripe; a small dark blotch at the tip of the lower jaw and a dark dot on the origin of the anal fin; a faded dark blotch on the humeral region; a nearly round dark blotch on the caudal fin base, which extends to the tip of the median rays of the caudal fin; upper and lower basal parts of the caudal fin with one small dark blotch; a silvery stripe along the sides of the body.

Distribution (fig. 22)

C. caliurus is known from a single specimen collected in the Paraguay Basin.

Cynopotamus kincaidi (Schultz, 1950)

(Fig. 24)

Charax limaesquamis Eigenmann & Ogle, 1907:33 (part; only the specimen No. 1694; erroneous identification).

Cryrtocharax kincaidi Schultz, 1950:60 (type-locality: Paraguay; type not seen; photograph and radiograph of the type examined).

Cynopotamus (Cynopotamus) kincaidi; Géry & Vu-Tân-Tuê, 1963b:241 (diagnosis in key).

Specimens studied (1): MZUSP — Rio Cuiabá, Santo Antonio do Leverger, Mato Grosso.

Diagnosis

D. ii, 10; A. iv-v, 42; P. i, 15; V. i, 7; 105-112 perforated scales on the lateral line; 30-31 scales above and 24-26 below the lateral line; about 46 teeth on the maxillary. This species is very similar to *C. amazonus* from which it differs by having a larger number of scales on the lateral line, and above and below the lateral line. It is sympatric with *C. caliurus* and *C. argenteus* in the Paraguay Basin.

Description

Body moderately large (S.L. 83-174 mm) and deep; dorsal outline of the trunk more curved than ventral. Snout conical, relatively short, just a little longer than orbital diameter. Maxillary bearing about 46 teeth along its lower border. Premaxillary with 8 small conical teeth between the canines of the external tooth row. Dentary with an external row of teeth and one small conical tooth situated before and slightly internal to the first canine; there are about 22 teeth in the posterior row on the dentary.

Scales numerous, 105-112 on the lateral line, 30-31 scales from the origin of the dorsal fin to the lateral line, and 24-26 from the origin of the anal fin to the lateral line; sheath of scales along the anal fin base anteriorly formed by 3-4 rows, and posteriorly by just one row of scales; the small scales on the surface of the caudal fin extend to about halfway the length of its lobes.

Dorsal fin relatively high, its anteriormost rays considerably longer than the posterior ones; anal fin with iv-v, 42 rays, its margin approximately straight, its anteriormost rays nearly twice as long as the last ones; origin of the anal fin situated vertically below the base of the fifth or sixth dorsal fin ray. Tips of the ventral fins reaching beyond the origin of the anal fin; pectorals longer than ventrals, their longest rays reaching beyond the middle of the latter; lower caudal lobe longer than upper.

Color in alcohol, dark brown above and lighter below; a silvery stripe on the sides of the body, becoming darker on the caudal peduncle, where it fuses with a nearly round dark blotch situated on the caudal base; a round dark blotch on the humeral region, a little smaller than the orbital diameter; lower jaw with a narrow dark stripe along its upper edge, extending to a point which roughly corresponds with the position of the fourth canine; tips of the dorsal and caudal fins with scattered dark pigments.

Distribution (fig. 22)

C. kincaidi has been recorded only in the Paraguay Basin.

Cynopotamus amazonus (Günther, 1868)

(Fig. 25)

Anacyrtus (Cynopotamus) amazonum Günther, 1868a:481 (type-locality: Xeberos; type not seen); 1868b:246.

Cynopotamus amazonum; Eigenmann & Eigenmann, 1891:58 (listed).

Cynopotamus amazonus; Fowler, 1945:163 (Jeberos, Peru; listed); Géry & Vu-Tân-Tuê, 1963b:241 (diagnosis in key).

Charax amazonum; Eigenmann, 1910:445 (listed).

Cyrtocharax amazonus; Fowler, 1950:310 (synonymy, distribution).

Cyrtocharax amazonum; Schultz, 1950:62 (diagnosis, distribution).

Anacyrtus limaesquamis Cope, 1878:686 (type-locality: Pebas, Peru; type not seen; data from the type examined); Eigenmann & Eigenmann, 1891:57 (listed); Boulenger, 1898:426 (Rio Juruá; listed).

Cyrtocharax limaesquamis; Fowler, 1907:454 (redescription); 1945:162 (Pebas, Contamana; listed); 1950:311 (synonymy, distribution).

Charax limaesquamis; Eigenmann & Ogle, 1907:33 (part; only the specimen No. 44835; erroneous identification); Eigenmann, 1910:444 (listed); La Monte, 1935:8 (Rio Juruá; listed).

Cynopotamus limaesquamis; Pellegrin, 1909:150 (Tefé, Tonantins; listed).

Cynopotamus argenteus (not of Valenciennes, 1837) Castelnau, 1855:74 (Rio Araguaia; listed).

Specimens studied (93: MZUSP — Igarapé do Pau-Roxo, Roraíma (2); Igarapé Boa Vista, Amazonas (1); Igarapé do 11, Pará (1); Igarapé do 5, Pará (1); Igarapé do Limão, Baião, Pará (1); Rio Jiparaná, Rondônia (1); Rio Jamari, Rondônia (1); Rio Araguaia, Aruanã, Goiás (1).

Diagnosis

D. ii, 9; A. iv, 36-41; P. i, 14-15; V. i, 7; 94-704 perforated scales on the lateral line; 23-28 scales above and 21-25 below the lateral line;

50-60 teeth on the maxillary; eyes very large, the orbital diameter equal to or just slightly smaller than the length of the snout; gibbosity very pronounced.

Description

Body moderately large (S.L. 82-170 mm) and deep; dorsal outline of the trunk more strongly curved than ventral. Snout conical, short, equal to or just slightly longer than orbital diameter. Maxillary curved, with a large number of teeth (50-60). Premaxillary with 7-9 small conical teeth situated in between the two canines of the external tooth row. Dentary with just one external row of teeth or with 1-2 small conical teeth situated near the mandibular symphysis and slightly internal to the first canine; posterior row on the dentary with 26-32 teeth.

Scales moderately numerous, 94-104 along the lateral line, 23-28 from the origin of the dorsal fin to the lateral line, 21-25 from the origin of the anal fin to the lateral line; the scale sheath on either sides of the anal fin base is formed by 4 rows of scales on the anterior part of the fin, but the rows are gradually reduced to 2 and 1 more posteriorly; small scales on the caudal fin extending to about 1/3 of the length of the caudal fin lobes.

Dorsal fin anteriorly elevated, its first rays about three times as long as the last ones; anal fin with iv, 36-41 rays, its lower edge convex at the anterior part due to the greater length of the first rays, which are about twice as long as the last ones; anal fin origin situated vertically below the base of the sixth dorsal fin ray; ventral fins long, their longest rays reaching to the origin of the anal fin; pectorals a little longer than ventrals, their longest rays surpassing the origin but not reaching the middle of the latter; lower caudal fin lobe slightly longer than upper.

Ground color in alcohol, dark yellow above and lighter below; a dark silvery stripe along the sides of the body, anteriorly narrow, becoming wider towards the caudal region, and reaching its maximum width at the caudal peduncle where it is darker and fuses with an approximately round dark blotch situated on the caudal base; the dark pigmentation of the caudal blotch prolongs into the median caudal rays; an oval shaped dark blotch on the humeral region; tip of the lower jaw with a small dark blotch; distal parts of the dorsal, anal and caudal fins with scattered dark pigments.

The regression data are in figures 37-45 and Appendix table 2.

Distribution (fig. 22)

This species occurs in the Amazon Basin, mainly in its large tributaries.

Geographic variation

The analysis of meristic and morphometric characters did not show significat differences among the samples from the different localities of the Amazon Basin.

Cynopotamus essequibensis Eigenmann, 1912

(Fig. 26)

Cynopotamus essequibensis Eigenmann, 1912:403 (type-locality: Potaro Landing, Guyana; type not seen); Boeseman, 1952:191 (Suriname River; listed); Géry & Vu-Tân-Tuê, 1963b:242 (diagnosis in key); Lowe, 1964 (Essequibo River; listed).

Cyrtocharax magdalenae essequibensis; Schultz, 1944:302 (diagnosis in key); 1950:63 (Kartabo, Guyana).

Specimens studied (15): ZMA — Marowijne River, Surinam (2); Pikien Saramacca River, Surinam (6); Nickerie River, Surinam (1); Coppename River, Surinam (4); Marowijne River, French Guyana (1).

Diagnosis

D. ii, 9; A. iv, 36-43; P. i, 14-15; V. i, 7; 91-100 perforated scales on the lateral line; 20-23 scales above and 17-21 below the lateral line; 49-59 teeth on the maxillary; eyes large, the orbital diameter equal to or slightly longer than the length of the snout; gibbosity very pronounced. This species is very closely related to *C. amazonus* but can be distinguished from it on the basis of scale counts.

Description

Body moderate (S.L. 105-160 mm) and very deep anteriorly, the depth decreasing considerably from behind the dorsal fin towards the tail; dorsal and ventral outlines of the trunk almost evenly curved. Snout short, equal to or just slightly shorter than orbital diameter. Maxillary with 49-59 teeth, its lower edge slightly convex. Premaxillary with 7-8 conical teeth interposed between the two canines of the external tooth row. Dentary with one external row of teeth or with an additional rudimentary inner row composed of 1 or 2 small conical teeth situated near the symphysis; posterior row on the dentary with 28-35 teeth.

Scales moderately numerous, 91-100 along the lateral line, which is almost straight for its entire extension; 20-23 scales from the lateral line to the origin of the dorsal fin, 17-21 from the lateral line to the origin of the anal fin; scale sheath along the anal fin base formed by 3 rows of scales anteriorly, and just one row posteriorly; small scales on the caudal fin restricted to the basal portion of the fin.

Dorsal fin extremely elevated, its anteriormost rays about 3.5 times as long as the last ray; anal fin almost falcate, its first rays much longer than the last ones; anal fin origin situated vertically below the base of the sixth or seventh ray of the dorsal fin; there are iv, 36-46 anal fin rays; pectoral fins a little longer than ventrals, their longest rays reaching beyond the origin of these fins; tip of the ventral fins reaching the origin of the anal fin; caudal fin lobes about equally developed.

Color in alcohol, dark brown above, light yellow below; lateral silvery stripe narrow at its origin and widening progressively towards the middle of the body; from below the dorsal fin backward, it becomes narrow again; a small and nearly round dark blotch on the caudal base and another one vertically elongated and larger on the humeral region; tip of the lower jaw and distal parts of the dorsal and caudal fins dark. In some specimens there is a dark dot on the base of the first dorsal fin ray. Some other specimens have, in addition to the caudal and humeral blotches, other isolated dark blotches on certain parts of the head but these apparently represent an abnormal coloration.

The regression data are shown in figures 37-45 and Appendix table 3.

Distribution (fig. 22)

C. essequibensis is known from the rivers of Guyana, Surinam and French Guyana.

Geographic variation

The comparison of the specimens from Surinam with the specimen from French Guyana and the specimens from Guyana (data from the literature) did not not reveal significant differences in both meristic and morphometric characters.

Cynopotamus bipunctatus Pellegrin, 1909

(Figs. 18B-C, 27)

Cynopotamus bipunctatus Pellegrin, 1909:13 (type-locality: mouth of Rio Suripa, Venezuela; type examined); Géry & Vu-Tân-Tuê, 1963a: 150 (redescription of the type).

Cyrtocharax bipunctatus; Schultz, 1950:62 (listed).

Cynopotamus (Hybocharax) bipunctatus; Géry & Vu-Tân-Tuê, 1963b: 241 (diagnosis in key); Leccia, 1970:70 (listed).

Specimens studied (1): MHNH — Rio Suripa, Venezuela.

Diagnosis

D. ii, 9; A. iv, 49; P. i, 14; V. i, 7; 104 perforated scales on the lateral line; 46 teeth on the maxillary.

Description

Body moderate (S.L. 91 mm) and deep; dorsal outline of the trunk conspicuosly more curved than ventral. Snout relatively long, longer than orbital diameter. Maxillary with 46 teeth, its toothed edge visibly convex. Premaxillary with 8 teeth in between the two canines of the external tooth row. Dentary with one external row of teeth and 2-3 small conical teeth which represent a rudimentary inner row, near the mandibular symphysis; posterior tooth row on the dentary with 24 teeth.

Scales relatively numerous, 104 along the lateral line, which is nearly straight on the sides of the body; 26 scales from the lateral line to the origin of the dorsal fin, 25 from the lateral line to the origin of the anal fin; scale sheath along either sides of the anal fin base formed by 5-6 rows of scales anteriorly, 3 rows on the median part and 2 rows on the posteriormost part of the fin; caudal fin with scales only on its basal portion.

Dorsal fin elevated, its first rays reaching beyond the tip of the last rays when the fin is depressed; anal fin with iv, 49 rays, its anteriormost rays much longer than the last ones; origin of the anal fin vertically below the base of the third or fourth ray of the dorsal fin; pectoral fins nearly as long as ventral fins, their longest rays reaching beyond the middle of the latter; tip of the ventrals reaching the origin of the anal fin.

Color in alcohol, dark brown, head silvery; an oval shaped dark blotch on the humeral region and a smaller one on the caudal base; a silvery lateral stripe, narrow at both ends and wider on the middle of the body; all fins pale.

Distribution (fig. 22)

C. bipunctatus is known only from the type-specimen, collected in the Suripa River, a tributary of the Apure in Venezuela.

Cynopotamus magdalenae (Steindachner, 1878)

(Figs. 18A, 28)

Anacyrtus (Cynopotamus) argenteus (not of Valenciennes, 1837) Steindachner, 1878:72 (erroneous identification).

Anarcyrtus magdalenae Steindachner, 1878:77 (type-locality: Rio Magdalena; type not seen; topotype examined). 1879:80 (Rio Cauca; listed).

Cynopotamus magdalenae; Eigenmann & Eigenmann, 1891:58 (listed).

Eucynopotamus magdalenae; Eigenmann, 1907:770 (listed); 1910:445 (listed).

Galeocharax magdalenae; Fowler, 1910:790 (listed).

Charax magdalenae; Eigenmann, 1922:159 (listed); Fowler, 1942:135 (Rio Magdalena; listed); Miles, 1947:169 (Rio Magdalena; listed).

Cyrtocharax magdalenae magdalenae; Schultz, 1944:302 (diagnosis in key); 1950:63 (diagnosis); Dahl, 1971:129 (biology; distribution).

Cynopotamus (Hybocharax) magdalenae; Géry & Vu-Tân-Tuê, 1963b: 241 (diagnosis in key).

Specimens studied (1): USNM — Rio Magdalena, Honda, Colombia.

Diagnosis

D. ii, 9; A. iv, 49-51; P. i, 15; V. i, 7; 125 perforated scales on the lateral line; 30 scales above and 30 below the lateral line; 42 teeth on the maxillary; snout long, much longer than orbital diameter. This species is very closely related to *C. argenteus* but has higher scale counts on the lateral line above and below the lateral line.

Description

Body large (S.L. 243 mm) and very deep; dorsal and ventral outlines of the trunk similarly curved. Snout long, much longer than orbital diameter. Maxillary with about 42 teeth, its lower adge nearly straight, except for the distal end. There are 8 conical teeth between the two canines of the external tooth row on the premaxillary. Dentary with one external row of teeth and one small conical tooth near the mandibular symphysis; there are about 27 teeth along the posterior tooth row on the dentary.

Scales small and very numerous, 125 along the lateral line; number of scales from the origin of the dorsal fin to the lateral line equal to that from the origin of the anal fin to the lateral line (30); the number of scale rows along the scale sheath on the anal fin base decreases from 3 on the anterior, to 1 on the posterior part of the fin; the scales on the caudal fin extend to about 1/3 of the length of the caudal fin lobes.

Dorsal fin very high, its anteriormost rays about 4 times as long as the last ones; anal fin with iv, 49-51 rays, its lower edge anteriorly convex, and almost straight from the median to the posterior part of the fin; anal fin origin situated vertically below the base of the fourth or fifth ray of the dorsal fin; pectoral fins longer than ventrals, the tip of their longest rays reaching the middle of these fins; ventral fins reaching only to the origin of the anus.

Color in alcohol, dark above, lighter on the sides and below; a nearly round dark blotch on the caudal base and a smaller one on the humeral region; a dark silvery stripe on the sides of the body, distinctly broader below the dorsal fin. All fins pale but there are vestiges of dark pigmentation on the posterior parts of the dorsal, anal, and caudal fins; a dark narrow stripe along the anterior border of the first dorsal fin ray.

Distribution (fig. 22)

This species occurs in the Magdalena and Cauca basins, Colombia.

Cynopotamus venezuelae (Schultz, 1944)

(Fig. 29)

Cyrtocharax magdalenae venezuelae Schultz, 1944:298 (type-locality: Rio Negro, Maracaibo Basin, Venezuela; type and syntypes examined); 1950:63 (synonymy).

Cynopotamus atratoensis venezuelae; Géry & Vu-Tân-Tuê, 1963b:242 (diagnosis in key); Leccia, 1970:70 (listed).

Specimens studied (1): USNM — Rio Palmar, Venezuela (3); Rio Negro, Venezuela (3); Rio Socuy, Venezuela (2); Rio Afran, Venezuela (1); Sinamaica, Venezuela (1); Rio Machango, Venezuela (1).

Diagnosis

D. ii, 9; A. iv, 40-46; P. i, 15-17; V. i, 7; 107-121 perforated scales on the lateral line; 26-29 scales above and 25-28 below the lateral line. 42-49 teeth on the maxillary; origin of the anal fin situated vertically below the base of the fifth or sixth ray of the dorsal fin. This species is very similar to *C. atratoensis* but it has fewer anal fin rays, and the origin of this fin is situated far posteriorly in relation to the origin of the dorsal fin.

Description

Body large (S.L. 181-237 mm) and very deep; dorsal outline of the trunk more curved than ventral. Snout long, longer than orbital diameter. Maxillary with 42-49 teeth, its lower edge just slightly curved. Premaxillary with 7-10 teeth in between the two canines of the external tooth row. Dentary with a rudimentary inner row formed by 1-3 small conical teeth near the mandibular symphysis and one external row which is posteriorly formed by 24-29 teeth.

Scales comparatively small and numerous; lateral line approximately straight from the caudal base to the middle of the body and somewhat curved from this point toward the posterior part of the head; 107-121 scales along the lateral line, 26-29 from the origin of the dorsal fin to the lateral line, and 25-28 from the origin of the anal fin to the lateral line; the scales along either sides of the anal fin base are arranged in two rows anteriorly and 1 row posteriorly; the scales of the body extend only to the basal part of the caudal fin.

Anteriormost dorsal fin rays much longer than the posterior ones, the last ray about 1/4 as long as the first or second ones; anal fin with iv, 40-46 rays, the first rays about 3 times as long as the last ones; lower edge of the anal fin slightly convex at the anterior region; origin of the anal fin situated vertically below the base of the fifth or sixth ray of the dorsal fin; pectoral fins longer than ventrals, their longest rays reaching beyond the middle of the latter; ventral fins reaching only to the origin of the anus; caudal fin lobes about equally developed or lower lobe slightly longer than upper in some specimens.

Ground color in alcohol, silvery, a little darker above; the silvery lateral stripe and the humeral and caudal dark blotches are also present; the fins are pale but the dorsal, anal and caudal fins present vestiges of dark pigmentation distally.

The regression data are found in figures 37-45 and Appendix table 4.

