

PART II

REVIEW OF THE SOUTH AMERICAN CICHLIDÆ

NOTICE

Please, this is NOT a published paper, so do not regard any names that are proposed herein as available in zoological nomenclature. Thank you!

The probable relationships of the genera may be expressed diagrammatically thus:—



Regan's (1906b) view of the relationships of American cichlid genera. '*C. multispinosum*' is probably a lapse for *C. spinosissimum*.

ABSTRACT

Forty-one genera and a minimum of c. 250 species of cis-Andean Recent cichlids are recognized.

Chief results of a taxonomic review of characters and each genus considered phylogenetically, implies as main outcome of the study, that views recently expressed about relationships of the genera *Cichla* Schneider, *Crenicichla* Heckel, and *Geophagus* Heckel, have alternatives.

Cichla, with at least five species, has many primitive traits, and its closer relationships need not be with other South American Cichlidae. The type-species of *Cichla*, *C. ocellaris* Schneider, is revised and found to be restricted in distribution to Guyana and Surinam. *Crenicichla* is not close to *Cichla*, but an advanced group. *Geophagus* is split into four genera, which are not closely inter-related.

A review of Fossil forms, chiefly from literature, indicates that all species are erroneously classified generically, and should be either assigned to other, Recent genera, or are decidedly distinct.

Recent genera distinguished include *Acarabobo* n. gen. (ex *Aequidens*), *Acarichthys* Eigenmann, *Acaronia* Myers, *Aequidens* Eigenmann & Bray (restricted), *Apistogramma* Regan, *Apistogrammoides* Meinken, *Astronotus* Swainson, *Australacara* n. gen. (ex *Cichlasoma*), *Batrachops* Heckel,

Biotodoma Eigenmann & Kennedy, *Biotoecus* Eigenmann & Kennedy, *Caquetaia* Fowler, *Chaetobranchoides* n. gen. (ex *Chaetobranchus*), *Chaetobranchopsis* Steindachner, *Chaetobranchus* Heckel, *Cichla*, *Cichlasoma* Swainson, *Claviforaminacara* n. gen. (ex *Aequidens*), *Coeruleacara* n. gen. (ex

Aequidens), *Coryphacara* n. gen. (ex *Cichlasoma*), *Crenicara* Steindachner (re-classified as geophagine), *Crenicichla*, *Gallochromis* n. gen. (ex *Geophagus*), *Geophagus* (restricted), *Guianacara* n. gen. (ex *Acarichthys*;

Odelemaria n. subgen.), *Gymnogeophagus* Ribeiro, *Heros* Heckel, *Hoplarchus* Kaup, *Krobia* n. gen. (ex *Aequidens*), *Margaritacara* n. gen. (ex *Geophagus*), *Mesonauta* Günther, *Nannacara* Regan, *Papiliochromis* Kullander, *Pharyngotocacara* n. gen. (ex *Aequidens*), *Pterophyllum* Heckel, *Retroculus* Eigenmann & Bray, *Satanoperca* Günther (re-validated from *Geophagus*), *Symphysodon* Heckel, *Taeniacara* Meinken, *Teleocichla* n. gen. (rheophilic, *Crenicichla*-like group), and *Uaru* Heckel.

Comparison with Old World cichlids suggests that studies of relationships among cichlids should be made on a familial, and not on a geographical basis.

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INTRODUCTION

This section examines two aspects of the South American Cichlidae. First, it lists all genera and described species, and also includes notes on known undescribed species. Such a listing has not been available since Regan's (1905a,c,d,e; 1906a,b) revision of the American Cichlidae, and even that comprehensive study is incomplete. Each entry has a reference to the original description and, in parenthesis, the type-species if a genus and the type-locality (as given in the original description) if a species. References to figures are restricted to a habitus figure, if given, or, when there are more such figures, to a figure of the holotype or a syntype.

Second, all genera have been re-examined with the aim of finding at least one apomorphic character state for each. It happens, that nearly all South American cichlid genera up to now were defined on the basis of questionable or plesiomorphic character states. This review, even if not completely successful from a cladistic view-point, has led to some re-arrangements of species, and recognition of a few genera in addition to those considered in current literature.

The context of the survey of the South American cichlid genera is the exploration of potential phylogenetically close relatives of *Cichlasoma*, but earlier hypotheses of relationships among South American cichlids (chiefly those of Stiassny 1982, Regan 1906b, Gosse 1976) are re-examined and commented upon. Thus, the generic descriptions are not exhaustive. Special attention is given to the phyletic status of *Cichla* and the validity of the geophagine group. As a major problem in South American cichlid taxonomy, the *Cichlasoma-Aequidens* group is treated at length in Part I. To avoid repetitions, the diagnostic value and phylogenetic significance of

some important characters are discussed after this introduction, with special consideration of those current in the literature.

Much of the data used derives from my mostly still unpublished studies of particular genera or species in connection with revisions of species groups or cichlid faunas. Complementary studies were made for this review, and I also made extensive use of existing literature, especially where African and Central American cichlids are involved. Register numbers are given for some of the material; a complete listing of the several thousand specimens surveyed poses some practical problems in production, and is not available, except in part and as personal communication on request.