C. venezuelae has been considered a subspecies of *C. magdalenae* (Schultz, 1944; 1950) but Géry & Vu-Tân-Tuê (1963b) considered it a subspecies of *C. atratoensis*. The latter was included by Schultz (l.c.) also as a subspecies of *C. magdalenae*. Both *C. venezuelae* and *C. atratoensis* differ considerably from *C. magdalenae* in anal fin and scale counts (table 4). With respect to these meristic characters, *C. atratoensis* and *C. venezuelae* are very closely related, although the latter has fewer anal fins rays and the origin of the anal fin decidedly more posterior. Unfortunately these species are represented by a restricted number of specimens and an adequate statistic analysis of the samples cannot be made. However, taking into consideration the above mentioned differences and especially the geographic distribution of these forms, it is evident that they cannot be considered as subspecies. As it has been demonstrated for the species of the genus *Roestes* (Menezes, 1974), *C. magdalenae, C. venezuelae* and *C. atratoensis* are strictly confined to fresh water and occur in isolated river basins and therefore are geographic and reproductively isolated.

Distribution (fig. 22)

C. venezuelae occurs in the rivers of the Maracaibo Basin, Venezuela.

Cynopotamus atratoensis (Eigenmann, 1907)

(Fig. 30)

Charax atratoensis Eigennman, in Eigenmann & Ogle, 1907:33 (type-locality: Truando, Colombia; type examined); 1910:445 (listed); 1922: 159 (listed); Fowler, 1942:135 (Atrato, Truando, and Sucio, Colombia; listed).

Cyrtocharax magdalenae atratoensis; Shultz, 1944:302 (diagnosis in key); 1950:63 (diagnosis); Dahl, 1971:129 (distribution).

Cynopotamus atratoensis atratoensis; Géry & Vu-Tân-Tuê, 1963b:242 (diagnosis in key).

Specimens studied (1): USNM — Truando, Colombia.

Diagnosis

D. ii, 9; A. iv, 45-47; P. i, 15-16; V. i, 7; 110-115 perforated scales on the lateral line; 44 teeth on the maxillary; origin of the anal fin situated vertically below the base of the second dorsal fin ray.

Description

Body large (S.L. 210 mm) and very deep; dorsal outline of the trunk more curved than ventral. Snout long, longer than orbital diameter. About 44 teeth on the maxillary; lower edge of the maxillary posteriorly curved. There are 7 teeth interposed between the two canines of the external row on the premaxillary. Dentary with just one small conical teeth near the mandibular symphysis, representing an inner row, in addition to the external row which has about 26 conical teeth along its posterior part.

Scales small and numerous, 110-115 on the lateral line, about 27 from the lateral line to the origin of the dorsal fin and 28 from the lateral line to the origin of the anal fin; scales along anal fin fin base arranged in 2 rows anteriorly and in 1 row posteriorly; small scales on the caudal fin extending to about 1/3 of the lengths of the upper and lower caudal fin lobes.

Anterior part of the dorsal fin greatly developed, the first rays about 4 times as long as the last ray; anal with iv, 45-47 rays, of which the first are much longer than the last ones; origin of the anal fin situated vertically below the base of the second dorsal fin ray; pectoral fins much longer than ventrals, their tips reaching beyond the middle of the latter; ventral fins reaching the origin of the anal fin.

General background color in alcohol, silvery, darker above; a silvery strip on the sides of the body, conspicuously darker on the caudal peduncle, where it fuses with an almost round dark blotch situated on the caudal base; humeral region with vestiges of a dark blotch; fins pale, with scattered dark pigments on the distal portions of the dorsal, anal and caudal fins.

Distribution (fig. 22)

C. atratoensis occurs in the Atrato Basin, Colombia.

Acestrocephalus Eigenmann, 1909

(Figs. 4, 7, 10, 13, 17)

Acestrocephalus Eigenmann, 1909:316. Type-species: *Xiphorhamphus anomalus* Steindachner, 1879:48 (Eigenmann, 1910:447).

Description

Body comparatively small (S.L. 41-102 mm); anterior dorsal region not elevated; dorsal outline regularly curved from the tip of the snout to the caudal base; lower part of the antorbital only in contact with the maxillary; first infraorbital relatively short, high on its median part; nasal bone tubular; cleithrum not notched, just with a slight sinuosity along its ventral edge; ectopterygoid with a bony crest on its median ventral surface; supraoccipital spine short; dentary with two rows of teeth, of which the first and the third are canines; these teeth are followed by a row of small conical teeth, slightly curved posteriorly, the number of which varies ontogenetically; the inner row of teeth on the dentary is formed by 9-11 small conical teeth; scales comparatively large and numerous, 71-77 along the lateral line, 12-14 above and 9-13 below the lateral line; anal fin comparatively short, with iv-v, 29-35 rays, its origin situated on the vertical which passes always behind the middle of the length of the dorsal in base.

The genus *Acestrocephalus* is represented by two allopatric species: *A. anomalus* and *A. sardina*. The former occurs in the Magdalena Basin, and the latter in the Amazon Basin (figs. 20, 32). They can be easily separated on the basis of some meristic counts. *A. sardina* has fewer anal fin rays (iv-v, 29-32 against iv, 33-35 of *A. anomalus*), fewer scales on the lateral line (71-72 against 73-77 of *A. anomalus*), and more scales below the lateral line (12-13 against 9-11 of *A. anomalus*).

Acestrocephalus anomalus (Steindachner, 1879)

(Figs. 4, 7, 10, 13, 17, 31)

Xiphorhamphus anomalus Steindachner, 1879b:84 (type-locality: Rio Cauca, Colombia; type not seen; specimens from the Magdalena examined).

Acestrocephalus anomalus; Eigenmann, 1909:316 (listed); 1910:447 (distribution); 1912:21 (redescription); 1922:165 (Magdalena Basin); Miles, 1947:173 (Rio Magdalena); Dahl, 1971:121 (Rio Magdalena).

Cynopotamus (Acestrocephalus) anomalus; Géry & Vu-Tân-Tuê, 1963b: 240 (diagnosis in key).

Specimens studied (10): CAS(IUM) — Apulo, Colombia (5); Girardot, Colombia (2); Peñas Blancas, Colombia (3).

Diagnosis

D. ii, 9; A. iv, 33-35; P. i, 12-14; V. i, 7; 73-77 perforated scales on the lateral line; 12-13 scales above and 9-11 below the lateral line; 34-37 teeth on the maxillary.

Description

Body relatively small (S.L. 41-68 mm) and low; dorsal and ventral outlines almost evenly curved. Snout elongate, equal to or just slightly longer than orbital diameter. Maxillary with 34-37 teeth, its lower edge curved. Premaxillary with 8-11 conical teeth between the two canines of the external tooth row. External tooth row on the dentary formed by one anterior canine, followed by one large conical tooth, one canine and a row of small conical teeth variable in number; inner row with 9-11 teeth.

Scales comparatively large, 73-77 on the lateral line, 12-13 from the origin of the dorsal fin to the lateral line, 9-11 from the origin of the anal fin to the lateral line; scales on either sides of the anal fin base forming a single longitudinal row, which extends to about the middle of the fin.

Dorsal fin anteriorly elevated, its first rays much longer than the last ones; anal fin with iv, 33-35 rays, which gradually decrease in size from the first to the last ones; origin of the anal fin situated vertically below the base of the seventh or eighth ray of the dorsal fin; pectoral fins a little longer than ventrals, their tips reaching the anterior border of the anus; upper and lower lobes of the caudal fin equally developed.

Color in alcohol, light brown, a little darker above; a narrow silvery stripe on the sides of the body, darker on the caudal peduncle where it fuses with an almost round dark blotch situated on the caudal base; there are vestiges of a dark humeral blotch. All fins pale.

The regression data are shown in figures 46-55 and Appendix table 5.

Distribution (fig. 32)

A. anomalus occurs in the rivers Cauca and Magdalena which form the Magdalena Basin.

Acestrocephalus sardina (Fowler, 1913)

(Fig. 33)

Charax sardina Fowler, 1913:567 (type-locality: Rio Madeira, Brasil; type not seen; specimen from the Rio Aripuanã, a tributary of the Madeira examined); Géry, 1972a:23 (redescription of the type).

Cyrtocharax sardina; Fowler, 1950:312 (listed).

Cynopotamus (Acestrocephalus) sardina; Géry, 1972a:28 (diagnosis in key).

Specimens studied (2): MZUSP — Rio das Mortes, Xavantina, Mato Grosso (1); Rio Aripuanã, Mato Grosso (1).

Diagnosis

D. ii, 9; A. iv-v, 29-32; P. i, 13-14; V. i, 7; 71-72 perforated scales on the lateral line; 12-14 scales above and 12-13 below the lateral line; 30-42 teeth on the maxillary.

Description

Body comparatively small (S.L. 90-102 mm) and low; dorsal outline slightly more curved than ventral. Snout elongate, a little longer than orbital diameter. Maxillary with 30-42 teeth, its lower edge almost straight, except for its posteriormost part. Premaxillary with 7-8 conical teeth between the two canines of the external tooth row. External row on the dentary as in *A. anomalus* but sometimes there is one additional large conical tooth behind the last canine; inner tooth row with 9-10 teeth.

Scales relatively large, 71-72 along the lateral line, 12-14 from the origin of the dorsal fin to the lateral line, 12-13 from the origin of the anal fin to the lateral line; scales on the base of the anal fin arranged in one longitudinal row which extends to about the fifteenth ray.

Dorsal fin high, its first rays about 2.5 times as long as the last ray; anal fin falcate, its anterior rays much longer than the posterior ones; there are iv-v, 29-32 anal fin rays; pectoral fins slightly longer than ventrals, their longest rays reaching beyond the insertion of the latter; ventral fins reaching to the origin of the anus; caudal fin lobes with about the same length.

Color in alcohol, dark yellow above, lighter below; upper part of the head dark, from the tip of the snout to the supraoccipital region; a dark silvery stripe on the sides of the body, extending from behind the upper part of the opercle to the caudal base, where it fuses with a nearly round caudal dark blotch; a small dark blotch vertically elongated on the humeral region and a dark dot on the base of the first dorsal fin ray; fins pale with scattered dark pigments mainly on the tips of the dorsal, anal and caudal fins.

In the original description of the species, Fowler (1913:566-568) mentions the presence of small denticles on the lower edge of the preopercle. Géry (1972a:23-24), based on the examination of the type-specimen, noticed that the denticles appear also on the edges of the cleithrum and suborpercle, but considered these structures as larval characters for the specimen measures only 32.5 millimiters. The specimen from the Aripuanã River, a tributary of the Madeira is adult (S.L. 90 mm) and does not have denticles on the edges of the cleithrum and of the opercular bones. Therefore, we may conclude that denticles and some other characters of the type-specimen are present only during the larval stage of the species.

Distribution (fig. 32)

Rio das Mortes and Madeira River basin.

Geographic variation

Although *A. sardina* is represented only by three specimens which have been collected in two different tributaries of the Amazon, it presumably has a wider distribution and possibly occurs also in other large Amazonian tributaries. One specimen from the Rio Negro and two specimens from the Rio Juruena recently studied by Géry (1972a) were tentatively assigned by him to *A. sardina.* Obviously, the taxonomic "status" of the species can be cleared out only after a complete study of its geographic differentiation, based on large series of specimens. However, since we did not find significant differences in the comparison between the specimen from the Rio Aripuanã and the specimen from the Rio das Mortes, it seems reasonable to assume that we are before a single species which possibly has a wide distribution in the Amazon Basin.

Galeocharax Fowler, 1910

(Figs. 3, 6, 9, 12, 16)

Galeocharax Fowler, 1910:790. Type-species: *Cynopotamus gulo* Cope, 1970:565.

Description

Body moderate to large (S.L. 22-220 mm); anterior dorsal region moderately elevated but not forming a typical gibbosity; dorsal outline slightly concave from the tip of the snout to the supraoccipital region, becoming convex from this point to the origin of the dorsal fin; lower part of the antorbital in close contact with the first infraorbital only; first infraorbital very elongate and comparatively deep, its anterior part overlaying a small portion of the posterior part of the premaxillary; nasal bone laminar; cleithrum not notched, its lower edge just sinuous; ectopterygoid without a bony crest along its median ventral part; supraoccipital spine moderate; dentary with two rows of teeth, the external row anteriorly formed by 4 large conical teeth, of which the first, the fourth, and especially the third are canines, and posteriorly by a row of small conical teeth slightly curved backward; the number of teeth along the posterior row on the dentary varies ontogenetically; inner row on the dentary with 7-11 small conical teeth; scales moderately numerous, 81-101 along the lateral line, 16-22 above and 14-22 below the lateral line; anal fin moderately long, with iv-v, 36-45 rays, its origin situated nearly on the vertical which crosses the middle of the dorsal fin base.

We recognize three species in *Galeocharax*: *G. humeralis, G. gulo* and *G. knerii.* With respect to most of the meristic characters, the last two resemble each other (table 4). Using these characters it is possible to separate only *G. humeralis,* which has 98-101 scales on the lateral line (80-86 in *gulo* and *knerii*), 20-22 scales above the lateral line (16-18 in *gulo* and *knerii*), 18-22 scales below the lateral line (14-17 in *gulo* and *knerii*). *G. gulo* and *G. knerii* can be distinguished from each other only on the basis of certain morphometric characters and of the number of teeth on the posterior row on the dentary, which is related to body size. *G. gulo* has fewer teeth in the posterior row on the dentary (fig. 55) and a deeper body (fig. 51).

Distribution (fig. 20)

Galeocharax is represented in the Amazon, Paraná (Paraná, Paraguay and Uruguay), and São Francisco basins.

Galeocharax humeralis (Valenciennes, 1834)

(Fig. 34)

Hydrocyon humeralis Valenciennes, 1834 (plate; (type-locality: America Meridionalis (Buenos Aires, Rio de La Plata); type not seen; topotypes examined); 1847:9 (text).

Xiphoramphus humeralis; Müller & Troschel, 1844:93 (listed); 1845:18 (listed).

Cynopotamus humeralis; Valenciennes, 1849:320 (Rio de La Plata, Buenos Aires; description); Kner, 1860:49 (part; only the specimens from Cuiabá, Rio Paraguay); Garman, 1890:13 (diagnosis; distribution); Eigenmann & Eigenmann, 1891:58 (listed); Goeldi, 1898: 467 (listed); Schultz, 1950:68 (diagnosis; distribution); Aramburu, 1953:299 (description); Ringuelet & Aramburu, 1961:32 (listed); Ringuelet, Aramburu & Aramburu, 1967:142 (description).

Cynopotamus (Acestrocephalus) humeralis; Géry & Vu-Tân-Tuê, 1963b: 240 (diagnosis in key).

Anacyrtus humeralis; Günther, 1864:348 (description); Perugia, 1891: 649 (Corrientes; Vila Maria, Rio Paraguay).

Eucynopotamus humeralis; Eigenmann, 1907:770 (listed); 1910:445 (distribution); Bertoni, 1939:56 (listed); 1945:257 (listed).

Galeocharax humeralis; Fowler, 1910:790 (listed); 1950:315 (synonymy; distribution).

Anacyrtus (Cynopotamus) knerii (not of Steindachner, 1878, part) Steindachner, 1878:65 (only the specimens from Cuiabá, Rio Paraguay).

Cynopotamus knerii (not of Stendachner, 1878) Eigenmann, McAtee & Ward, 1907:143 (Bahia Negra and Corumbá, Rio Paraguay); Ringuelet & Aramburu, 1961:32 (listed).

Eucynopotamus knerii Bertoni, 1914:13 (listed); 1939:56 (listed); Pozzi, 1945:257 (distribution).

Eucynopotamus gulo (not of Cope, 1870) Bertoni, 1939:56 (listed).

Specimens studied (8): NMW — Cuiabá, Mato Grosso (1); MLP — San Pedro, Buenos Aires, Argentina (2); Rosario, Santa Fé, Argentina (3); Parana Pavón, Entre Rios, Argentina (1).

Diagnosis

D. ii, 9; A. iv-v, 42-45; P. i, 14-15; V. i, 7; 98-101 perforated scales on the lateral line; 20-22 scales above and 18-22 below the lateral line; 47-52 teeth on the maxillary; 9-10 teeth along the inner row on the dentary.

Description

Body moderate (S.L. 90-137 mm); dorsal and ventral outlines of the trunk similarly curved. Snout long, much longer than orbital diameter. Maxillary with 47-52 teeth, its lower edge convex. Premaxillary with 8-9 teeth between two canines of the external tooth row. Inner row of teeth on the dentary with 9-10 teeth.

Scales comparatively small and numerous, 98-101 on the lateral line, 20-22 scales from the origin of the dorsal fin to the lateral line, 18-22 from the origin of the anal fin to the lateral line; scale sheath on both sides of the anal fin base formed by 4 rows of scales anteriorly, this number decreasing to 2 and 1 respectively on the median and posterior parts of the fin; scales present on the caudal fin base and extending to about 1/4 of the length of the caudal fin lobes.

Dorsal fin moderately elevated, its anteriormost rays about 2.5 times as long as the last rays; anal fin truncate, its rays gradually decreasing in size from the first to the last ones; number of anal fin rays, iv-v, 42-45; origin of the anal fin situated vertically below the base of the fifth or sixth ray of the dorsal fin; pectoral fins longer than and reaching the middle of, ventrals; ventral fins reaching only to the anterior border of the anus; caudal fin lobes equally developed.

Color in alcohol, yellowish, darker above and lighter on the sides and below; a nearly round dark blotch on the humeral region and a similar one on the caudal base; a dark silvery stripe along the sides of the body, extending from the humeral blotch to the caudal base where it becomes wider and fuse with the caudal blotch; fins with the same ground color of the body, but the dorsal, anal and caudal fins have scattered dark pigments.

The regression data are in figures 46-55 and Appendix table 6.

Distribution (fig. 32)

G. humeralis is restricted to the Paraguay and Lower Paraná basins.

Geographic variation.

The comparison between the specimen from the Paraguay Basin with the specimens from the Lower Paraná Basin did not show significant differences.

Galeocharax gulo (Cope, 1870)

(Fig. 35)

Cynopotamus gulo Cope, 1870 (type-locality: Pebas, Peru; type not seen; topotypes examined); Fowler, 1907:459 (redescription of the type); 1939:268 (description); 1945:164 (Pebas, Contamana, Rio Marañon); Eigenmann & Allen, 1942:259 (synonymy, distribution).

Eucynopotamus gulo; Eigenmann, 1907:770 (listed); 1910:445 (listed); Pearson, 1937:92 (Tingo de Pauca, Pusoc, Peru).

Galeocharax gulo; Fowler, 1910:790 (listed); 1950:314 (synonymy, distribution).

Cynopotamus (Acestrocephalus) gulo; Géry & Vu-Tân-Tuê, 1963b:240 (diagnosis in key).

Anacyrtus knerii (not of Steindachner, 1878) Boulenger, 1887:274 (Canelos, Ecuador); 1898:426 (Rio Juruá); Eigenmann & Eigenmann, 1891:57 (listed).

Cynopotamus knerii Garman, 1890:13 (Tabatinga; diagnosis); Eigenmann & Eigenmann, 1891:58 (listed); Pellegrin, 1909:150 (Tocantins); Pearson, 1924:49 (Rio Beni); Eigenmann & Allen, 1942:259 (distribution); Fowler, 1945:158 (distribution).

Anacyrtus humeralis (not of Valenciennes, 1834) Perugia, 1897:26 (Rio Beni, Bolivia); ? Pellegrin, 1899:157 (Rio Apure, Venezuela).

? Cynopotamus humeralis (not of Valenciennes, 1834) Schultz, 1944:296 (Venezuela); Leccia, 1970:70 (Venezuela).

Eucynopotamus humeralis; La Monte, 1935:8 (Rio Purus).

Charax goeldii Fowler, 1913:568 (type-locality: Rio Madeira, Brasil; type not seen); Géry, 1972a:25 (redescription of the type).

Cyrtocharax goeldii; Fowler, 1950:311 (synonymy, distribution).

Cynopotamus (Acestrocephalus) goeldii; Géry & Vu-Tân-Tuê, 1963b:240 (diagnosis in key).

Cynopotamus molossus (not of Kner, 1860) Schultz, 1950:68 (part; erroneous identification).