As will be shown, there are no 'key characters' that conveniently put the assemblage of South American cichlids in a neat phylogenetic order. There is a large number of species and more or less distinct lineages distinguishable only by consideration of a great many characters distributed through all organ systems. Even staying by skeletal, colour, dental and few other sources of characters, the data base becomes enormous and complex, especially since character state polarity decisions are often not possible. As explained in Part I, I am phylogenetically oriented. That means to me above all a search for differences in homologous characters between samples of specimens. Such are thought to define evolutionary unique units of organisms. Differences between taxa in homologous characters are the only clue to evolutionary history (phylogeny) of taxa. Assuming evolution as a mechanism for character transformation, one of two states is more different from that of the evolutionarily unaffected state than is the other. Decision as to which one, is the major problem of phylogenetic systematics working with lower level groups, such as species or genera, whereas homology is the major problem at higher levels.

There is only one straightforward way to polarity resolution, viz. outgroup comparison, although ontogenetical considerations may provide alternatives (cf. Fink 1981a). The likelihood of the same character transformation occurring twice or more often is ideally negligible.

A rare character state, ie. one found in few taxa, has likely a younger evolutionary history than one that is widespread, especially if there are otherwise no or few character state differences between those very few taxa. This is the 'commonality principle', which is outgroup dependent, but the only really good basis for polarity estimates. Its problem is that if a group and outgroup under study includes a majority of forms with a state responsible for their differentiation and only a few without this innovation and hence rarer, the conclusion would not be accurate until a still larger outgroup is consulted. To avoid those mistakes, there are several approaches.

One that has been emphasized in this paper, is consideration of a general reductive tendency among teleosts. A common regressive trait is more likely derived than a rare supranumerical or complete trait. To a large extent such reductions are related to ontogeny insofar as the adult state agrees with the young or juvenile state among outgroup taxa. Reductions have, however, a disagreeable particular tendency to be expressed in homoplasy, which should be detectable by considering parsimony, ie. character states contradicting a phylogeny are homoplastic if more character states support the very phylogeny, but homoplasy is hardly evident on its own.

Staying by phylogenetic principles and requiring that derived characters should be unique and preferably neither regressive nor losses to be accepted as apomorphic, it becomes virtually impossible to find anything phylogenetically useful. I have therefore no phylogeny to conclude with. Rather, the survey suggests to me that whereas American and African cichlids for the most part appear distinct, there are examples of African cichlids, notably *Hemichromis* and *Tylochromis*, that in some respects agree better with American than with other African cichlids, and so a continent-based phylogeny runs the risk of promoting paraphyly. No certain results after five year's moderate study weigh light against the inconclusiveness of massive efforts by many people to elucidate relationships of African cichlids. I do think that I have a lot many new characters, here, however, that are not studied on African cichlids, and also polarity interpretations differing from those made for African cichlids. So, besides that suggestions for an improved classification of the American Cichlidae is offered, there is some hope also that here is an opening towards a holistic cichlid systematics.

The approach is thus primarily descriptive even if brevity is required by page availability.

Regretfully, Van Couvering's (1982) paper, which contains considerations of higher level cichlid systematics, was received too late for discussion (no literature search made after December 31 1982). Although Van Couvering also considers *Cichla* a primitive cichlid, our reasons for arriving at that shared conclusion are occasionally contradictory. There is a great discrepancy here in experience basis, as Van Couvering's comparative material consists chiefly in Old World cichlids.

Outgroups used for polarity decisions in the following are only occasionally specifically referred to. A material list is available from the author. Principal comparative material includes Asian, Madagascan, and African cichlids, and other percoid families. *Etoplus* Cuvier, studied particularly on *E. maculatus* (Bloch), but also to some extent *E. suratensis* (Bloch), and the related Madagascan *Paretropus* Bleeker, are, like *Ptychochromis oligacanthus* (Bleeker) thought to be primitive because of the well-developed pseudobranch, the last-mentioned species also has a probable epibranchial 2 tooth-plate. *Etoplus* is, however, osteologically very different from all other cichlids in many respects. Further, especially percichthyids, serranids, labroids, centropomids, percids, embiotocids, and lutjanids have been called in as representing possible cichlid relatives. African cichlid material includes *Hemichromis fasciatus* (Peters), *Oreochromis mossambicus* (Peters), and casual material of several other genera.

CHARACTERS

There is certainly no limit to characters useful in taxonomy, except that imposed by imagination. The few chosen here for discussion were selected as being well-known to cichlid students or have been proposed as important by other workers. Generic descriptions contain references to many other characters.

Lip shape

This character has been observed previously with regard to the continuity or discontinuity of the lower lip fold, used by Jordan & Evermann (1898) and Pellegrin (1904) to separate *Cichlasoma* and *Heros*. The value of the character was criticized already by Pellegrin, and I am not sure of its significance. It has not before been noted that the upper lip fold may be continuous or interrupted as well. Continuous lip folds are generally a character of plesiomorphic forms, such as *Caquetaia*, *Satanoperca acuticeps*, and chaetobranchines, but also noted in *Apistogramma*. *Cichla*, like all African cichlids examined has the fold interrupted (or rather, not continuous over the jaw symphysis).