Specimens studied (34): MZUSP — Rio Solimões, Fonte Boa, Amazonas (12); Rio Solimões, Anamã, Amazonas (1); Rio Solimões, Ilha de Baruruá, Amazonas (2); Rio Solimões, Coari, Amazonas (2); Rio Juruá, Amazonas (3); Rio Amazonas between Santarém, Pará and Parintins, Amazonas (5); Rio Tocantins, Estreito, Maranhão (2); Rio das Mortes, Xavantina, Mato Grosso (1); Rio São Francisco, Bahia (1); Rio São Francisco, Pirapora, Minas Gerais (2); USNM — Rio Ampiyacu, Peru (2); Shansho Cano, Peru (1).

Diagnosis

D. ii, 9-10; A. iv-v, 36-43; P. i, 13-16; V. i, 7; 80-86 perforated scales on the lateral line; 16-18 scales above and 14-17 below the lateral line; 38-45 teeth on the maxillary; 7-9 teeth along the inner row on the dentary.

Description

Body moderate to large (S.L. 21-220 mm); dorsal and ventral outlines of the trunk almost equally curved. Upper part of the head very depressed at the interorbital region, considerably broader than the lower part. Snout long, much longer than orbital diameter. Maxillary with 38-54 teeth, its lower edge convex. Premaxillary with 7-10 conical teeth between the two canines of the external row. Inner row of teeth on the dentary with 7-11 teeth.

Scales larger and less numerous than in the previous species; 80-89 on the lateral line, 16-18 from the origin of the dorsal fin to the lateral line, 14-17 from the origin of the anal fin to the lateral line; scales along either sides of the anal fin base arranged in 2 rows anteriorly and in 1 row posteriorly; caudal fin with scales only on its basal portion.

Dorsal fin high, its first rays almost 3 times as long as the last ones; anal fin with iv-v, 36-43 rays, which gradually decrease in size from the first to the last ones; origin of the anal fin situated vertically below the base of the sixth or seventh ray of the dorsal fin; ventral fins much shorter than pectorals, their longest rays reaching only to the origin of the anus; pectorals long, their tips reaching beyond the insertion of the ventrals; lower caudal lobe slightly longer than upper.

Color in alcohol identical to that of *G. humeralis*.

The regression data are shown in figures 46-55 and Appendix table 7.

Distribution (fig. 32)

This species occurs in the Amazon and São Francisco basins. The presence of *G. gulo* in the São Francisco represents a first record.

Geographic variation

G. gulo is predominantly distributed along the main course of the Amazon and no differences were found in either meristic or morphometric characters when the samples from Peruvian, Upper, Middle and Lower Amazon were compared. One specimen from the Rio Madeira, originally described as *Charax goeldii* (data from Géry, 1972a, p. 27) did not differ from specimens from the Tocantins and other Amazonian samples. This suggests that *G. gulo* probably occurs in the other main tributaires of the Amazon.

The specimens from the São Francisco were shown not to differ significantly from the Amazonian specimens. Although the São Francisco Basin is apparently isolated from the Amazonian Basin, the direct communication between the Rio Sapão, a tributary of the São Francisco, and the Rio do Sono, a tributary of the Tocantins, in the lowlands of Goiás, provides an easy explanation for the homogeneity of the populations.

Galeocharax knerii (Steindachner, 1878)

(Figs. 3, 6. 12, 16, 36)

Cynopotamus humeralis (not of Valenciennes, 1834) Kner, 1860:49 (part; only the specimens from Oriçanga; erroneous identification); Campos, 1945:454 (Rio Mogi-Guaçu).

Anacyrtus (Cynopotamus) knerii Steindachner, 1878:65 (part; only the specimens from Oriçanga, Rio Mogi-Guaçu; type not seen; topotypes examined).

Cynopotamus knerii; Eigenmann & Norris, 1900:395 (Rio Piracicaba); Fowler, 1950:309 (synonymy, distribtuion).

Galeocharax knerii; Fowler, 1910:790 (listed).

Note:

The original description of *G. knerii* (Steindachner, 1878:65) is based on the specimens collected by Natterer in Cuiabá, Rio Paraguay and Irisanga (=Oriçanga), erroneously identified by Kner as *Cynopotamus humeralis,* according to Steindachner (l.c.). Among the specimens collected by Natterer, only those from Oriçanga, located near the Rio Mogi-Guaçu, can actually be considered as *Galeocharax knerii.* The remaining ones correspond to *G. humeralis* which, as demonstrated above, is restricted to the Paraguay and Lower Paraná basins.

In order to designate the type-species of *G. knerii,* we tried to obtain, on loan, the specimens collected by Natterer in Oriçanga, which are deposited at the Wien Museum. We contacted Drs. Marcus Knoflachen of the Zoölogisch Institut and Paul Kähsbauer of the Zoölogisch Museum but they were unable to locate the specimens. I was informed that except for types, it is extremely difficult, at present, to locate any specimen in the collection. In any case, the type-locality of *Galeocharax knerii* is restricted to Oriçanga and the specimens from this locality must be actually considered as the types.

Specimens studied (108): MZUSP — Jupiá, São Paulo (9); Rio Paraná, Mato Grosso (4); Ilha Solteira, Mato Grosso (1); Ilha Solteira, São Paulo (15); Franca, São Paulo (1); Emas, São Paulo (24); Piracicaba, São Paulo (17); Barra Bonita, São Paulo (1); Salto de Itapura, São Paulo (1); Usina do Limoeiro, São Paulo (26); Jurumirim, São Paulo (2); Pouso Alegre, Minas Gerais (1).

Diagnosis

Di. ii, 9; A. iv-v, 39-45; P. i, 14-15; V. i, 7; 81-86 perforated scales on the lateral line; 16-18 scales above and 15-17 below the lateral line; 36-51 teeth on the maxillary; 7-11 teeth along the inner row on the dentary.

Description

Body moderate to large (S.L. 22-220 mm); dorsal and ventral outlines of the trunk identically curved; body proportionally less deep than in *G. gulo* (fig. 47); upper part of the head depressed but just slightly wider than the lower part; interorbital distance proportionally smaller than in

G. gulo (fig. 50). Maxillary with 36-51 teeth, its lower edge convex. Premaxillary with 6-10 teeth between the two canines of the external tooth row. Inner row of teeth on the dentary wiith 7-11 teeth; teeth in the posterior row on the dentary proportionally more numerous than in *G. gulo* (fig. 55).

Scales identical to those of *G. gulo;* 81-86 along the lateral line, 16-18 from the origin of the dorsal fin to the lateral line, 15-17 from the origin of the anal fin to the lateral line; scale sheath along both sides of the anal fin base formed by 3 rows of scales anteriorly, the number of scale rows decreasing to 2 and 1 respectively on the median and posterior parts of the fin; scales on caudal fin restricted just to the basal portion.

Dorsal fin high, its anteriormost rays about 3.5 times as long as the last ones; anal fin with iv-v, 39-45 rays, the anterior ones longer than the posterior; origin of the anal fin situated vertically below the base of the eighth or nineth ray of the dorsal fin; pectoral fins longer than ventrals and reaching beyond the origin of these fins; ventrals short, their tips failing to reach the origin of the anus; caudal fin lobes about equally developed.

Color in alcohol identical to that of the other two species of the genus, but the dark humeral blotch is comparatively smaller, and the silvery lateral stripe darker and broader.

The regression data are presented in figures 46-55 and Appendix table 8.

Distribution (fig. 32)

G. knerii is restricted to the rivers of the Upper Paraná basin.

Geographic distribution

No significant differences were found in meristic and morphometric characters in the comparison of the samples from the different river systems of the Upper Paraná basin.

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APPENDIX

List of localities and study material. The number of specimens and the range of standard length in mm are in parentheses. The number after each locality indicates its geographical position as it appears in figure 1.

Cynopotamus argenteus

MZUSP 1547 (1, 210) — Brasil: RS, Itaqui, Rio Uruguay — 51
MZUSP 10412 (1, 237) — Idem
MLP 1-III-46-9 (1,58) — Argentina: Buenos Aires, San Pedro, Rio Paraná — 54
MLP 15-IV-45-5 (1, 176) — Idem
MLP 9-XII-40-26 (1, 150) — Argentina: Buenos Aires, Ensenada, Rio de La Plata — 55
MLP 5-IV-43-34 (1, 97) — Argentina: Buenos Aires, Palo Blanco (not precisely located)
MLP 3-X-32-13 (2, 98-122) — Argentina: Rio de La Plata (not precisely located)
MLP 16-IV-32-2 (1, 145) — Idem
MLP 4-X-32-19 (1, 210) — Idem
MLP 3-X-32-11 (1, 178) — Idem
IUM 9961 (1, 177) — Paraguay: Asunción, Laguna Pasito, Rio Paraguay — 50

Cynopotamus caliurus

CAS(IUM) 14682 (1, 84) — Paraguay: Asunción, Laguna Pasito, Rio Paraguay — 50

Cynopotamus kincaidi

MZUSP 4400 (1, 83) — Brasil: MT, Santo Antonio do Leverger, Rio Cuiabá — 35
USNM 1694 (1,174) — Paraguay: Rio Paraguay (not precisely located)

Cynopotamus amazonus

MZUSP 10413-14 (2, 107-170) — Brasil: RR, Igarapé do Pau-Roxo — 14
MZUSP 10415 (1, 156) — Brasil: AM, Igarapé Boa Vista — 22
MZUSP 10416 (1, 125) — Brasil: Pa, Igarapé do 11 — 30
MZUSP 10417 (1, 130) — Brasil: Pa, Igarapé do 5 — 29
MZUSP 10418 (1, 143) — Brasil: Pa, Baião, Igarapé do Limão — 28
MZUSP 10419 (1, 82) — Brasil: GO, Aruanã, Rio Araguaia — 37
MZUSP 2536 (1, 152) — Brasil: RO, Rio Jiparaná — 33
MZUSP 2538 (1, 153) — Brasil: RO, Rio Jamari — 32

Cynopotamus essequibensis

ZMA 106.347 (2, 105-107) — Surinam: Brokopondo, Marowijne Creek — 19
ZMA 106.348 (4, 126-160) — Surinam: Saramacca, Coppename River — 17
ZMA 106.350 (1, 150) — Surinam: Nickerie, Stondansie Fall — 16
ZMA 105.585 (6, 110-150) — Surinam: Brokopondo, Pikien Saramacca River — 18
ZMA 106.351 (1, 125) — Surinam: Nickerie, Fallawatra River — 15
ZMA 106.349 (1, 160) — French Guyana: Marowijne, Kamaloea Creek — 20

Cynopotamus bipunctatus

MNHN 98-21 (1, 91) — Venezuela: Rio Apure — 13

Cynopotamus magdalenae

USNM 121394 (1, 243) — Colombia: Honda, Rio Magdalena — 3

Cynopotamus venezuelae

USNM 121391 (1, 233) — Venezuela: Sinamaica — 10
USNM 121392 (1, 207) — Venezuela: Toturna, Rio Palmar — 11
USNM 121393 (2, 212-236) — Venezuela: Rio Socuy — 6
USNM 121394 (2, 181-195) — Venezuela: Maracaibo, Rio Palmar — 11
USNM 121395 (1, 190) — Venezuela: Rosario, Rio Afran — 7
USNM 121397 (1, 234) — Venezuela: Lagunillas, Rio Machango — 12
USNM 121398 (3, 205-237) — Venezuela: Rio Negro — 8

Cynopotamus atratoensis

USNM 1664 (1, 210) — Colombia: Truando, Rio Atrato — 1

Acestrocephalus anomalus

CAS(IUM) 12837 (2, 65-66) — Colombia: Girardot, Rio Magdalena — 4
CAS(IUM) 12838 (3, 41-50) — Colombia: Peñas Blancas, Rio Magdalena — 5
CAS(IUM) 12839 (3, 48-57) — Colombia: Apulo, Rio Magdalena — 2
MZUSP 10420-21 (2, 68) — Idem

Acestrocephalus sardina

MZUSP 10422 (1, 102) — Brasil: MT, Xavantina, Rio das Mortes — 36
MZUSP 10423 (1, 90) — Brasil: MT, Aripuanã, Rio Aripuanã — 34

Galeocharax humeralis

MZUSP 4413 (1, 137) — Brasil: MT, Santo Antonio do Leverger, Rio Cuiabá — 35
MLP 1-III-46-10 (1, 90) — Argentina: Buenos Aires, San Pedro, Rio Paraná — 54
MLP 1-III-46-11 (1, —)— Idem
MLP 28-V-40-59 (1, 110) — Argentina: Santa Fé, Rosario, Rio Paraná — 52
MLP 28-V-40-60 (1, 130) — Idem
MLP 28-V-40-61 (1, 133) — Idem
MLP 3-VI-43-13 (1, 113) — Argentina: Entre Rios, Paraná Pavón, Rio Paraná — 53

Galeocharax gulo

MZUSP 10424-33 (10, 21-44) — Brasil: AM, Fonte Boa, Rio Solimões — 24
MZUSP 10438 (1, 108) — Idem
MZUSP 10434 (1, 95) — Brasil: Anamã, Rio Solimões — 27
MZUSP 10437 (1, 103) — Brasil: AM, Jacaré, Rio Solimões — 25
MZUSP 10435-36 (2, 97-133) — Brasil: AM, Ilha de Baruruá, Rio Solimões — 23
MZUSP 10439-40 (2, 117-140) — Brasil: AM, Ilha Sorubim, Rio Solimões — 26
MZUSP 1683 (1, 147) — Brasil: Rio Juruá (not precisely located)
MZUSP 10441-43 (3, 117-172) — Idem
MZUSP 10444-47 (4, 138-169) — Brasil: between Santarém, PA and Parintins, AM (not precisely located)
MZUSP 4987 (1, 44) — Brasil: MA, Estreito, Rio Tocantins — 31
MZUSP 10448 (1, 40) — Brasil: Idem

MZUSP 10449 (1, 108) — Brasil: MT, Xavantina, Rio das Mortes — 36
MZUSP 10586-87 (2, 195-205) — Brasil: MG, Pirapora, Rio São Francisco — 38
MZUSP 1919 (1, 220) — Brasil: Idem
USNM 124884 (1, 55) — Peru: Rio Ampiyacu — 21
USNM 124890 — (1, 155) — Peru: Idem
USNM 124899 (1, 137) — Peru: Shansho Cano (not precisely located)

Galeocharax knerii

MZUSP 10450-58 (9, 22-153) — Brasil: SP, Jupiá, Rio Paraná — 42
MZUSP 10476-81 (12, 80-181) — Brasil: MT, Jupiá, Rio Paraná — 41
MZUSP 10488-501 (14, 85-190) — Brasil: SP, Ilha Solteira, Rio Paraná — 39
MZUSP 2073 (1, 195) — Brasil: SP, Franca, Rio Grande — 46
MZUSP 10502-10 (9, 94-140) — Brasil: SP, Emas, Rio Mogi-Guaçu — 48
MZUSP 10511 (1, —) — Idem
MZUSP 10514-27 (14, 119-180) — Brasil: Idem
MZUSP 1969 (1, 155) — Brasil: SP, Piracicaba, Rio Piracicaba — 45
MZUSP 326 (1, 220) — Idem
MZUSP 2031 (1, 218) — Idem
MZUSP 10529-41 (14, 82-198) — Idem
MZUSP 10556 (1, 135) — Brasil: SP, Barra Bonita, Rio Tietê — 43
MZUSP 10557 (1, 150) — Brasil: SP, Salto de Itapura, Rio Tietê — 40
MZUSP 10558-83 (26, 83-200) — Brasil: SP, Usina do Limoeiro, Rio Pardo — 47
MZUSP 10584-85 (2, 218-233) — Brasil: SP, Jurumirim, Rio Paranapanema — 44
MZUSP 1660 (1, 154) — Brasil: MG, Pouso Alegre, Rio Sapucaí — 49

INDEX

(Synonyms in italics)

ABBREVIATIONS USED IN FIGURES 2-13

acs — accessory suprapreopercle
an — antorbital
ang — angular
ar — articular
auf — auditory foramen
bas — basioccipital
br — branchiostegal rays
cb — coronomeckelian bone
cf — cranial fontanel
cl — cleithrum
d — dentary
eb — epiphyseal bar
ect — ectopterygoid
ectc — ectopterygoid bony crest
ep — epiotic
es — extrascapular
et — ethmoid
exo — exoccipital
fr — frontal
hm — hyomandibular
ih — interhyal
inf — infraorbital
int — interopercle
la — lapillus
lc — lagenar capsule
let — lateral ethmoid
m — maxillary
mes — mesopterygoid
met — metapterygoid
n — nasal
op — opercle
opi — opisthotic
orb — orbitosphenoid
pa — parasphenoid
par — parietal
pcl — postcleithrum
pf — posttemporal fossa
pl — palatine
pm — premaxillary
po — preopercle
post — posttemporal
pro — prootic
prv — prevomer
ps — pterosphenoid
pt — pterotic
q — quadrate
sc — saccular capsule
scl — supracleithrum
sf — subtemporal fossa
si — simplectic
so — supraoccipital
sop — subopercle
sp — sphenotic
ss — sphenotic spine

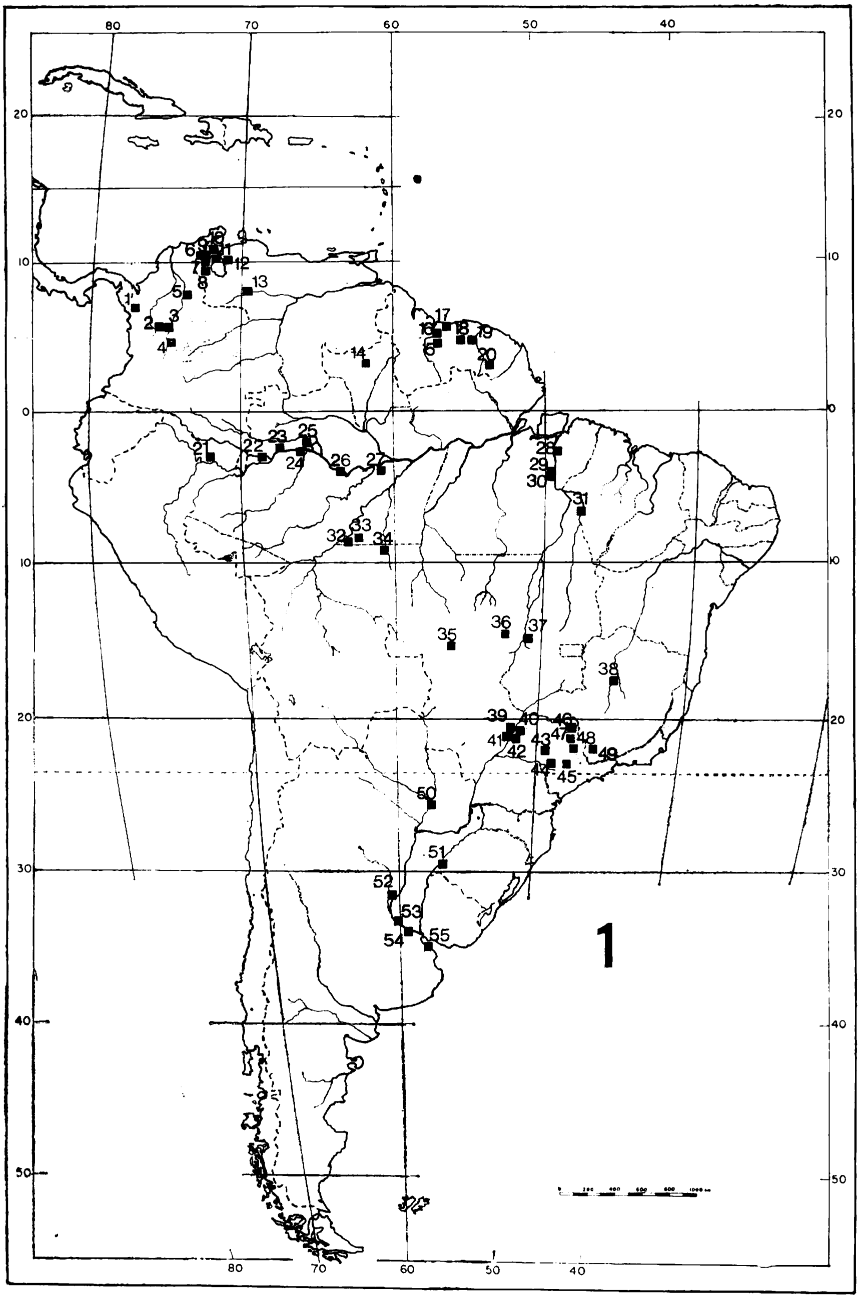
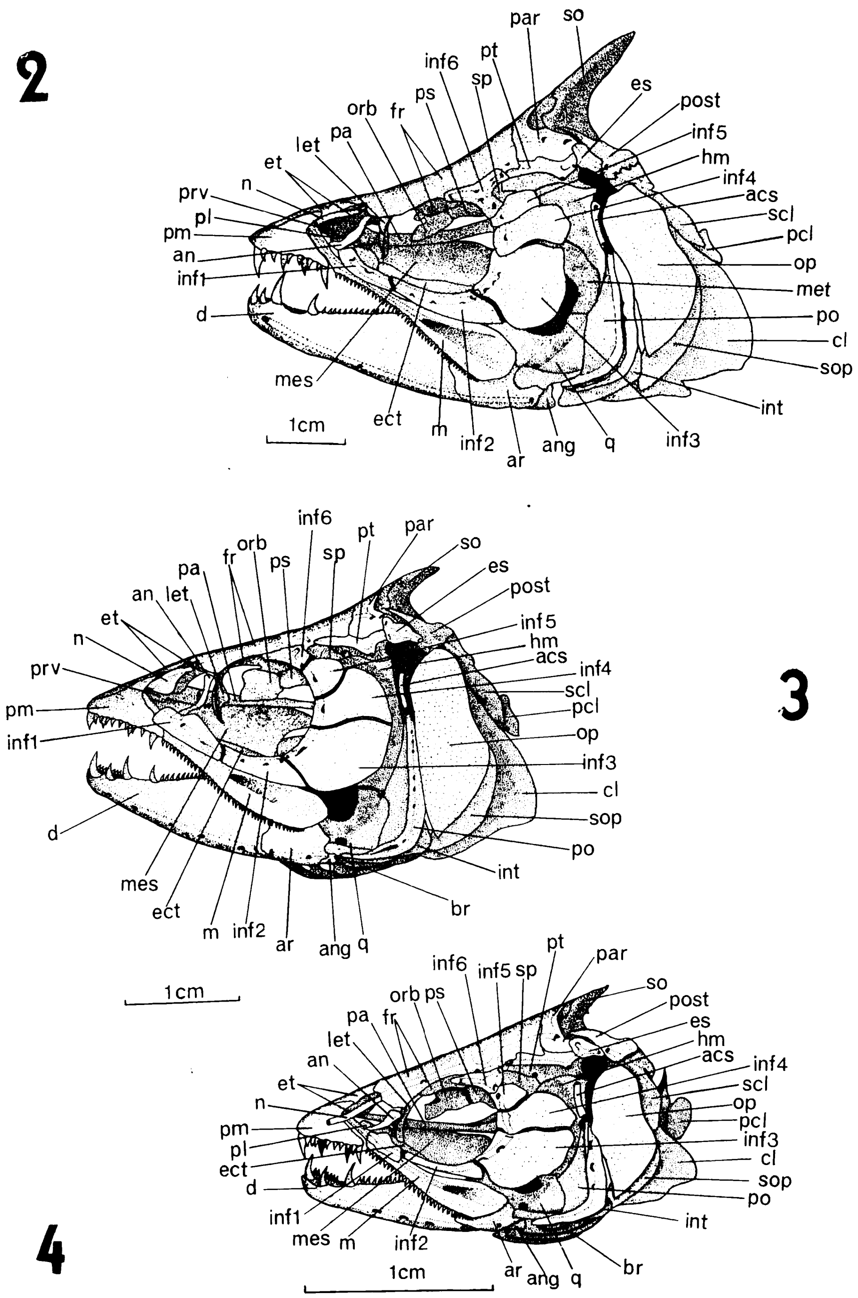
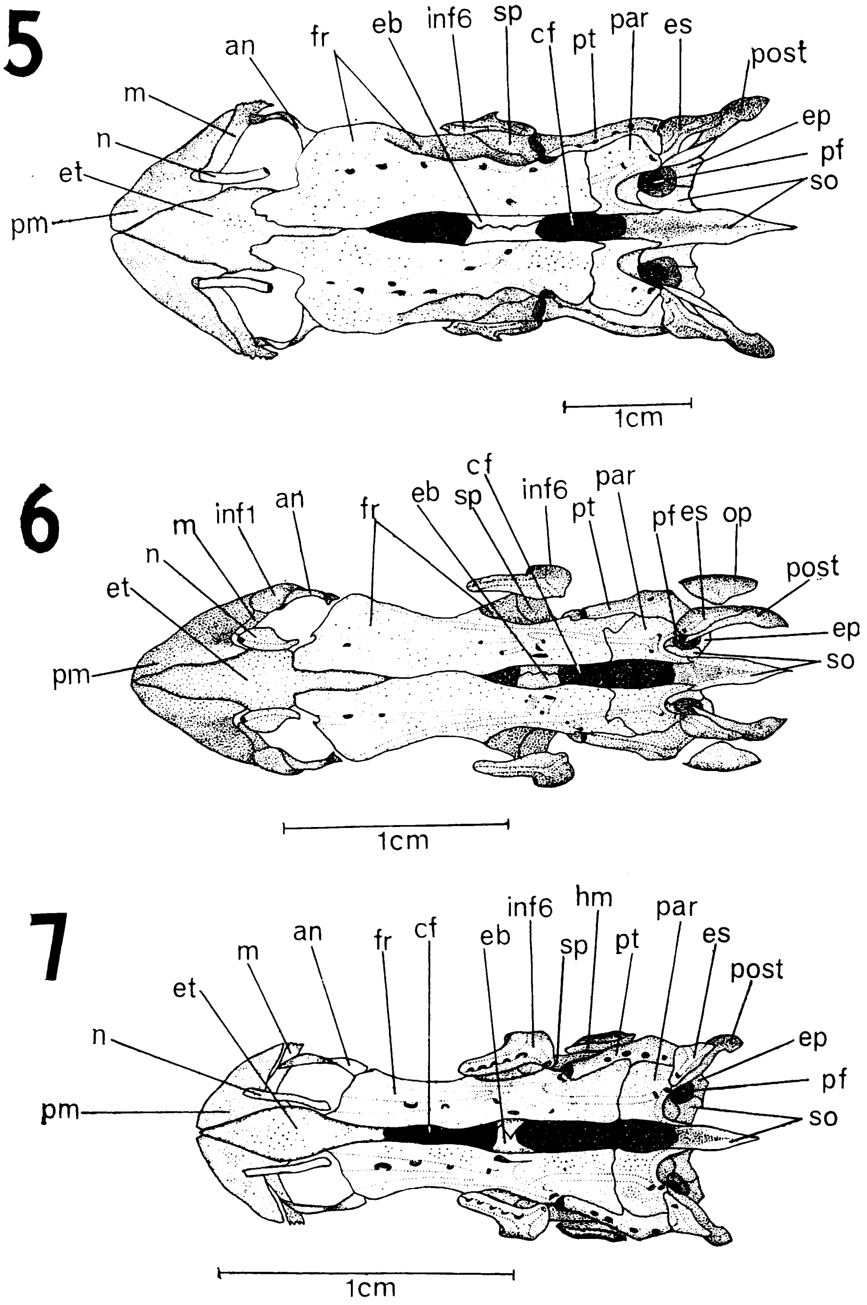


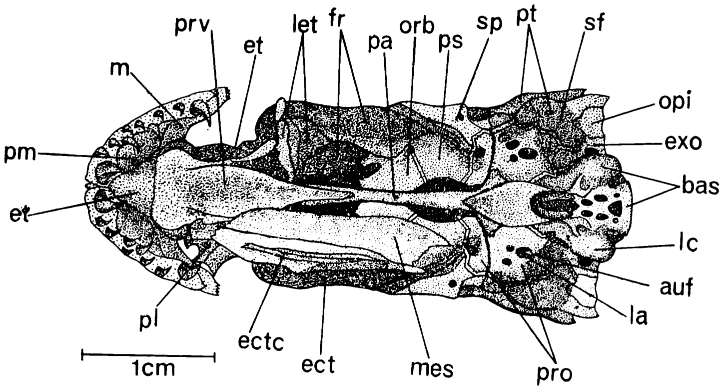
Fig. 1. Localities from which material has been available for this study. Details are presented in the Appendix.



Lateral view of the skull. 2, *Cynopotamus argenteus* (Valenciennes), MZUSP 10412; 3, *Galeocharax knerii* (Steindachner), MZUSP 10511; 4, *Acestrocephalus anomalus* (Steindachner), MZUSP 10420.



Dorsal view of the cranium. 5, *Cynopotamus argenteus* (Valenciennes), MZUSP 10412; 6, *Galeocharax knerii* (Steindachner), MZUSP 10511; 7, *Acestrocephalus anomalus* (Steindachner), MZUSP 10420.



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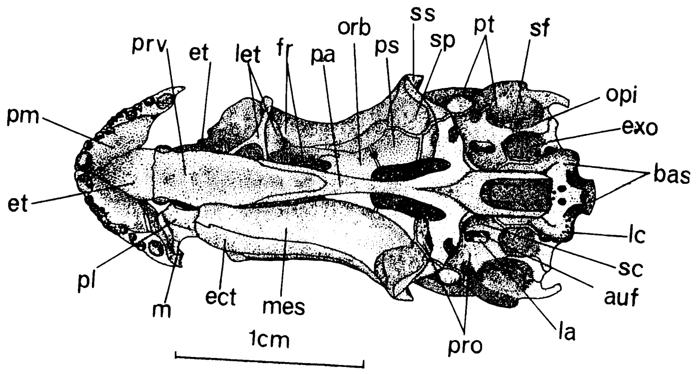

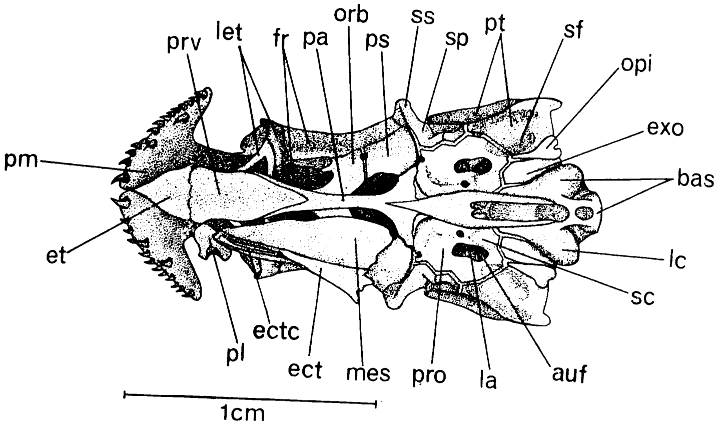

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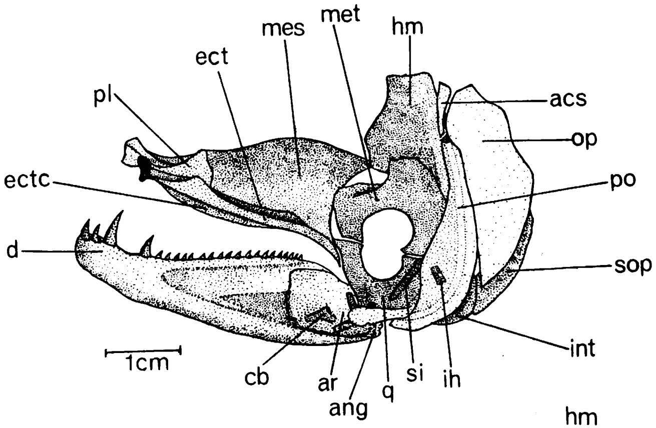
Ventral view of the cranium. 8, *Cynopotamus argenteus* (Valenciennes), MZUSP 10412; 9, *Galeocharax knerii* (Steindachner), MZUSP 10511; 10, *Acestrocephalus anomalus* (Steindachner), MZUSP 10420.



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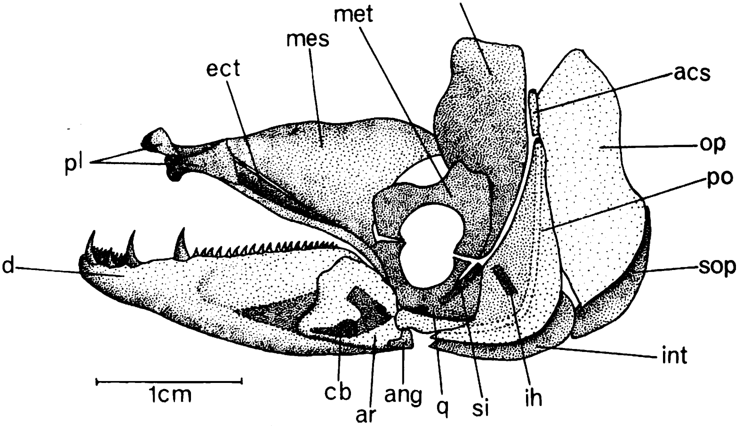

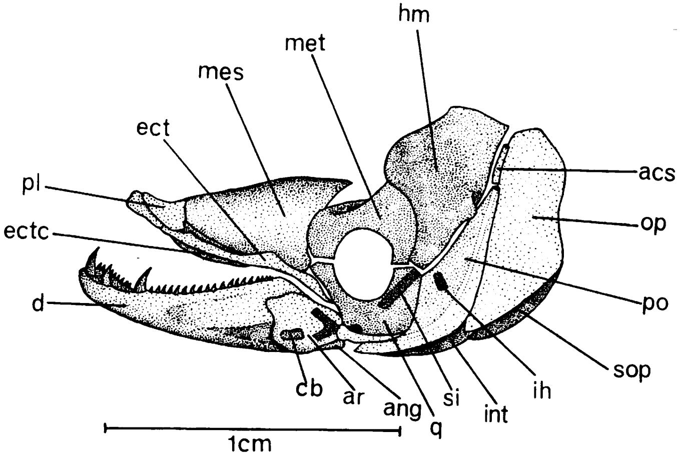

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Lateral bones of the face. 11, *Cynopotamus argenteus* (Valenciennes), MZUSP 10412; 12, *Galeocharax knerii* (Steindachner), MZUSP 10511; 13, *Acestrocephalus anomalus* (Steindachner), MZUSP 10420.

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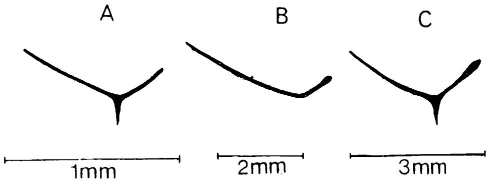

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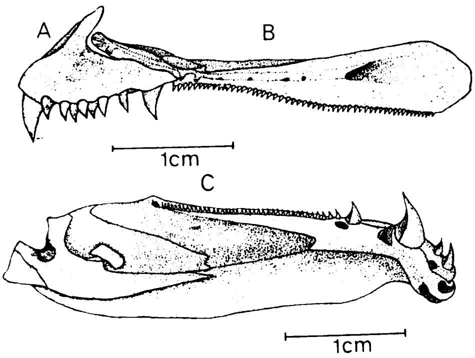

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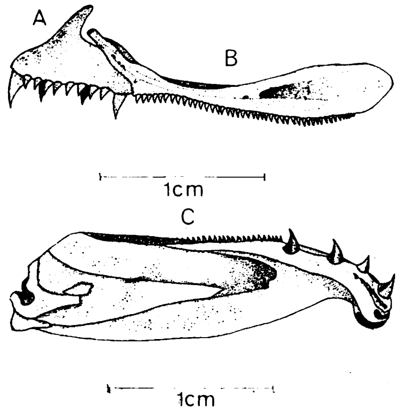

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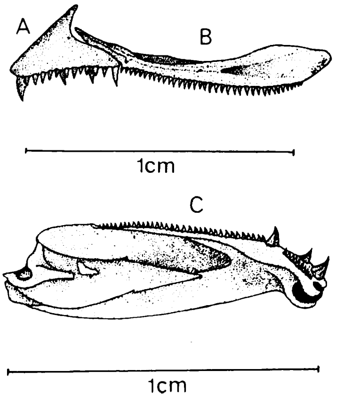

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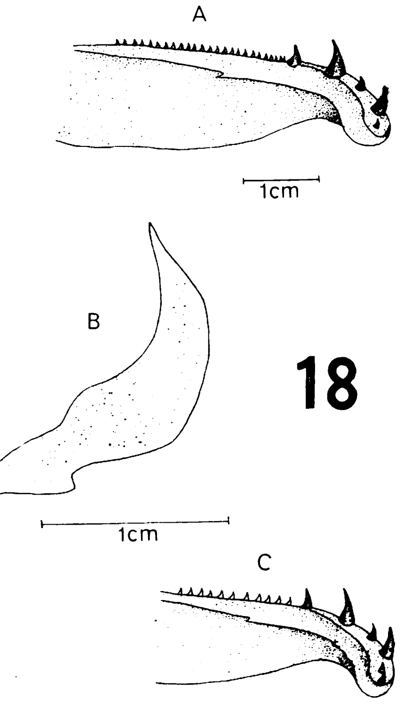

Fig. 14. Vertical section through the left ectopterygoid to show the presence (A and C) and absence (B) of the ventral bony crest; A, *Cynopotamus argenteus*, MZUSP 10412; B, *Galeocharax knerii*, MZUSP 10511; C, *Acestrocephalus anomalus*, MZUSP 10420. Fig. 15. External view of the left premaxillary (A) and maxillary (B) and inner view of the left half of the lower jaw (C) of *Cynopotamus argenteus*. Fig. 16. Same of *Galeocharax knerii*. Fig. 17. Same of *Acestrocephalus anomalus*. Fig. 18. A, inner view of the left half of the lower jaw of *Cynopotamus magdalenae*, USNM 123934; B, external view of the cleithrum of *Cynopotamus bipunctatus*, MNHN 98-21; C, inner view of the left half of the lower jaw of same.

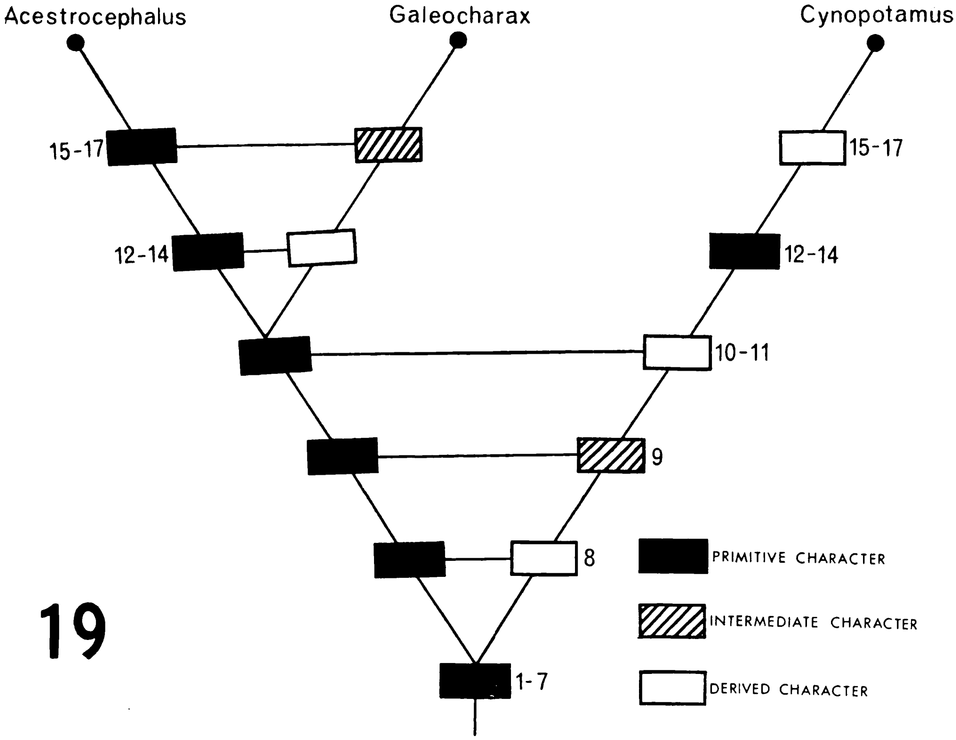

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Fig. 19. Phylogeny of the genera of the subfamily Cynopotaminae.