A character of more importance here, is the mode of attachment of the lower lip fold. It is seen that in all American cichlids except *Cichla*, *Astronotus* and *Retroculus*, and in all Old World cichlids surveyed, except *Hemichromis*, the lower lip fold attaches laterally or caudomedially on the upper lip fold at some distance from the distal maxillary-premaxillary connection. This type is designated as 'American'. The 'African' type, exemplified by *Cichla*, *Astronotus* and *Retroculus* alone among American cichlids, differs in that the lower lip fold attaches to the maxilla caudally and the upper lip dorsally, and not covering the upper lip (Fig. 105). In tilapiines I find a somewhat intermediate condition, with very weakly developed lips, and the lower overlying the tip of the upper. I am uncertain whether the state is exactly comparable to that of South American cichlids. Haplochromines, *Ptychochromis* and *Tylochromis* have typical *Cichla*-like lips. *Etoplus* lips, however, resemble the South-American.

The African type agrees well with percoid lip appearance in general; the American type is clearly derived although further work, perhaps best through ontogenetic series, is needed to investigate the possible identity of the state in tilapiines and *Etoplus*, with the American type.

Suborbital bones

The suborbital series, as are termed here the canal bearing bones making up the lower margin of the orbit, offers some good characters with regard to fusion of bones

and reduction of the number of canal foramina. The rostralmost bone in the series is called, as usual, a lachrymal. The succeeding are called infraorbitals (1-6). Where the first suborbital element is considered to be consisting of the original lachrymal plus the first infraorbital, it is nevertheless termed lachrymal, although the next infraorbital is the second. The sixth infraorbital here, is usually called dermosphenotic in the literature.

The most primitive condition, as ascertained by outgroup comparisons, is that of *Cichla*, in which the lachrymal and first infraorbital are joined, a circumstance first noted by Günther (1862), and the first infraorbital is also very wide. There are four lateralis foramina on the lachrymal, and the caudalmost opens jointly with the rostral foramen of the canal on the first infraorbital (Fig. 110).

The same pattern is seen in *Retroculus*, all African cichlids examined except *Hemichromis*, in *Ptychochromis* and *Etroplus*. In the African cichlids, however, the lachrymal and first infraorbital are completely coalesced, so as to form one single bone, although the canal configuration remains the same. In the remaining genera listed, the first infraorbital is much narrower than in *Cichla*.

All South American cichlids except *Retroculus* and *Cichla*, have four lachrymal lateralis foramina. I consider the median pair in *Cichla* and *Retroculus* as homologous to the single median opening in the remainder, and the caudalmost to represent the posterior foramen of the first infraorbital which is completely fused with the original lachrymal. The canal configuration lends some support to this hypothesis, but *Astronotus* (Fig. 101) seems to provide a missing link condition in possessing separate although contiguous lachrymal and first infraorbital, although only three lachrymal foramina.

Support for the hypothesis that the lachrymal and first infraorbital are fused in all South American cichlids except *Cichla*, *Astronotus* and *Retroculus*, comes also from a count of the infraorbitals which remain in relatively constant position and size and are five, except in some further evolved forms.

These latter offer two further advancements. First, terminal coalescence chiefly of infraorbitals 3 and 4, although a foramen is retained medially on the resulting bone. Second, the number is reduced in minute forms, whereby the first infraorbital to go is the sixth. The single remnant in *Taeniacara* (Fig. 126) may be the third and fourth, but further study is needed to ascertain its origin. *Biotoecus* apparently lacks infraorbitals completely.

Hemichromis is of interest for having only four lachrymal pores like American cichlids, and also five infraorbitals.

Preopercular lateralis canal foramina

All American cichlids except 'Aequidens' *pauloensis*, *Astronotus*, *Cichla*, *Retroculus*, and the chaetobranchines have six preopercular lateralis foramina, whereas those mentioned and all Old World forms have seven. One of the foramina on the lower limb is evidently lost or fused with another in the majority of the American Cichlidae. If this reduction is homologous escapes analysis from observation of canal courses, as these vary widely.

Dental lateralis canal foramina

The majority of the Old World cichlids, as well as *Cichla*, crenicichlines, *Retroculus*, geophagines, *Tnarichthys*, *Astronotus*, and chaetobranchines among the American, have five dental lateralis foramina. Among Africans I have noted *Hemichromis* as having only four dental foramina. The rostralmost pore is invisible in intact tilapiines surveyed, but the foramen shows well in cleared and stained *Oreochromis*. Four dental foramina is regarded as advanced over five. *Taeniacara* has only three, apparently the result of progressive reduction.