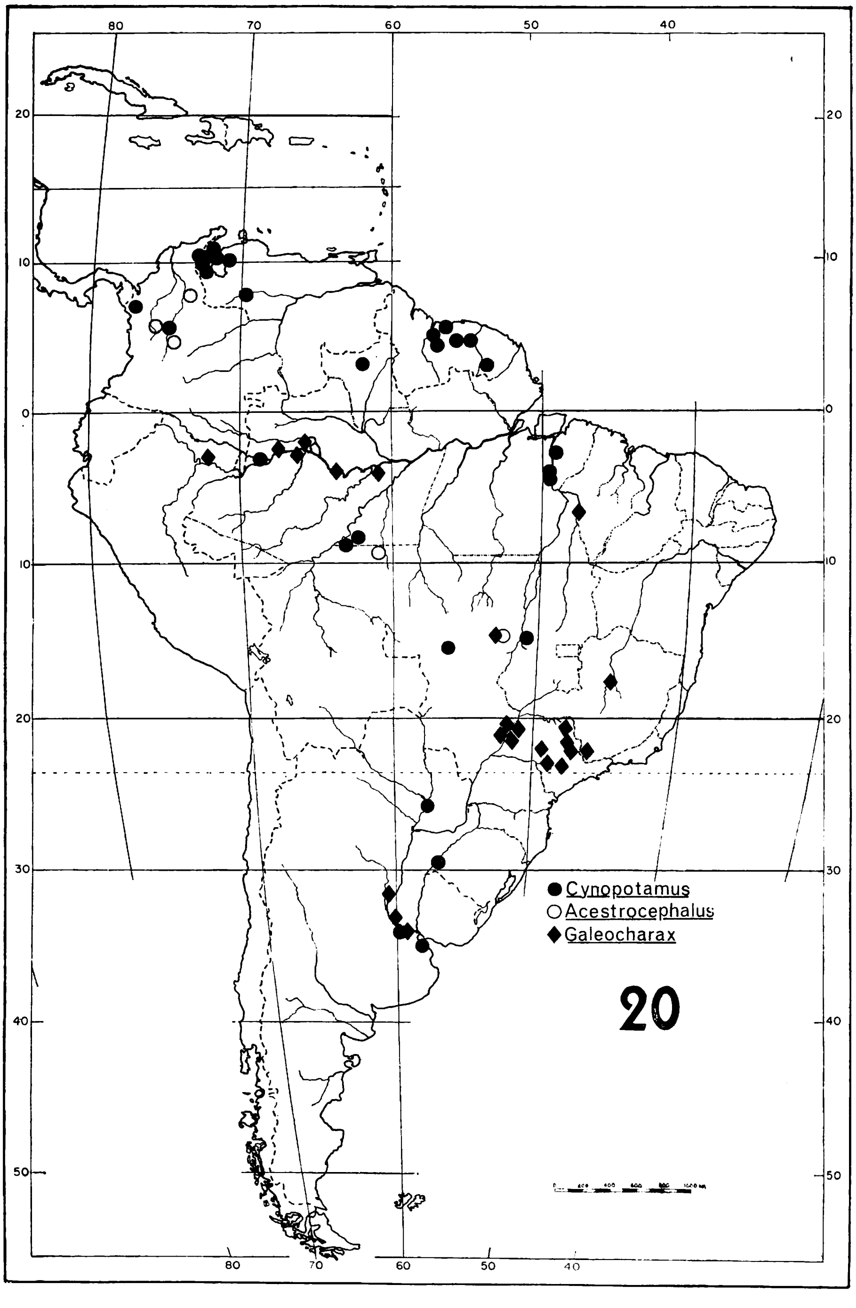

Fig. 20. Geographic distribution of *Cynopotamus, Galeocharax,* and *Acestrocephalus.*

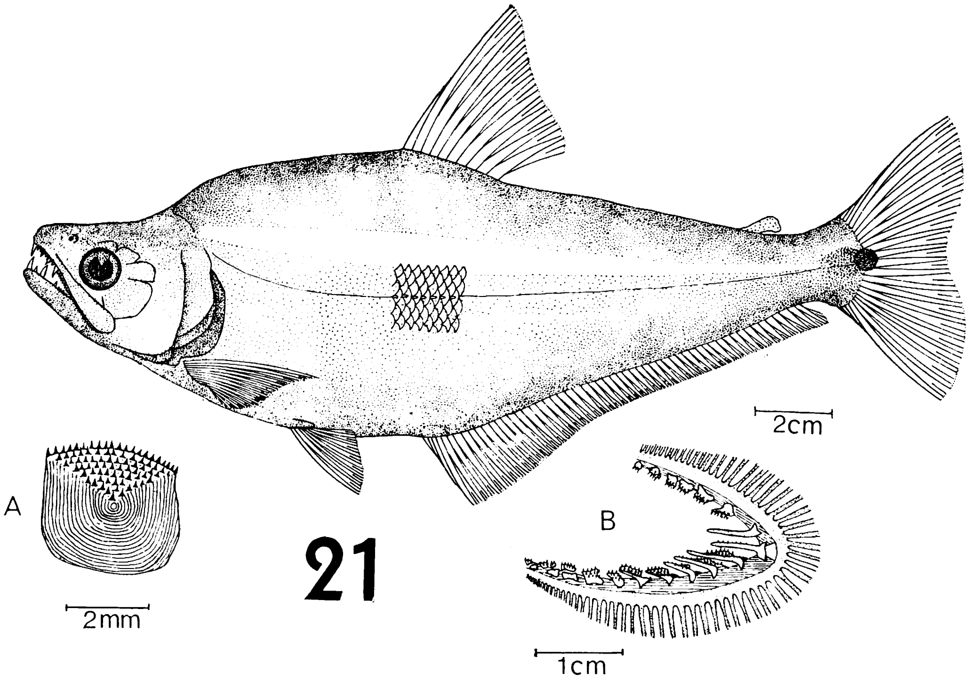

Fig. 21. *Cynopotamus argenteus* (Valenciennes), 58 mm S.L., MLP 1-III-46-9; A, scale from the dorsal region of the body; B, gill rakers on the first gill arch.

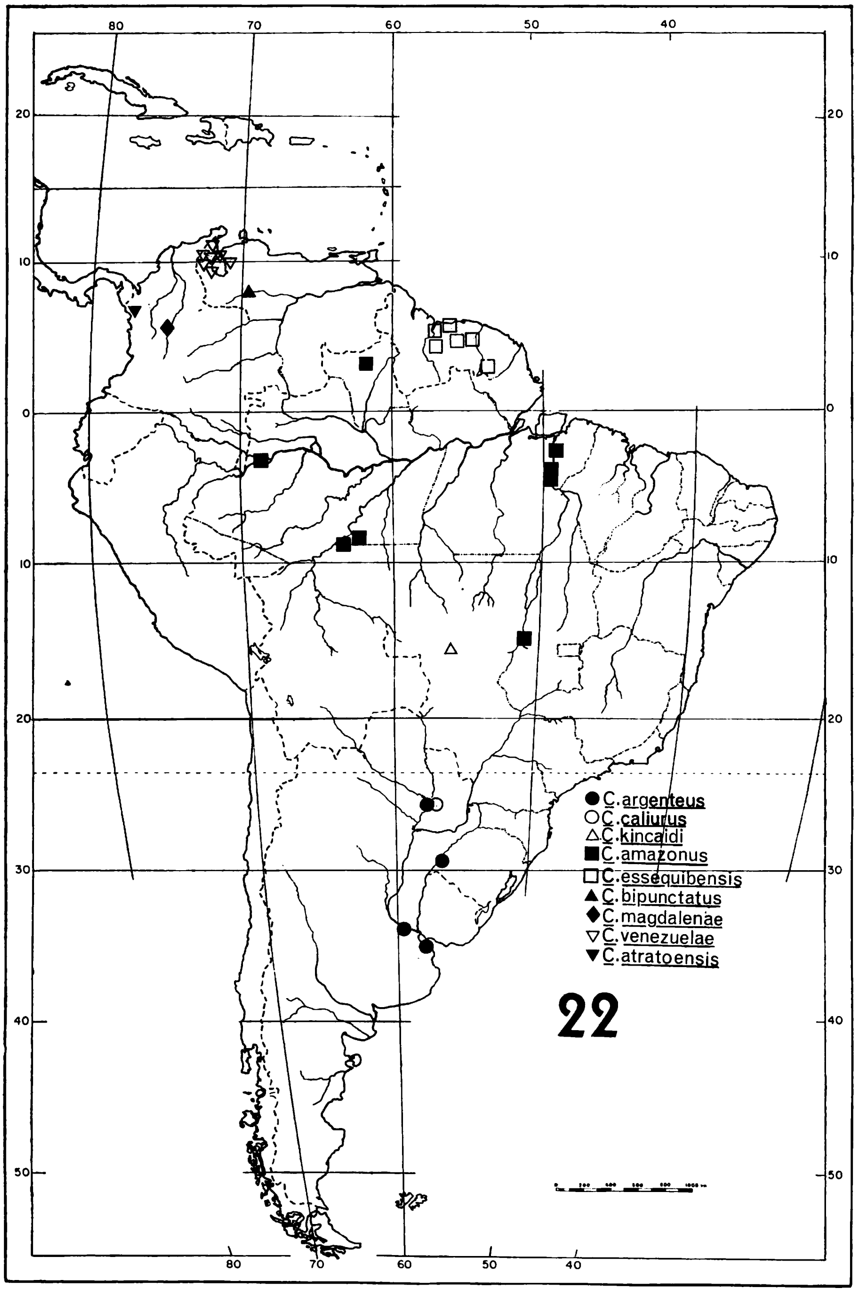

Fig. 22. Geographic distribution of the species of *Cynopotamus*.

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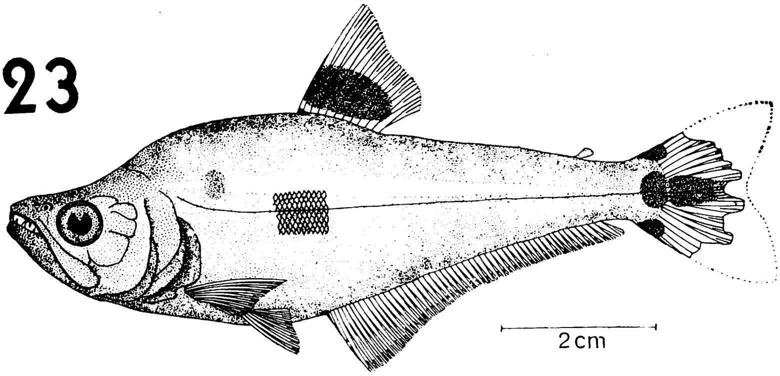

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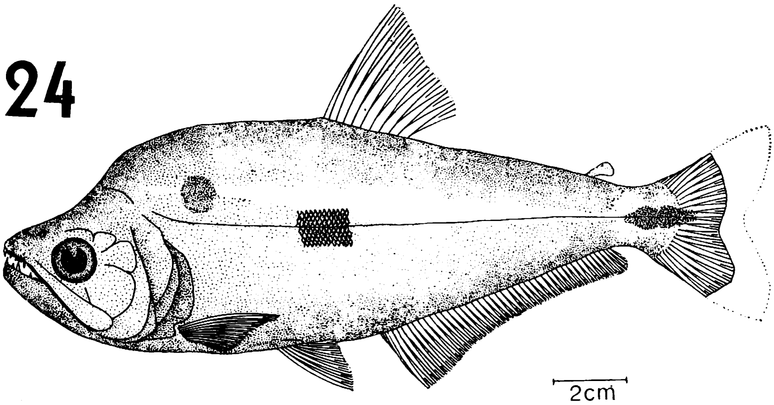

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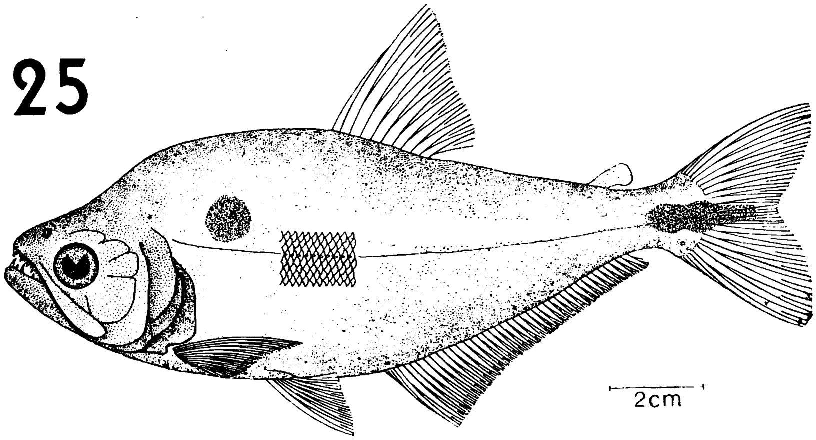

Fig. 23. *Cynopotamus caliurus* (Eigenmann, McAtee & Ward), 84 mm S.L., CAS(IUM) 15682, holotype. Fig. 24. *Cynopotamus kincaidi* (Schultz), 174 mm S.L., USNM 1694. Drawing based on the photograph of the holotype. Fig. 25. *Cynopotamus amazonus* (Günther), 143 mm S.L., MZUSP 10418.

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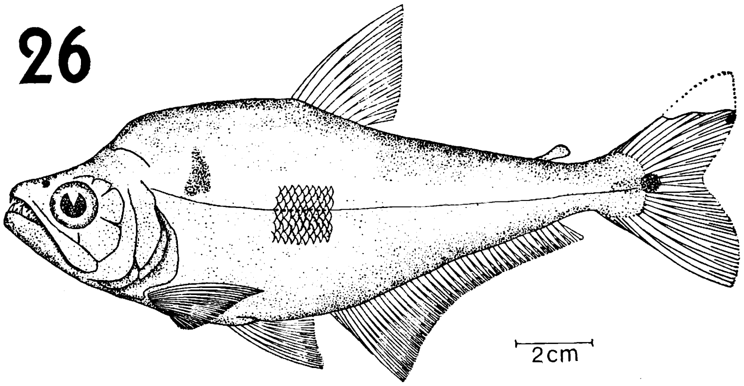

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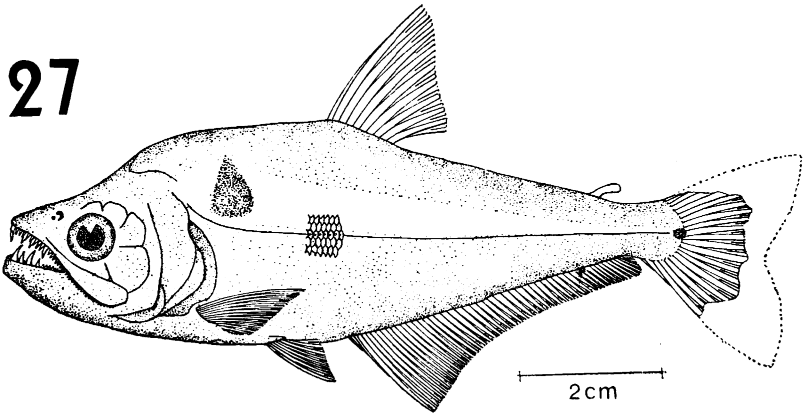

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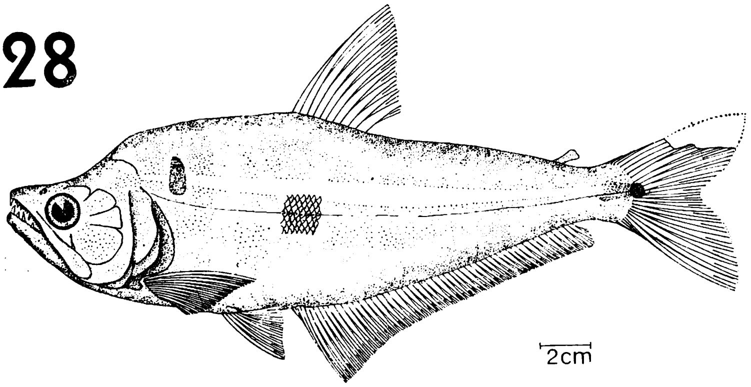

Fig. 26. *Cynopotamus essequibensis* Eigenmann, 160 mm S.L., ZMA 106.348. Fig. 27. *Cynopotamus bipunctatus* Pellegrin, 91 mm S.L., MNHN 98-21, holotype. Fig. 28. *Cynopotamus magdalenae* (Steindachner), 243 mm S.L., USNM 79185.

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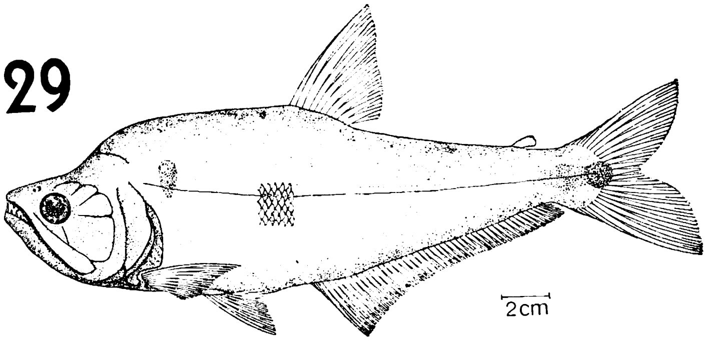

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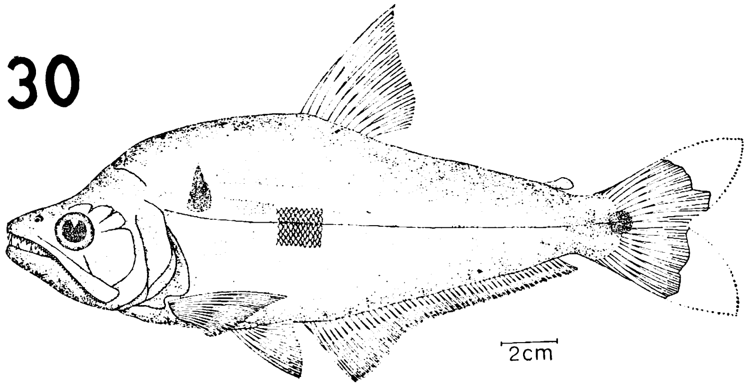

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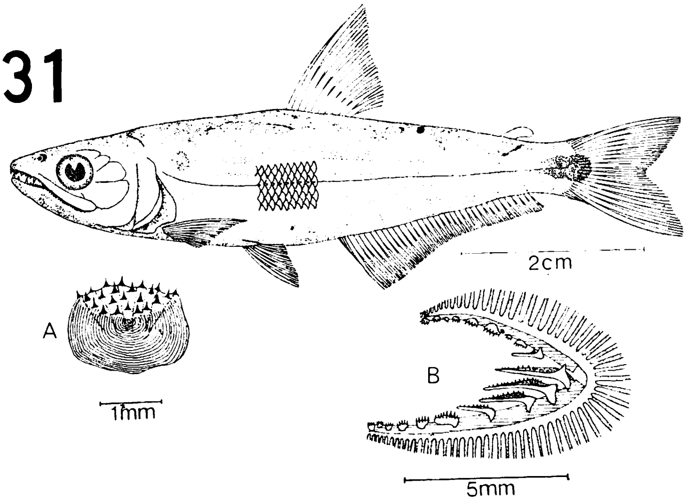

Fig. 29. *Cynopotamus venezuelae* (Schultz), 233 mm S.L., USNM 121391. Fig. 30. *Cynopotamus atratoensis* (Eigenmann), 210 mm S.L., USNM 1664, holotype. Fig. 31. *Acestrocephalus anomalus* (Steindachner), 68 mm S.L., MZUSP 10420; A, scale from the dorsal region of the body; B, gill rakers on the first gill arch.

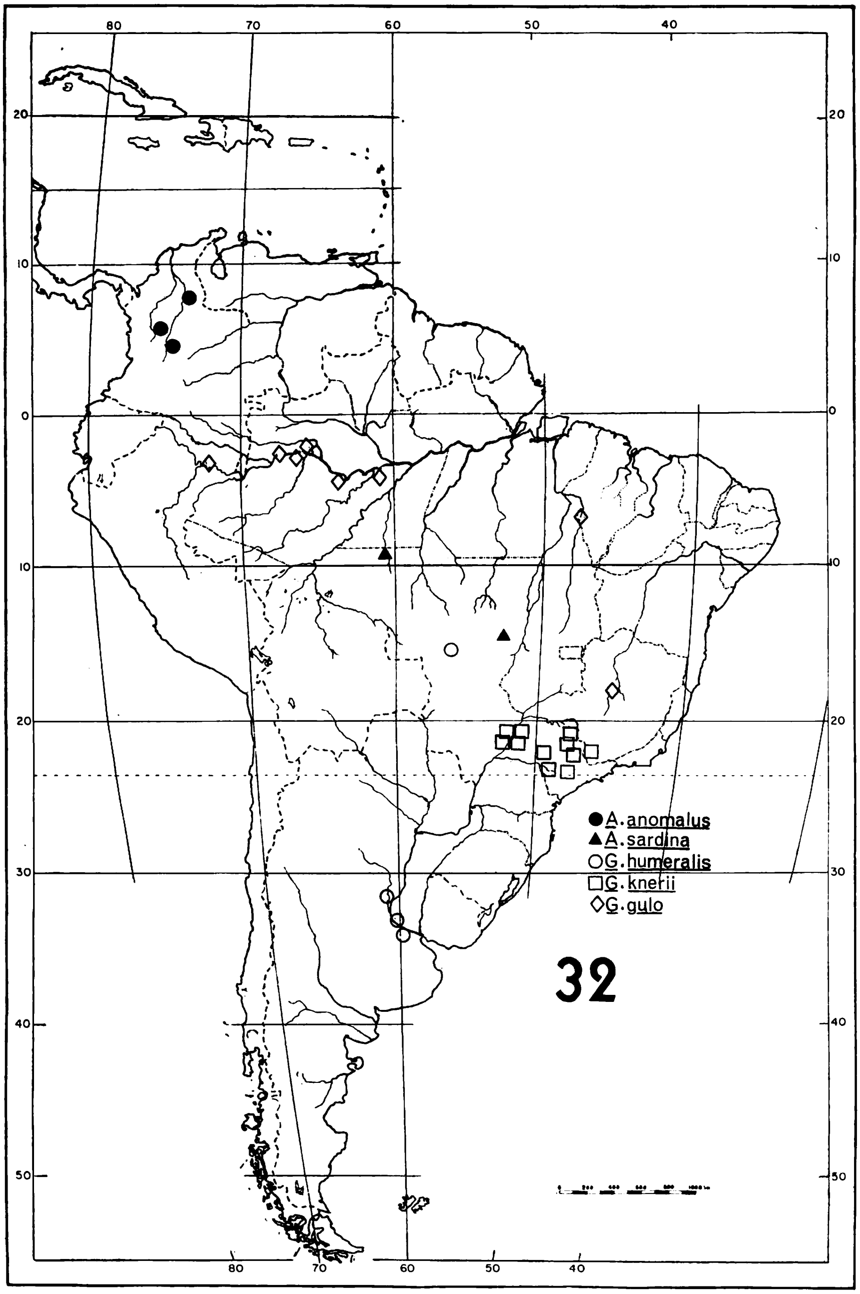

Fig. 32. Geographic distribution of the species of *Acestrocephalus* and *Galeocharax*.

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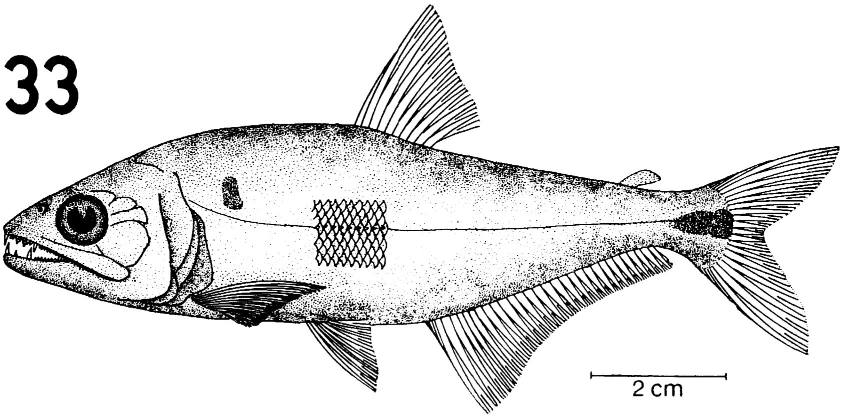

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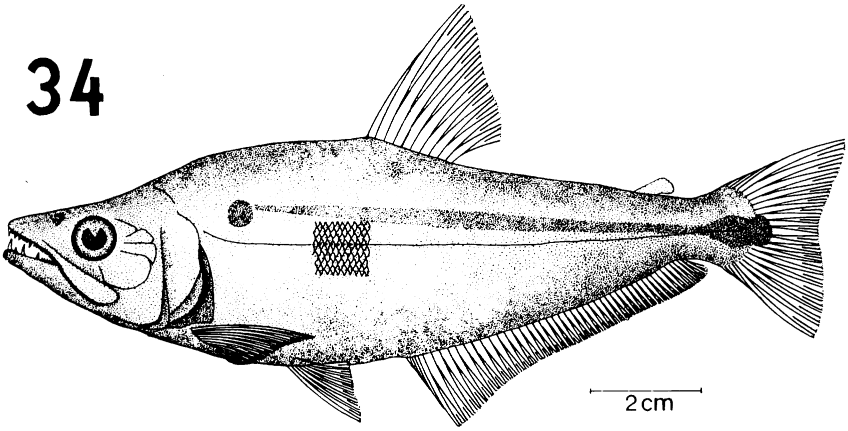

Fig. 33. *Acestrocephalus sardina* (Fowler), 102 mm S.L., MZUSP 10422. **Fig. 34.** *Galeocharax humeralis* (Valenciennes), 130 mm S. L., MLP 28-V-40-60.

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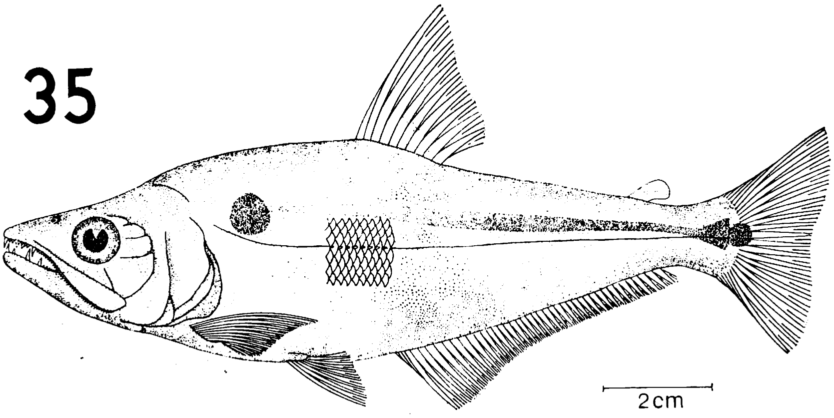

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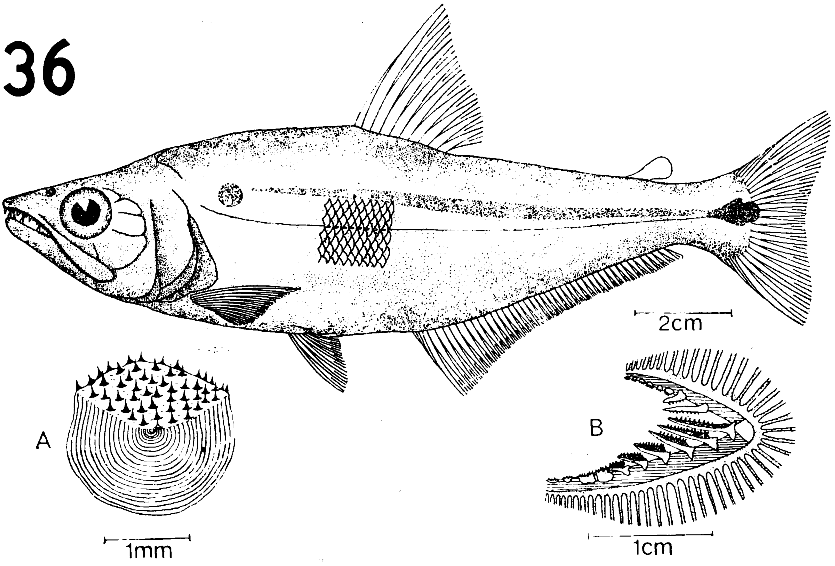
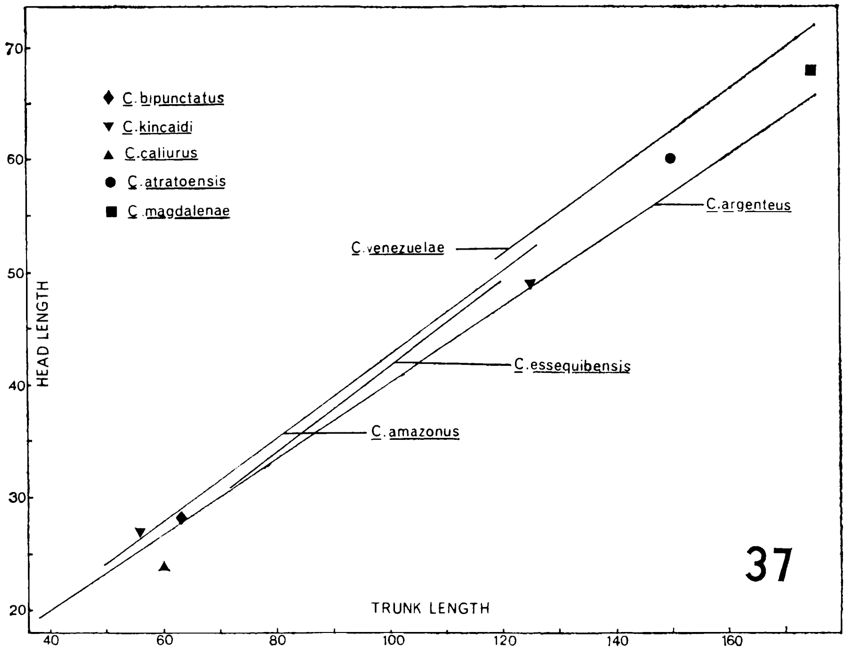
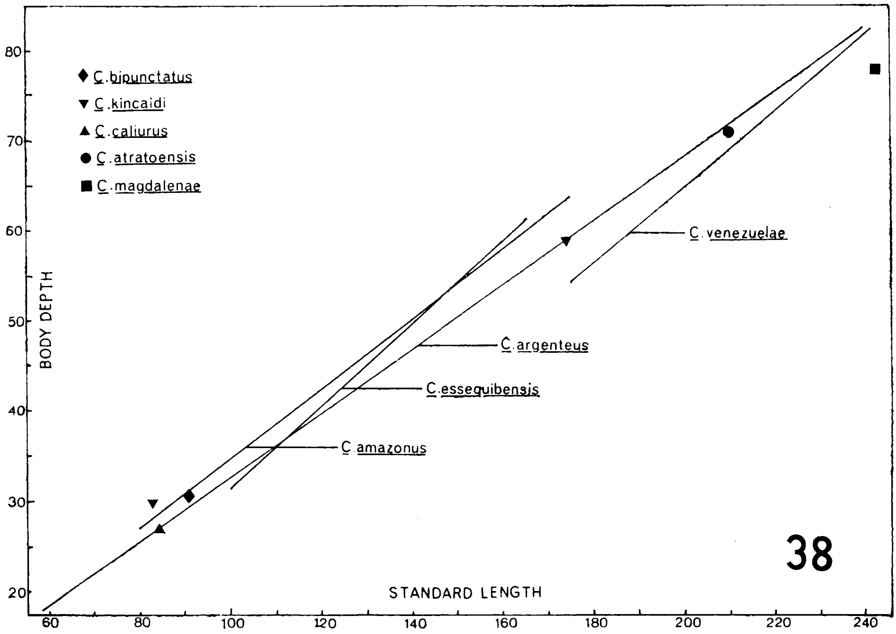
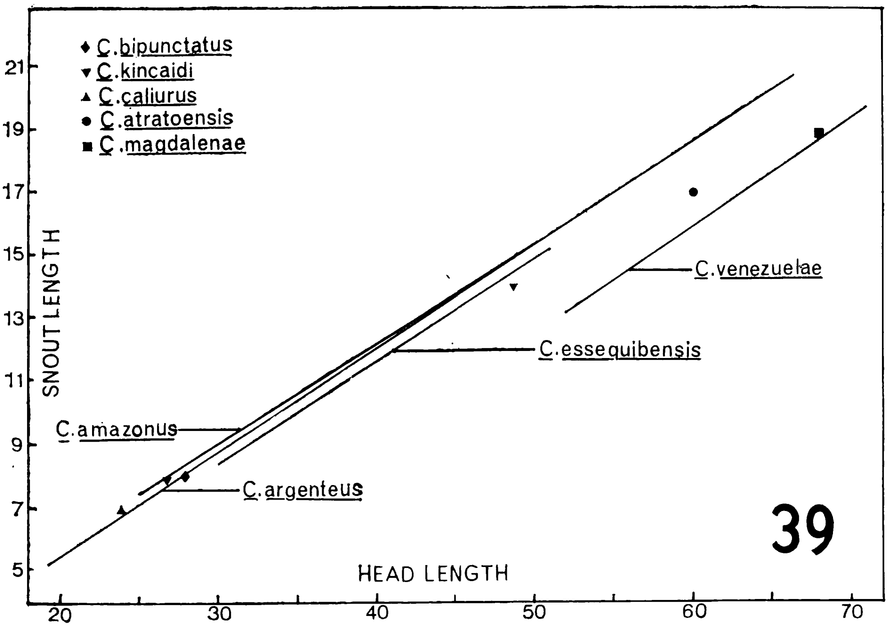


Fig. 35. *Galeocharax gulo* (Cope), 133 mm S.L., MZUSP 10435. Fig. 36. *Galeocharax knerii* (Steindachner), 153 mm S.L., MZUSP 10458; A, scale from the dorsal region of the body; B, gill rakers on the first gill arch.





Linear regression for all species of *Cynopotamus*. 37, head length on trunk length; 38, body depth on standard length.



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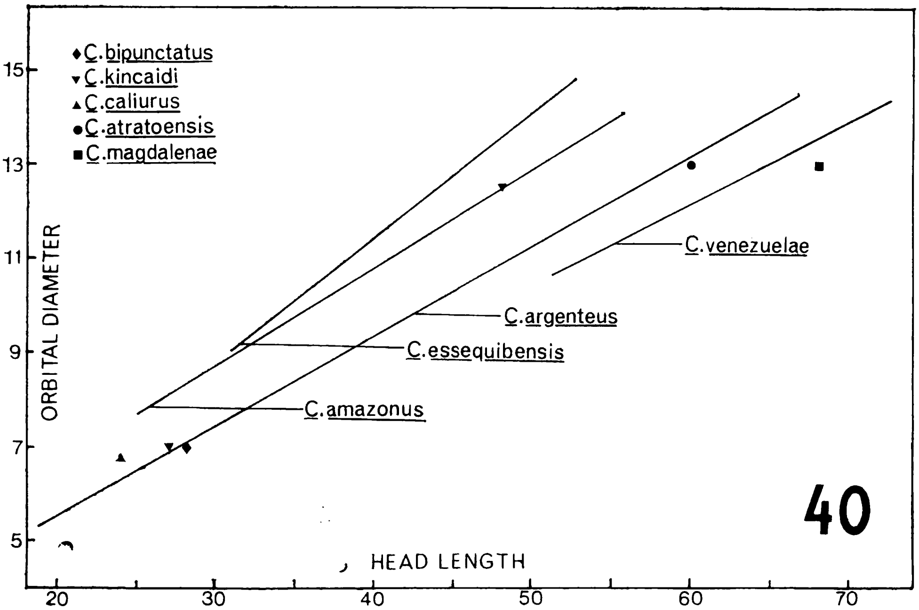

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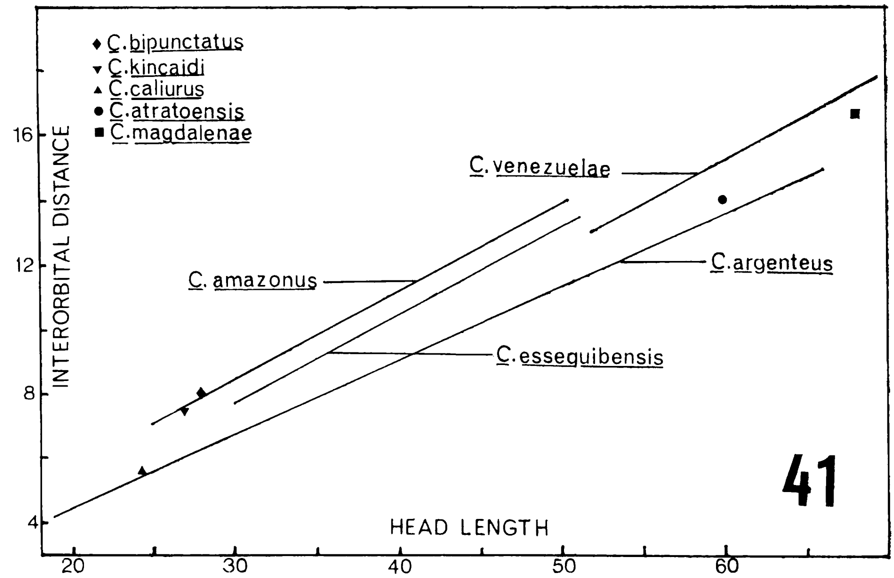
Linear regression for all species of *Cynopotamus*. 39, snout length on head length; 40, orbital diameter on head length.