Lateral line on caudal-fin

All South American, and all African cichlids that I surveyed, have one or two lateralis tubes continuing the lower lateral line on the caudal-fin base, occasionally more, rarely absent (minute forms), between rays V1 and V2. Lack in *Etroplus* is apparently associated with otherwise very reduced lateral lines. In at least some African (*Hemichromis*, tilapiines) and almost all American cichlids, there are also tubes

on the dorsal and ventral lobes separate from the median series; very long sequences in the forms with well-scaled caudal-fin, reduced to one or two or lost in forms with only half or less of the caudal-fin lobes scaly. In chaetobranchines the sequences are long despite reduced squamation compared to *Cichla*, whereas in *Astronotus* the tube series reach only the middle of the fin although the fin is scaly to the end.

The branches vary in position. The lower is always between rays V4-5, except in occasional aberrant specimens, and in chaetobranchines. The upper is modally running between rays D2-3 (most cichlasomines), or D3-4 (eg., *Hopliarchus*, *Krobia*, geophagines), rarely D1-2 (*Coeruleacara*, *Pharyngotocacara*). The rarer position as well as reduced number of tubed scales are regarded as apomorphic features, although parallel reduction is assumed to have occurred. I am uncertain about polarity in the case of the commoner positional conditions.

The ventral section is the more persistent and is, for instant, relatively frequent in *Cichlasoma*, whereas in that genus the dorsal is rare and relatively shorter.

A well developed triradiate caudal-fin lateral line is found in African cichlids only in *Tylochromis*, in which there are long sequences between rays D2-3, V1-2, and V3-4. In *Hemichromis*, I find a tube between rays V4-5 in one specimen, and in some *Oreochromis* specimens there is a tube between rays D2-3 and V4-5.

Among other percoid families, at least centropomids (Greenwood 1976; pers. obs.) serranids (*Epinephelus*; pers. obs.), and pempherids (Tominaga 1968) feature a median caudal-fin lateral line, carried on to the hind edge of the fin; in the centropomid *Lates* it is also triradiate (Greenwood 1976).

In *Crenicichla vittata*, the lower lateral line sequence is continued past the middle of the caudal-fin, but in this species like in all other *Crenicichla*, *Batrachops* and *Teleocichla*, dorsal and ventral lobe branches are missing.

In chaetobranchines all lateral line sequences are long, and they may be showing a truly ancestral state.

Flank lateral line

Most cichlids have, on each side of the body, a long anterior, epaxial lateral line section, and a shorter posterior lateral line section. In South American cichlids generally, the terminal scales lie in the same or proximate transverse vertical series. In some African cichlids, the upper may extend caudad onto the caudal peduncle or the lower rostrad to the pectoral region, and some benthic forms in Lake Tanganyika have a third line on the caudal peduncle. A few forms on both continents have a continuous lateral line from head to caudal-fin like the majority of fishes that have a complete lateral line. Those include *Cichla* and the benthic rheophilic genera *Teleocichla* in South America, *Teleogramma* and *Gobiocichla* Kanazawa in West Africa. In *Cichla*, the condition is plesiomorphic, being percoid; in the rheophilic forms it is derived and related to the attenuate shape.

Minute forms in both South America (eg. *Apistogramma*) and Africa (eg. *Nanochromis* Pellegrin) have rudimentary lateral lines with only a pore on scales posteriorly in the upper and anteriorly in the lower. As the pore is the ontogenetical precursor of the tube, the character state is related to body size in these fishes, and not of any greater systematic importance. Only in *Etroplus* is there an apparent case of extreme reduction of the lateral line to complete loss or a few scales anteriorly in the humeral region.

The position of the upper lateral line relative to the dorsal-fin base is traditionally an important character in the taxonomy of South American cichlids, but is clearly an expression of size of scales as well as body depth.

In forms with very small scales, the lateral line scales are longer than the other flank scales; apparently there is a critical minimum length for the tubes. This character is seen in such different fishes as eg., *Teleogramma* (African) and *Hopliarchus*, and varies within genera with the size of the not tubed scales. It has thus hardly any phylogenetic value *per se*.

Caudal-fin skeleton

I find very little variation in the caudal-fin skeleton between South American forms studied, but a good deal of individual variation. The cichlid caudal skeleton is rather generalized, but lacking a urodermal and with modally two epurals.

The caudal fin skeleton of 108 species of cichlids from both the New and the Old World were studied by Vandewalle (1973). He considered chiefly the number of hypurals and the presence/absence of a parhypural spine. Fusion of hypurals was found chiefly in several small and/or benthic and rheophilic African forms, although Vandewalle himself related the fusion to adaptive radiation in the Great Lakes of East Africa.

Monod (1968) studied the caudal skeleton of *Astronotus* and a few other cichlids. In sections of juveniles of an unidentified Ethiopian cichlid he found a hypural 6 as an early ontogenetic feature. His figured *Astronotus* has three epurals, and is likely abnormal.

Stiassny (1982) drew attention to a cartilage plate in *Cichla* connecting hypurals 2 and 3 distally, which she considered apomorphic for the genus. Little data is available on the cartilagenous plates in the caudal-fin skeleton of other families, but I find the median plate in some geophagines, and rudiments in *Crenicichla* and *Aequidens*. I believe rather that it may be an ancestral feature.