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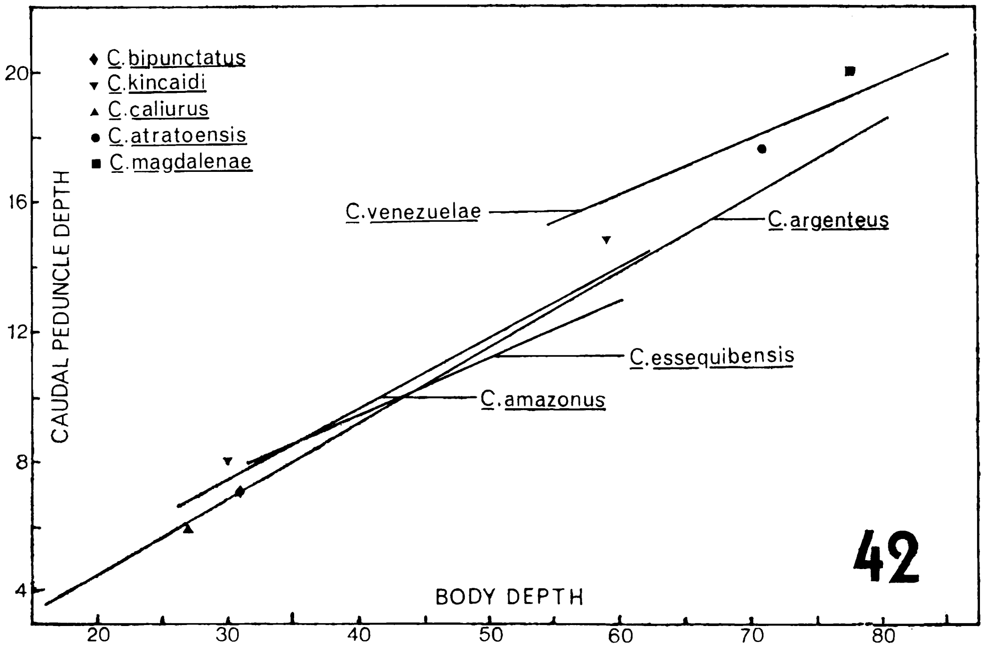

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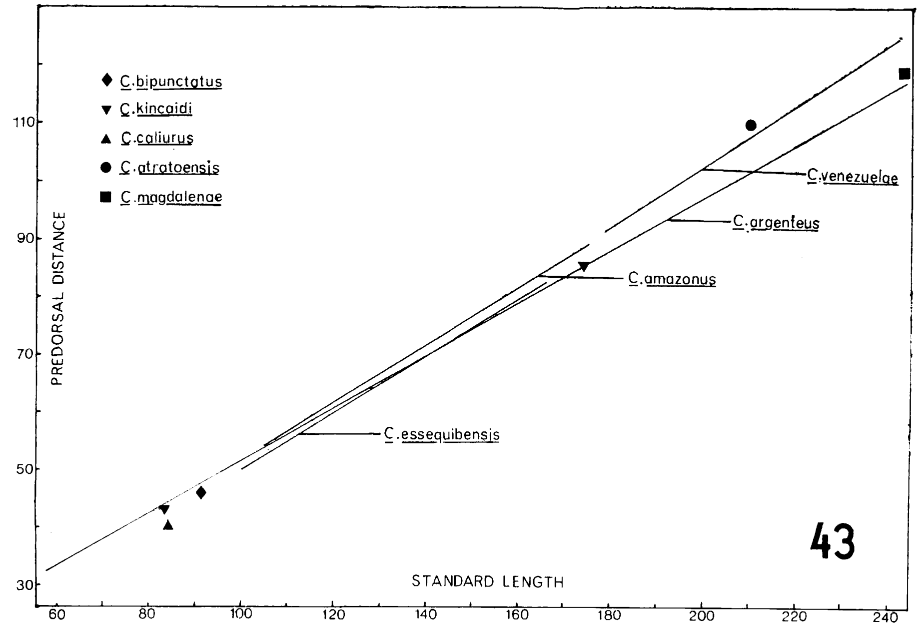
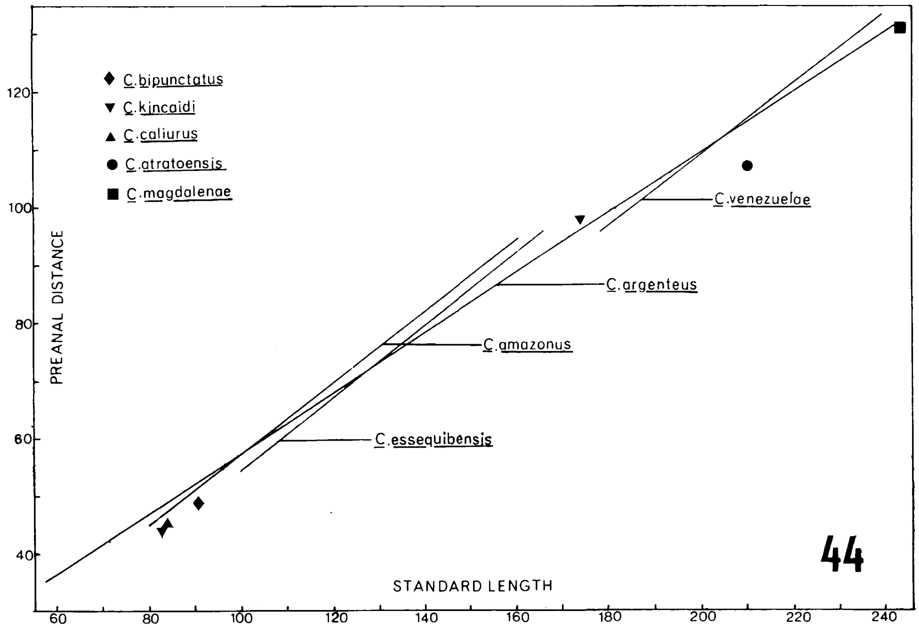
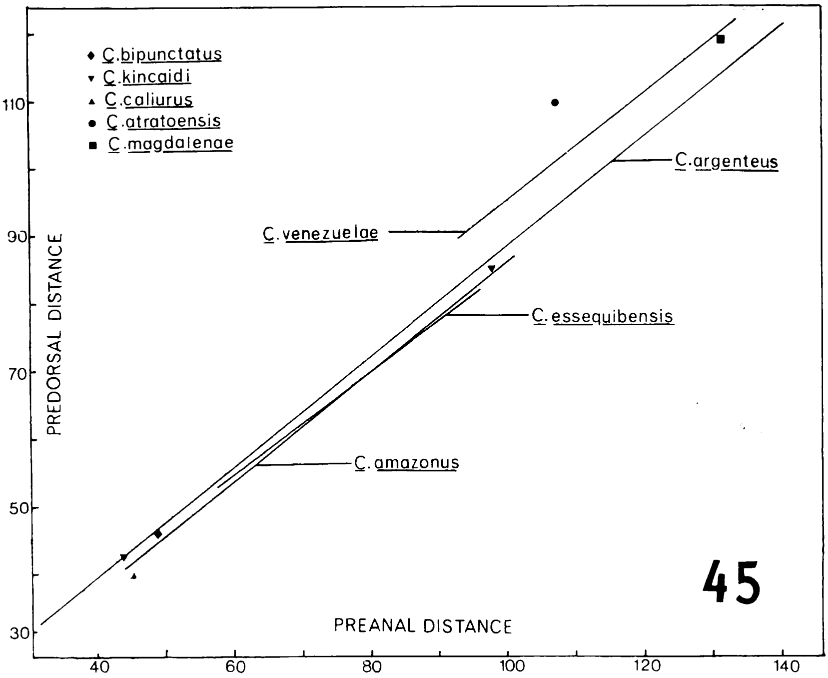
Linear regression for all species of *Cynopotamus*. 41, interorbital distance on head length; 42, caudal peduncle depth on body depth.





Linear regression for all species of *Cynopotamus*. 43, predorsal distance on standard length; 44, preanal distance on standard length.



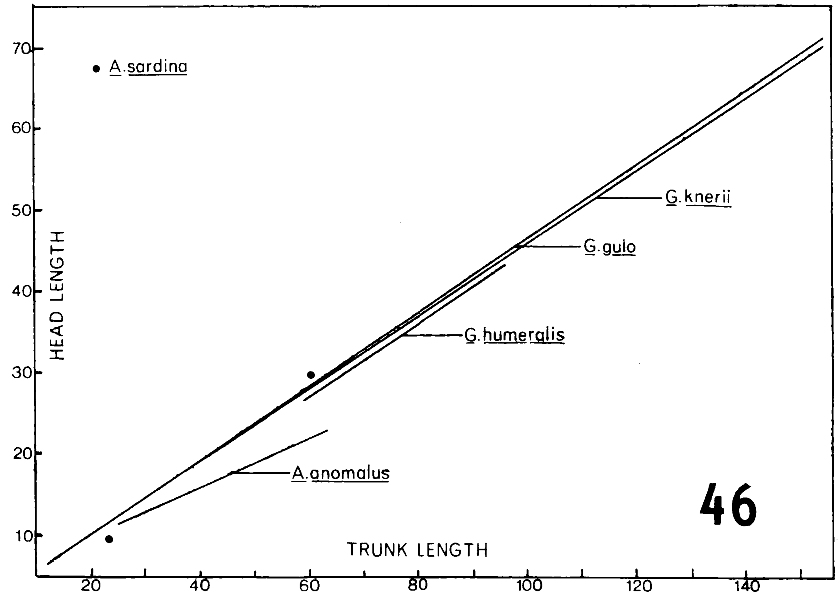
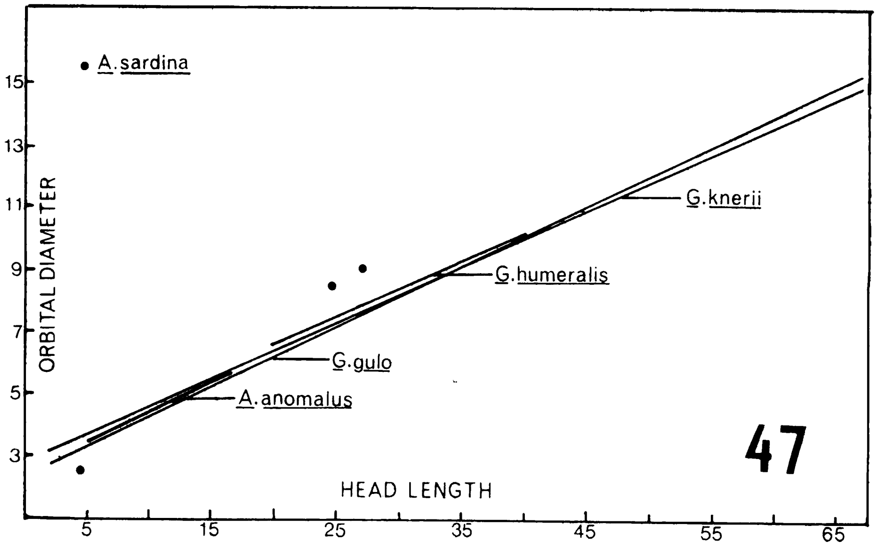
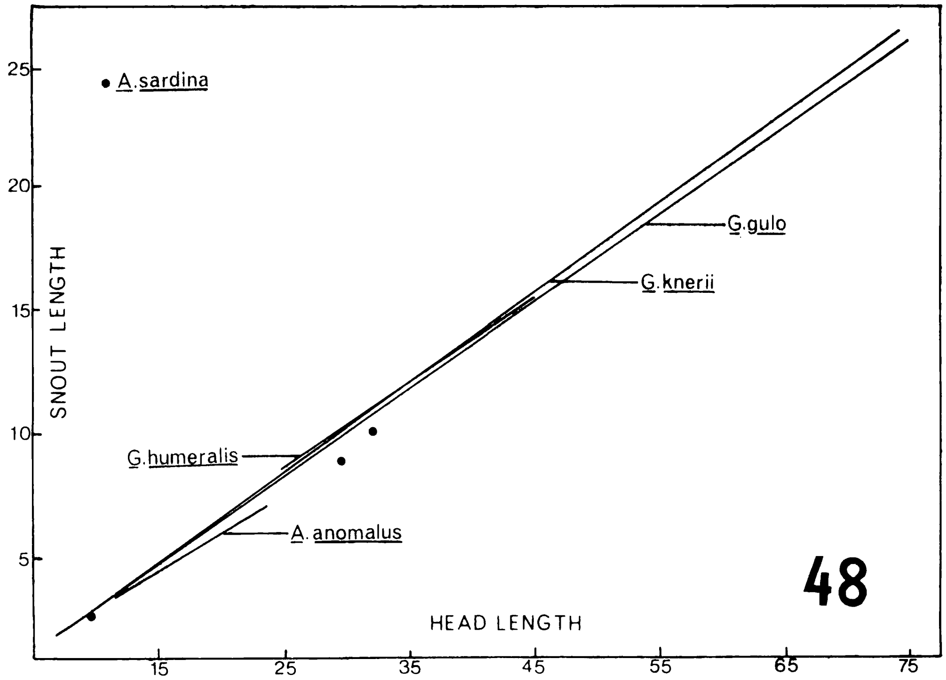
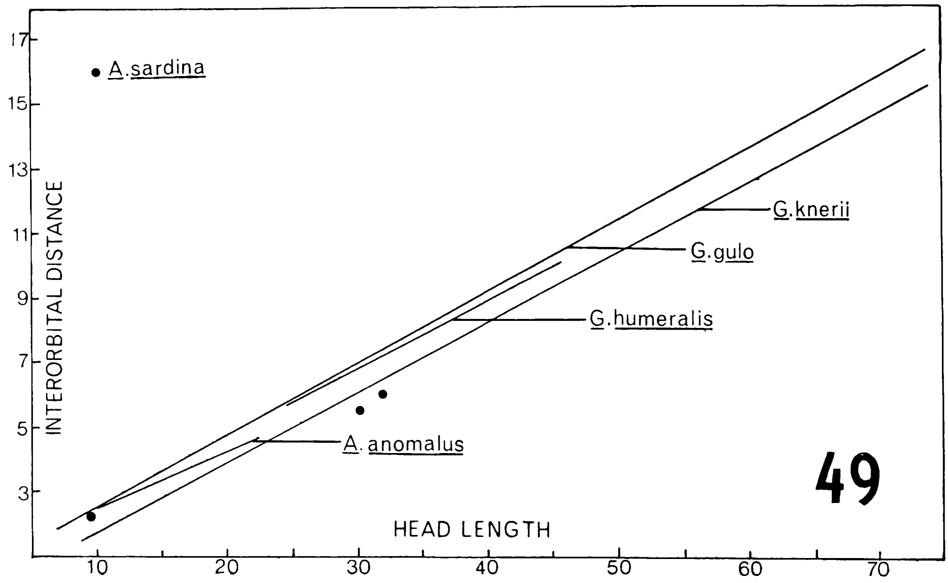


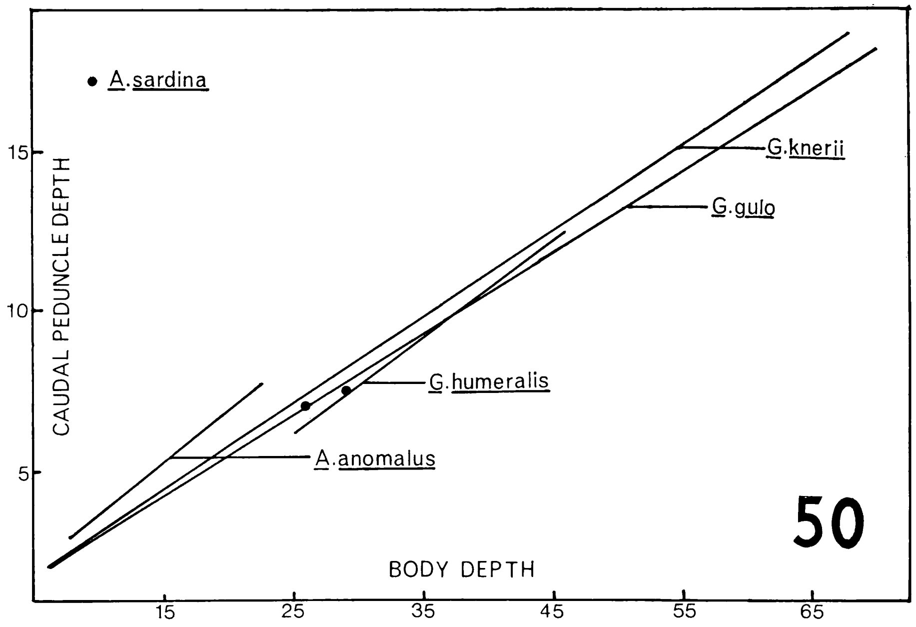
Fig. 45. Linear regression of predorsal distance on preanal distance for all species of *Cynopotamus*. 46, Linear regression of head length on trunk length for all species of *Galeocharax* and *Acestrocephalus*.



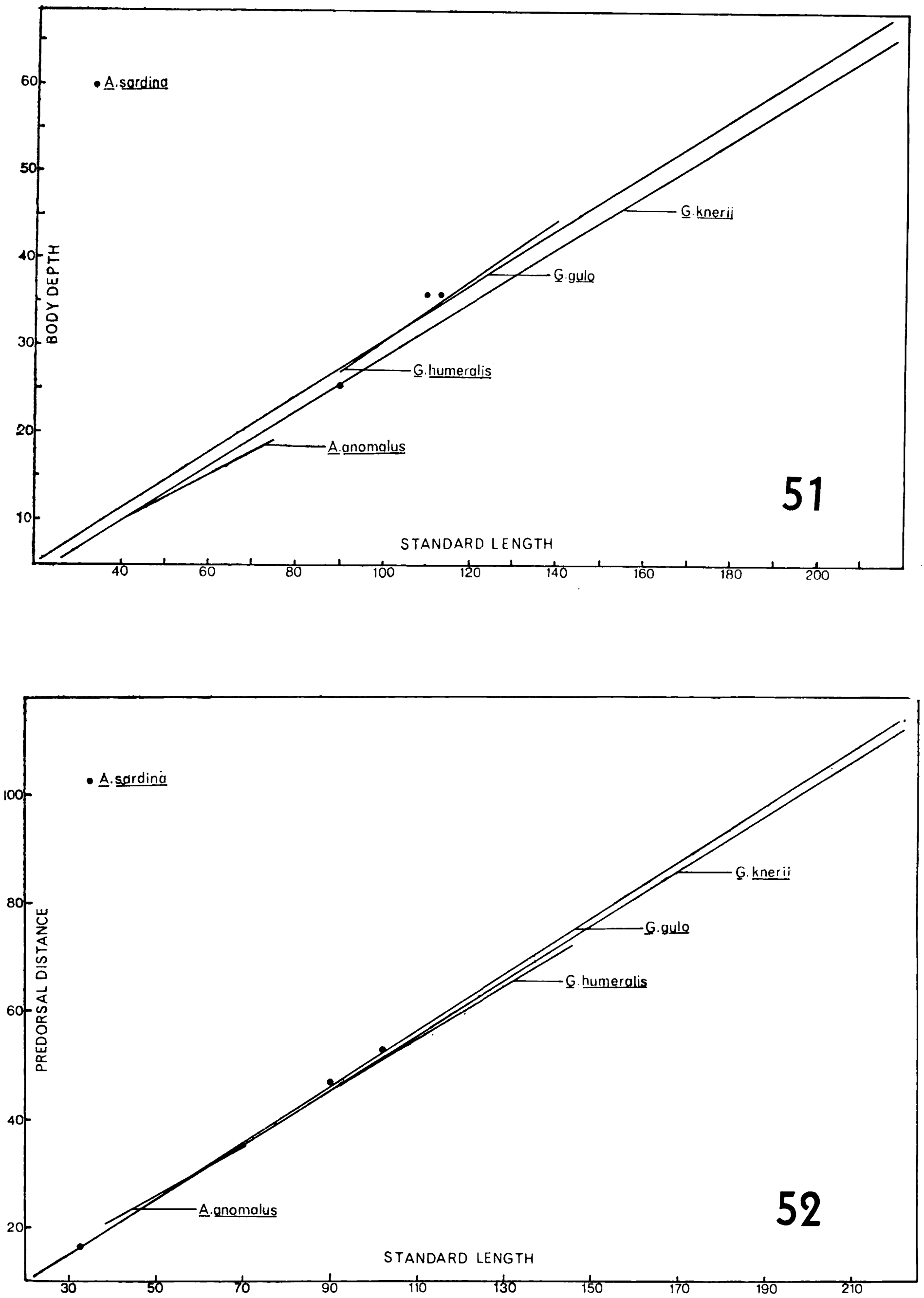


Linear regression for all species of *Galeocharax* and *Acestrocephalus*. 47, orbital diameter on head length; 48, snout length on head length.