The parhypural spine is well developed in many cichlids, in some it is lost completely. There are also intermediate forms which show individual variation in the development of the parhypurapophysis, which is then at most rather bud-like. Presence of a parhypural spine is an ancestral condition, but loss obviously has occurred in different lineages in both Africa and America.

Anal-fin spines

The number of anal-fin spines has a central position as a character in cichlid taxonomy.

The majority of the cichlids have three anal-fin spines, but not *Etroplus*, *Paretroplus*, some *Oreochromis*, several L. Tanganyika genera, *Astatoreochromis*, *Lamprologus* (Zaire, L. Tanganyika) in the Old World, with from variably 3 or 4, in *Oreochromis* and *Astatoreochromis*, to 12 in *Etroplus*.

There is a similar situation in the Neotropical group, although the almost invariably polyacanth Central American species produce a relatively higher proportion of polyacanth forms. The variation is from 3-4 (eg. *Apistogramma*) to about 12 (*Herotilapia*; *Archocentrus*).

The anal-fin spine number has been used repeatedly to distinguish otherwise similar genera, whereby 'more than three' has been regarded as a state derived over three. From my studies of the South American cichlids, from Whitehead's (1962) analysis of some *Oreochromis*, and from the variability in *Astatoreochromis* Pellegrin (Greenwood 1979), it is clear that three and four or more spines may occur in the same species as well as in the same genus. There is no evidence either, that a polyacanth anal-fin would necessarily be advanced over a triacanth. See part I for further discussion.

Supraneurals

Perciforms likely have primitively three supraneurals (Johnson 1981), although cichlids have two, one or none.

Reduced numbers may be correlated with the development of a rostrad pointing spine on the first pterygiophore (*Gymnogeophagus*) or on the remaining supraneural (*Oreochromis*), or a caudad directed spinous supraoccipital process (*Crenicichla*), but as in the case of *Guianacara*, one and two supraneurals may occur in closely related forms not showing any apparent shape differences.

Two supraneurals is an ancestral trait, but losses have probably occurred in parallel.

The character was first noted by Vandewalle (1971). Later Gosse (1976) used it for separating some geophagine genera.

Branchial apparatus

A prominent character state in South American cichlid systematics is the laminar ventral expansion of the first epibranchial in a group of genera, here included in the geophagines. The second epibranchial has a similar shape, in all cichlids, but the depth varies, as does that of the first epibranchial lamina.

As it is found that *Geophagus* *auctt.*, defined by the lobe of which the first epibranchial lamina forms the skeletal support, is polyphyletic, the value of the lobe

as an indicator of phyletic relationships is open to doubt, and other characters that may defend the group have been investigated.

It is also seen, that some forms, by other characters close to *Geophagus*, lack the lobe and the lamina, and that apparently unrelated forms may have ventral edge modifications of the first epibranchial (*Claviforaminacara*). On the other hand, a kind of lobe associated with the second epibranchial is fairly frequent among African cichlids and found also in *Chaetobranchoides*.

The primitive cichlid condition of the first epibranchial is probably a long slender element, as in *Cichla*, and *Ptychochromis*. Advanced states include above all shortening (as in *Cichlasoma*) and modifications like the laminar expansions, probably in independent lineages.

Primitive branchial arch characters distinguished include a long rod-like interarcual cartilage in *Satanoperca*, but reduction and loss has evidently occurred at different rates in different lineages. A cartilagenous first pharyngobranchial is a specialization of crenicichlins; otherwise this element varies in shape, either stick-like or expanded at the epibranchial end.

The second pharyngobranchial lacks teeth in *Symphysodon*, apparently a specialization, as this form also has few jaw teeth.

Ptychochromis has a small loose tooth-plate associated with the second pharyngobranchial caudad to it and lateral to the third pharyngobranchial, that may represent a second epibranchial tooth-plate, a structure figured in approximately the same position in *Lates* by Greenwood (1976), but it has not been observed in other cichlids. In two chaetobranchine genera, otherwise weakly toothed cichlids, there is a tooth-plate on the second basibranchial, but I am uncertain about its significance.

Other tooth-plates in the pharynx are the three upper pharyngeal tooth-plates, mostly as described in Part I, although in primitive forms like *Cichla* and *Chaetobranchopsis* the third pharyngobranchial is dorsoventrally compressed, and in *Cichla* the second pharyngobranchial lies lateral to the third, instead of rostral to it. The fourth tooth-plate is only loosely associated with the third in *Cichla*, as a primitive character. In some forms, primitively there is a series of tooth-plates dorsally along the fourth ceratobranchial, particularly many in *Etoplus* and *Ptychochromis*, but reductions in number and loss may be parallel in different lineages.

Gill-rakers along the margin of the lower pharyngeal tooth-plate, in crenicichlins and some geophagines, are judged as ancestral, although they are not known from other percoids.