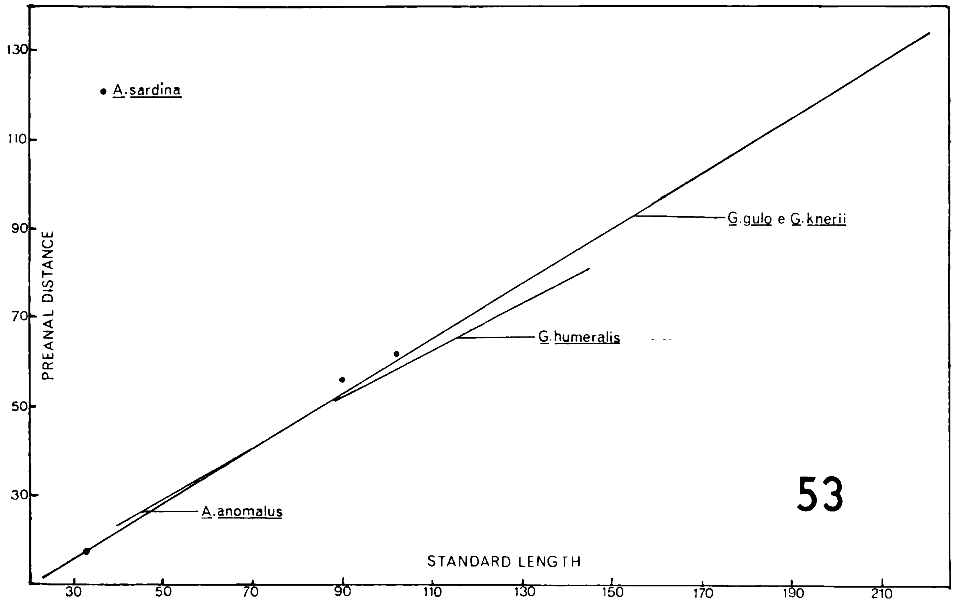




Linear regression for all species of *Galeocharax* and *Acestrocephalus*. 49, interorbital distance on head length; 50, caudal peduncle depth on body depth.



Linear regression for all species of *Galeocharax* and *Acestrocephalus*. 51, body depth on standard length; 52, predorsal distance on standard length.



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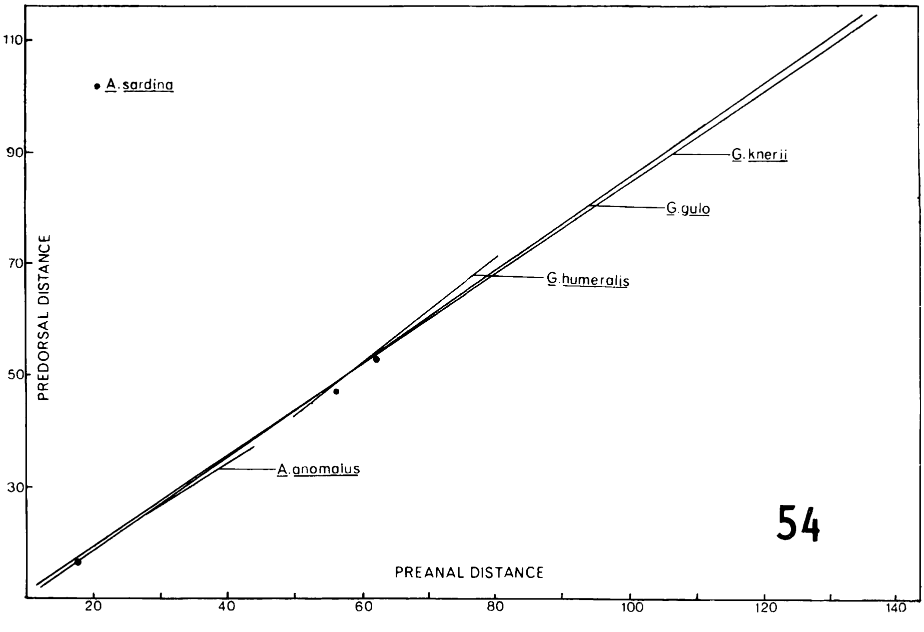

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Linear regression for all species of *Galeocharax* and *Acestrocephalus*. 53, preanal distance on standard length; 54, predorsal distance on preanal distance.

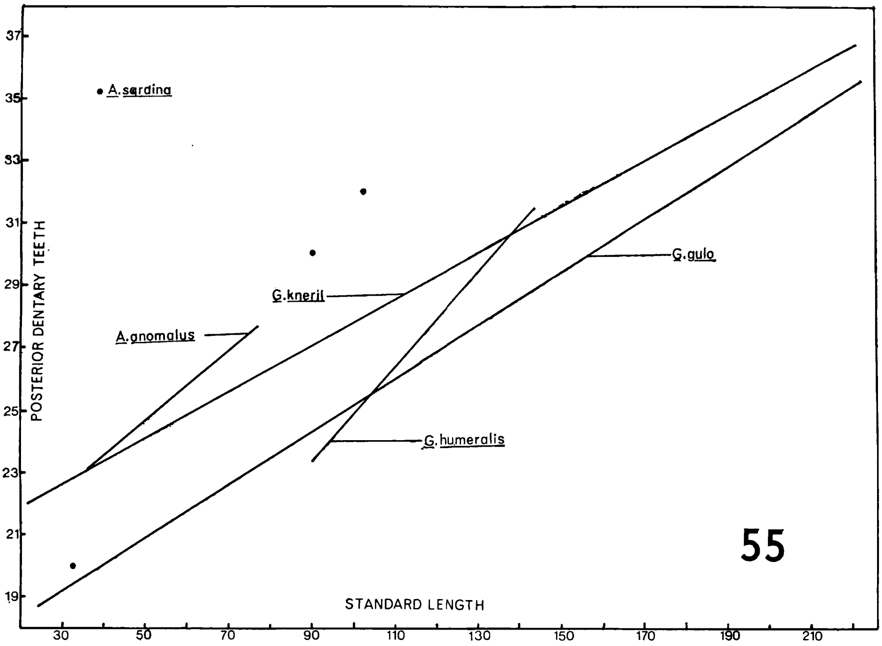

Fig. 55. Linear regression of number of posterior dentary teeth on standard length for all species of *Galeocharax* and *Acestrocephalus*.

TABLE 1 - CHARACTERS USED IN FIGURE 19

Number	Character	Character state		
		Primitive	Intermediate	Derived
1	Scales	Ctenoid	-	-
2	Accessory suprapreopercle	Present	-	-
3	Circumorbital series	Incomplete	-	-
4	Inner row of teeth on the premaxillary	Formed by two teeth	-	-
5	Gill rakers	In part laminar	-	-
6	Rhinosphenoid	Absent	-	-
7	Orbitosphenoid	In contact with parasphenoid	-	-
8	Cleithrum	Sinuous	-	Notched
9	Inner row of teeth on the dentary	Present	Rudimentary	-
10	Sphenotic	With prominent spine	-	Without spine
11	Dilator groove	Reduced	-	Long
12	Ectopterygoid bony crest	Present	-	Absent
13	Nasal	Tubular	-	Laminar
14	First infraorbital	Short	-	Long
15	Supraoccipital spine	Short	Moderate	Long
16	Anterior dorsal region	Not raised	Slightly raised	Strongly raised in form of gibbosity
17	Number of anal fin rays	Low	Moderate	High

TABLE 2 - TOTAL RANGE OF MERISTIC VALUES FOR ALL SPECIES OF THE GENUS *CYNOPOTAMUS*

SPECIES	ANAL FIN RAYS	PECTORAL FIN RAYS	LAT. LINE SCALES	SCALES ABOVE LATERAL LINE	SCALES BELOW LATERAL LINE	MAXILLARY TEETH	POST. DENTARY TEETH
C. argenteus	46-53	13-15	106-112	24-26	22-24	45-55	23-38
C. caliurus	50	13	115	25	23	45	24
C. kincaidi	45	15	105-110	30-31	24-26	46	22
C. amazonus	36-41	14-15	94-104	23-28	21-25	50-60	26-32
C. magdalenae	49-51	15	125	30	30	42	27
C. atratoensis	45-47	15-16	110-115	27	28	44	26
C. venezuelae	40-46	15-17	107-121	26-29	25-28	42-49	24-29
C. essequibensis	36-43	14-15	91-100	20-23	17-21	49-59	28-35
C. bipunctatus	49	14	104	26	25	46	24

TABLE 3 - TOTAL RANGE OF MERISTIC VALUES FOR
ALL SPECIES OF THE GENUS *ACESTROCEPHALUS*

SPECIES	ANAL FIN RAYS	PECTORAL FIN RAYS	LAT. LINE SCALES	SCALES ABOVE LATERAL LINE	SCALES BELOW LATERAL LINE	MAXILLARY TEETH	INNER DENTARY TEETH
A. anomalus	33-35	12-14	73-77	12-13	9-11	34-37	9-11
A. sardina	29-32	13-14	71-72	12-14	12-13	30-41	9-10

TABLE 4 - TOTAL RANGE OF MERISTIC VALUES FOR
ALL SPECIES OF THE GENUS *GALEOCHARAX*

SPECIES	ANAL FIN RAYS	PECTORAL FIN RAYS	LAT. LINE SCALES	SCALES ABOVE LATERAL LINE	SCALES BELOW LATERAL LINE	MAXILLARY TEETH	INNER DENTARY TEETH
G. humeralis	42-45	14-15	98-101	20-22	18-22	47-52	9-10
G. gulo	37-45	13-16	80-86	16-18	15-17	38-52	7-11
G. knerii	36-43	14-16	80-86	16-18	14-17	38-54	7-9

APPENDIX TABLE 1 - Regression data from *Cynopotamus argenteus*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	12	0.33 ± 0.0128	6.55 ± 1.4964	0.98
BODY DEPTH x STANDARD LENGTH	12	0.35 ± 0.0120	-3.16 ± 1.9617	0.98
SNOUT LENGTH x HEAD LENGTH	12	0.33 ± 0.0087	-0.97 ± 0.4004	0.99
ORBITAL DIAMETER x HEAD LENGTH	12	0.19 ± 0.0116	1.73 ± 0.5302	0.96
INTERORBITAL DISTANCE x HEAD LENGTH	12	0.22 ± 0.0137	-0.06 ± 0.6268	0.96
PREDORSAL DISTANCE x PREANAL DISTANCE	11	0.81 ± 0.0382	7.50 ± 3.3370	0.98
PREANAL DISTANCE x STANDARD LENGTH	11	0.52 ± 0.0145	5.10 ± 2.2962	0.99
PREDORSAL DISTANCE x STANDARD LENGTH	11	0.45 ± 0.0138	6.14 ± 2.1890	0.99
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	12	0.23 ± 0.0114	-0.04 ± 0.6309	0.97

N - Number of specimens

b - Regression coefficient ± its standard deviation

a - Regression constant ± its standard deviation

r^2- Coefficient of determination

APPENDIX TABLE 2 - Regression data from *Cynopotamus amazonus*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	9	0.37 ± 0.0311	5.52 ± 2.9975	0.95
BODY DEPTH x STANDARD LENGTH	9	0.38 ± 0.0249	-3.64 ± 3.4319	0.97
SNOUT LENGTH x HEAD LENGTH	9	0.32 ± 0.0195	-0.46 ± 0.8157	0.97
ORBITAL DIAMETER x HEAD LENGTH	9	0.20 ± 0.0297	2.49 ± 1.2419	0.87
INTERORBITAL DISTANCE x HEAD LENGTH	9	0.26 ± 0.0298	0.49 ± 1.2482	0.91
PREDORSAL DISTANCE x PREANAL DISTANCE	9	0.80 ± 0.0192	5.78 ± 1.5438	0.99
PREANAL DISTANCE x STANDARD LENGTH	9	0.62 ± 0.0238	-5.27 ± 3.2819	0.98
PREDORSAL DISTANCE x STANDARD LENGTH	9	0.50 ± 0.0241	1.60 ± 3.3151	0.98
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	9	0.21 ± 0.0103	0.92 ± 0.5098	0.98

APPENDIX TABLE 3 - Regression data from *Cynopotamus essequibensis*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	15	0.38 ± 0.0253	3.44 ± 2.3457	0.94
DOBY DEPTH x STANDARD LENGTH	15	0.45 ± 0.0365	-13.34 ± 4.7980	0.92
SNOUT LENGTH x HEAD LENGTH	15	0.32 ± 0.0238	-1.26 ± 0.9242	0.93
ORBITAL DIAMETER x HEAD LENGTH	15	0.26 ± 0.0171	0.78 ± 0.6660	0.94
INTERORBITAL DISTANCE x HEAD LENGTH	15	0.27 ± 0.0195	-0.46 ± 0.7593	0.93
PREDORSAL DISTANCE x PREANAL DISTANCE	15	0.77 ± 0.0400	8.24 ± 2.9668	0.96
PREANAL DISTANCE x STANDARD LENGTH	15	0.62 ± 0.0246	-8.45 ± 3.2678	0.98
PREDORSAL DISTANCE x STANDARD LENGTH	15	0.49 ± 0.0186	0.55 ± 2.4452	0.98
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	15	0.17 ± 0.0146	2.32 ± 0.6777	0.91

APPENDIX TABLE 4 - Regression data from *Cynopotamus venezuelae*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	11	0.36 ± 0.0390	7.59 ± 5.9563	0.90
BODY DEPTH x STANDARD LENGTH	11	0.41 ± 0.0406	-18.87 ± 8.7750	0.92
SNOUT LENGTH x HEAD LENGTH	11	0.34 ± 0.0369	-4.66 ± 2.3358	0.90
ORBITAL DIAMETER x HEAD LENGTH	11	0.17 ± 0.0224	1.98 ± 1.4223	0.86
INTERORBITAL DISTANCE x HEAD LENGTH	11	0.27 ± 0.0238	-1.17 ± 1.5071	0.93
PREDORSAL DISTANCE x PREANAL DISTANCE	10	0.79 ± 0.0636	15.52 ± 7.4975	0.95
PREANAL DISTANCE x STANDARD LENGTH	10	0.62 ± 0.0477	-15.20 ± 10.2028	0.95
PREDORSAL DISTANCE x STANDARD LENGTH	11	0.52 ± 0.0252	-2.58 ± 5.4489	0.97
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	11	0.16 ± 0.0386	6.05 ± 2.7637	0.68

APPENDIX TABLE 5 - Regression data from *Acestrocephalus anomalus*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	10	0.31 ± 0.0208	3.51 ± 0.8643	0.96
BODY DEPTH x STANDARD LENGTH	10	0.26 ± 0.0138	-0.73 ± 0.7975	0.97
SNOUT LENGTH x HEAD LENGTH	10	0.30 ± 0.0350	-0.11 ± 0.5740	0.90
ORBITAL DIAMETER x HEAD LENGTH	10	0.19 ± 0.0283	1.41 ± 0.4648	0.85
INTERORBITAL DISTANCE x HEAD LENGTH	10	0.17 ± 0.0225	0.72 ± 0.3692	0.88
POSTERIOR DENTARY TEETH x STANDARD LENGTH	10	0.10 ± 0.0521	19.37 ± 3.0156	0.34
PREDORSAL DISTANCE x PREANAL DISTANCE	10	0.82 ± 0.0420	1.80 ± 1.4108	0.97
PREANAL DISTANCE x STANDARD LENGTH	10	0.56 ± 0.0311	0.73 ± 1.8014	0.97
PREDORSAL DISTANCE x STANDARD LENGTH	10	0.47 ± 0.0162	1.92 ± 0.9368	0.99
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	10	0.32 ± 0.0271	0.40 ± 0.4007	0.94

APPENDIX TABLE 6 - Regression data from *Galeocharax humeralis*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	6	0.45 ± 0.0579	-0.13 ± 4.7850	0.93
BODY DEPTH x STANDARD LENGTH	6	0.34 ± 0.0524	-4.43 ± 6.2867	0.91
SNOUT LENGTH x HEAD LENGTH	6	0.34 ± 0.0478	-0.09 ± 1.7832	0.93
ORBITAL DIAMETER x HEAD LENGTH	6	0.18 ± 0.0284	2.09 ± 1.0595	0.91
INTERORBITAL DISTANCE x HEAD LENGTH	6	0.21 ± 0.0235	0.35 ± 0.8748	0.95
POSTERIOR DENTARY TEETH x STANDARD LENGTH	6	0.15 ± 0.0163	9.92 ± 1.9592	0.95
PREDORSAL DISTANCE x PREANAL DISTANCE	6	0.93 ± 0.0675	-3.96 ± 4.6261	0.98
PREANAL DISTANCE x STANDARD LENGTH	6	0.50 ± 0.0440	8.15 ± 5.2762	0.97
PREDORSAL DISTANCE x STANDARD LENGTH	6	0.47 ± 0.0326	2.74 ± 3.9116	0.98
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	6	0.29 ± 0.0346	-1.28 ± 1.2918	0.94

APPENDIX TABLE 7 - Regression data from *Galeocharax gulo*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	34	0.45 ± 0.0070	1.05 ± 0.5635	0.99
BODY DEPTH x STANDARD LENGTH	33	0.32 ± 0.0020	-1.43 ± 0.2260	0.99
SNOUT LENGTH x HEAD LENGTH	34	0.35 ± 0.0045	-0.67 ± 0.1679	0.99
ORBITAL DIAMETER x HEAD LENGTH	34	0.19 ± 0.0039	1.39 ± 0.1460	0.98
INTERORBITAL DISTANCE x HEAD LENGTH	34	0.22 ± 0.0035	0.30 ± 0.1321	0.99
POSTERIOR DENTARY TEETH x STANDARD LENGTH	32	0.08 ± 0.0034	16.62 ± 0.4117	0.95
PREDORSAL DISTANCE x PREANAL DISTANCE	34	0.83 ± 0.0082	1.85 ± 0.5798	0.99
PREANAL DISTANCE x STANDARD LENGTH	34	0.61 ± 0.0075	-2.69 ± 0.8891	0.99
PREDORSAL DISTANCE x STANDARD LENGTH	34	0.51 ± 0.0046	-0.52 ± 0.5375	0.99
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	33	0.25 ± 0.0040	0.48 ± 0.1431	0.99

APPENDIX TABLE 8 - Regression data from *Galeocharax knerii*

REGRESSION	N	b	a	r^2
HEAD LENGTH x TRUNK LENGTH	107	0.44 ± 0.0059	1.47 ± 0.5264	0.98
BODY DEPTH x STANDARD LENGTH	103	0.31 ± 0.0038	-2.45 ± 0.4715	0.98
SNOUT LENGTH x HEAD LENGTH	107	0.36 ± 0.0040	-0.63 ± 0.1612	0.98
ORBITAL DIAMETER x HEAD LENGTH	107	0.18 ± 0.0035	1.89 ± 0.1446	0.96
INTERORBITAL DISTANCE x HEAD LENGTH	107	0.21 ± 0.0042	-0.42 ± 0.1725	0.96
POSTERIOR DENTARY TEETH x STANDARD LENGTH	107	0.07 ± 0.0043	20.46 ± 0.5498	0.74
PREDORSAL DISTANCE x PREANAL DISTANCE	107	0.82 ± 0.0071	2.27 ± 0.5443	0.99
PREANAL DISTANCE x STANDARD LENGTH	107	0.61 ± 0.0049	-3.09 ± 0.6347	0.99
PREDORSAL DISTANCE x STANDARD LENGTH	107	0.50 ± 0.0038	-0.52 ± 0.4903	0.99
CAUDAL PEDUNCLE DEPTH x BODY DEPTH	103	0.26 ± 0.0046	0.46 ± 0.1678	0.97