Further aspects of the gill-rakers and associated elements are discussed under *Cichla* and *Chaetobranchoides*, and next:

Microgillrakers (microbranchiospines)

Stiassny (1981b) considered microgillrakers with toothed lateral edges and truncated top to be an autapomorphy of the Cichlidae. In regard to variation, she noted varying distribution on the gill-arches, which includes presence on both sides of all four as well as complete absence. The complete set in *Cichla*, she (1982) considered derived, although of 'typical cichlid type', and unusual in that they lie above the proximal part of the gill-filament heads (her Fig. 15 shows the position overlying the proximal part of the gill-rod, however). The microgillrakers are small ($80 \mu \times 60 \mu$ average size according to Stiassny 1981b), and although presence/absence and general form is readily verified under a dissection microscope, a comparative study using light and electron microscopy and a large number of taxa should be made before more far-going systematic conclusions are attempted.

I have noted, however, that the 'typical cichlid' form characterizes only some African groups, eg. *Astatotilapia* (Stiassny 1981b), *Tilapia* (Gosse 1956), and *Oreochromis* (pers. obs.); but those of *Hemichromis* resemble rather those of *Cichlasoma*. In most cichlids they are apparently round-tipped; in *Etoplus* with the lateral edge toothed, but commonly only the basal portion of the edges toothed. The microgillrakers of *Cichla* resemble those of *Crenicichla*; at least in the former occasionally with teeth on the dorsal edge; form variable, narrow or squarish, in the latter case with lateral surface teeth. In chaetobranchines and *Astro-*

notus they are plates with truncated bottom and rounded top, with many small teeth on the exposed surface and some along the lateral edge ventrally.

Complete absence as in, eg. *Claviforaminacara* and some *Geophagus* is a derived condition. Contrary to Stiassny, I feel that a complete set, as in *Cichla*, is the original cichlid condition, with parallel loss in different lineages. As in *Cichlasoma* they are usually absent from the first arch, but in *Etroplus* and *Acaronia* present externally on all four arches. Commonly also absent from the inside of the fourth arch.

Considering that there is much variability in form and distribution on arches, as well as gradual ontogenetic appearance (Stiassny 1981b) and that they are likely subject to a reductive tendency, microgillrakers are for the moment only of potential value to intrafamilial cichlid taxonomy.

Considering the shape variation, Stiassny's claim for a cichlid autapomorphy is negated. Microgillrakers occur also in centropomids (Greenwood 1976; 'supralamellar plates'), pomadasyids (Stiassny 1981b), gerreids (Stiassny 1981b; pers. obs.), citharinids (Gosse 1956, Vari 1979), and *Phractolaemus* (Thys 1961). Some hesitation may be called for in recognizing the mere presence in some cichlids as an apomorphy for the family.

Branchiostegal rays

McAllister (1968) gave a variation of five to six branchiostegal rays in Cichlidae. Checking McAllister's reference list, it seems like the count of six comes from Jordan & Evermann (1898), who merely cite Gunther (1862), who gives a variation of five or six branchiostegal rays for the family. The count of six is, however, taken from Valenciennes' (1858) description of *Glyphisodon zillii* (= *Tilapia zillii* (Gervais)). The record should be checked.

All cichlids that I have examined have five branchiostegal rays, three anterior ceratohyal, two posterior ceratohyal. In forms of which alizarin material available, more primitive genera (*Astronotus*, *Chaetobranchopsis*, larger geophagines, *Crenicichla*, *Cichla*) the fifth ray has its proximal end more or less medial to the anterior ceratohyal (see also Barel et al. 1976, Fig. 5), otherwise it is ventral, as in *Cichlasoma*. There is much variation in the shape of the hyoid arch elements within the family, awaiting deeper study.

Van Couvering (1982) uncritically accepted McAllister's record of branchiostegal ray number of the Cichlidae. She found seven rays in the holotype of *Kalyptochromis namulodentis* Van Couvering, 1982 (early Miocene, Kenya), but noted some uncertainty about the count that should maybe be emphasized. I would agree, however, that the five branchiostegals in cichlids represent a derived condition, though not unique among perciforms (cf. McAllister 1968).

In Labroids the lateral rays tend to cluster on the anterior ceratohyal, (one on the posterior, four on the anterior ceratohyal according to McAllister 1968) although five is apparently the common number (cf. McAllister 1968, Rognes 1973). Embiotocids have rarely five, usually six, with two ventral anterior ceratohyal (McAllister 1968).

Lower percoids tend to have six or seven branchiostegal rays, a few families also a foramen in the anterior ceratohyal (the beryciform foramen), in McAllister's (1968) records. As the variation is chiefly in the rostralmost rays, below the rostral slender shaft of the anterior ceratohyal, cichlids are apparently advanced over lower percoids and embiotocids in having lost one of these rays, but retaining, evidently, the general set of posterior rays with regard to position and number.

Dentition

Teeth have received much attention in the taxonomy of African cichlids, which display a great variety of tooth shapes. Aside from casual observations by Regan and Pellegrin of the more obvious deviations from the generalized type in *Aequidens* and *Cichlasoma*, South American cichlid teeth have had little impact on the taxonomy. As indicated below, however, there is quite some diversity, which involves relative sizes of teeth in the linguad series compared to those of the labiad series, relative depressibility, reduction of number tooth-series as well as of number of teeth, and different shapes.

The most common shape is caniniform, i.e., a pointed, slightly recurved tooth with circular base, and it is assumedly primitive for the South American forms. This tooth-shape occurs also in African cichlids, but tricuspid or bicuspid teeth in these may have a long phyletic history, as judged from their widespread occurrence and presence in the presumably primitive *Etroplus* and *Ptychochromis*.

Scales

Any areas of cycloid scales or loss of scales are considered derived, though probably cycloid squamation developed independently in several lineages of cichlids. Loss of scales, especially prepelvic and nape scales is commonly associated with minute body size (eg., *Biotoecus*, *Taeniacara*), but not obligatory in small forms. A special case is encountered in the naked nape midline of *Cichla* and *Geophagus harperi*. Rheophilic forms, especially *Teleocichla*, have the anterior head and chest scales deeply embedded in the skin.

Small scales (= higher number of squ. long. scales) appear among cichlids for the most part primitive, as a percoid character state, but there are several aspects to this character. Scale counts follow vertebral counts and body shape (also correlated). Stout-bodied species have relatively larger scales than elongate fishes which include a greater magnitude of sideways bending of the body in their motions. Thus, the small scales of *Crenicichla* may be correlated with locomotion mode, whereas they must have some other explanation in the deep-bodied, rigid *Symphysodon*.

Preopercular scales

Preopercular scales are rare amongst cichlids, and different in appearance and arrangement in different genera (Figs. 100, 115, 123). In eg. *Acarabobo* they correlate with biserial cheek squamation whereas related genera have mostly triserial cheek squamation and naked preoperculum. However, also in *Etroplus* and *Archocentrus centrarchus* they show some relation to the cheek squamation, continuing it over the preoperculum. In *Pterophyllum* the scales are like those on adjacent cheek, but not continuous with the remaining head squamation, and restricted to the lower limb of the preoperculum. Although the correlation with biserial cheek squamation may be an apomorphy *per se*, preopercular scales are common among other percoids, and as both *Etroplus* and *Archocentrus centrarchus* appear to be primitive cichlids, preopercular scales are primarily to be seen as ancestral.

Fin shapes

Species of the genus *Cichlasoma* have a fairly modal cichlid finnage. Deviations have received some taxonomic appraisal, such as the lower percoid shape of the dorsal-fin of *Cichla*. It has not been recognized that the other fins of *Cichla* also show lower percoid resemblances. I regard the finnage of *Cichla* as indicative of the ancestral cichlid condition, although it should be noted that the supposedly also primitive *Etroplus* and *Ptychochromis* have very different dorsal- and anal-fin shapes, approaching the modal. *Tylochromis* has extremely long second and third anal-fin spines, but relatively very short first anal-fin spine, not unlike centropomids; in other fins it is close to *Geophagus*.

Fin shapes vary greatly among perciforms and among cichlids, and are reasonably related to body shape. However, a straight, or emarginate posterior border of the caudal-fin, a common cichlid condition, seems a likely ancestral character, and is useful as it singles out a more limited number of forms with rounded caudal-fin. Produced marginal or median caudal-fin rays are, however, also advanced features, sometimes species specific (within *Apistogramma*), and occurring in different lineages.

The pectoral-fin of South American cichlids usually have the fourth ray longest, but in *Crenicichla*, with strongly rounded pectoral-fin, one of the median rays is the longest, possibly an autapomorphy.

The pelvic-fin may be very long, reaching well above the anal-fin, or short, but its length is likely correlated to body shape and manoeuvring environment. Character states show an erratic distribution, however, and polarity decisions are conjectural.

The pelvic-fin usually has the outer branch of the first ray the longest, in African as well as American cichlids; commonly, the first ray is also much produced. In *Crenicichla*, with the first and second rays subequal in length or the second the

longest, the fin is very small considering the length of the fish and is probably reduced to fit the cylindrical shape of the body. In *Acarichthys*, with the second branch of the first ray longest and the second ray nearly as long, some other explanation of the broad tip is called for.

The anal- and dorsal-fins are greatly modified in some deep-bodied strongly compressed forms, especially *Symphysodon* and *Pterophyllum*, with graduated spine length and longer soft than spinous portion, but also to some extent *Heros*. In these the fin shape relates to the body shape and the fins do not provide independent character states.

Produced dorsal-fin lappets occur in a number of geophagines. Virtually all cichlids (but not *Cyrtocara sensu stricto* in Lake Malawi) have lappets at all known sizes. These may be short or long in relation to the extraspinous extension, but the restriction of the produced anterior lappets in a group, otherwise including forms with differentiated spine lengths, suggests that they may be the result of shortened spines as much as lengthening of the lappets. So, the long lappets in males of some *Apistogramma* species are not necessarily advanced over the modal cichlid condition in congenetics.

Caudal-fin counts

All cichlids except *Nannacara* have 16 principal caudal-fin rays (i,7,7,i), but few African genera were examined. The basal and highest number in perciforms is 17 (i,8,7,i). Some apparently have fewer, eg., priacanthids, nandids (i,7,7,i), scarids (i,6,5,i) and embiotocids (i,6,6,i). This character is useful only for delimiting *Nannacara*. It seems that within the percoids, there is a reductive tendency.

Procurrent caudal-fin rays occur in numbers of two to ten at least. There is a 'natural break' between those with modally three, and those with more. The character may be correlated with the length of the caudal peduncle, and low numbers are typical also of minute species. In- and outgroup comparisons suggest, however, that high numbers are ancestral.

Vertebrae

Pellegrin (1904) divided cichlids into three groups according to vertebral numbers: isospondylous (1:1 abdominal:caudal), opisthopolyspondylous (<1:1 abdominal:caudal) and proteropolyspondylous (>1:1 abdominal:caudal). Since, vertebral numbers have been reported for many cichlids, but little used or subjected to analysis. Intrafamilial variation has been shown to be considerable, with total counts from 23, in *Apistogramma* species, to 41 in large *Crenicichla*; abdominal:caudal ratios vary, with the majority isospondylous or with slight deviations from unity, few genera proteropolyspondylous or opisthopolyspondylous.

No cichlid has the 'basal percoid' count of 10+14-15, the taxonomic significance of which has been subject to much discussion (Gosline 1956; Johnson 1981), many have higher counts, but 23 is very rare. The tendency is clearly regressive (Johnson 1981), as is evident in cichlids, among which otherwise regressed and/or minute forms have the lower counts. Patterson (1964) related vertebral number in perciforms to a change in body proportion giving increased maneuverability, and, most importantly, considered the 10+14-15 formula possibly a parallel acquisition in several groups.

As the low numbers (10+14-15) are apparently derived, as lower numbers are exceptional among perciforms and as cichlids always have at least 11, usually more abdominal vertebrae, and modal total counts in the range 28-32, it seems clear that the relatively many vertebrae of cichlids are ancestral in a wider group, as in percids, centrarchids and many labrids, and that high numbers are ancestral among cichlids. The question is if there is some basal count, and if the rare extremely high counts (>c. 35) might not after all be secondary.

Whereas terete cichlids do have higher numbers, eg. *Crenicichla*, there are terete forms with low numbers, eg. *Taeniacara*; also whereas deep-bodied species tend to higher caudal vertebral numbers (eg., *Symphysodon*), there are also reverse instances (*Etoplius suratensis* with 17+14 according to Günther (1862) and Pellegrin (1904)). Large species generally have more vertebrae than small, but *Acarania* is then quite exceptional; and *Crenicara* still have higher numbers than other dwarf cichlids.

Most recently, Stiassny (1982) declared proteropolspondyly and high vertebral counts in *Crenicichla* and *Cichla* a synapomorphy of these genera.

The majority of the cichlids are iso- or opisthopolspondyloous. Besides *Cichla* and *Crenicichla*, a few haplochromines (Stiassny 1982), some *Satanoperca* and one *Etoplus* species are proteropolspondyloous to various degrees.

Cichla is different from *Crenicichla* in having a closed hemal canal below the last three vertebrae; besides, the vertebral ratio shows very little abdominal dominance, one, two, rarely three vertebrae only. *Cichla* can be distinguished by more vertebrae but hardly by vertebral number ratio from *Satanoperca*; and the high count is ancestral.

Crenicichla have consistently 2-6/7 more abdominal than caudal vertebrae. Total number is probably to some extent related to size, but there is also regional variation (Kullander 1982c); in reduced numbers (in the probably advanced *lepidota-saxatilis* assemblage) there is still a positive ratio abdominal to caudal (18+14 in *C. britskii*, the most regressed species so far known), showing that regression is in both caudal and abdominal numbers.

The character state in *Crenicichla* and *Batrachops* appears unique among percoids and is therefore apomorphic within a larger group. The state(s) is clearly not identical with that of *Cichla* as total vertebral numbers are not identical throughout *Crenicichla*, the difference in ratio is clearly greater in *Crenicichla*, and in *Cichla* a complexity is present in the abdominal hemal canal.

Some caution in relation to which group *Crenicichla* should be considered derived, is suggested by *Teleocichla* which are otherwise highly specialized and probably sister-group of some forms now in the catch-all *Crenicichla*. *Teleocichla* species have as many or more caudal as abdominal vertebrae.

I am uncertain of how many vertebrae there really are in some haplochromines thought by Stiassny (1982) and Greenwood (1979) to be derived in increase of abdominal vertebrae, in one group coupled with decrease of caudal vertebral number, so it is difficult to tell whether they are comparable. The supposed ancestral number $12-14+15-16 = 17-19$, as modal, is rather low in the abdominal count, and no reason other than 'common' is given for regarding it as plesiomorphic.

Conclusively, what alone may be clear about cichlid vertebral number is a reductive trend in total number. Ratios abdominal:caudal number tend to relative constancy among species otherwise decided to be closely related, but no particular intrafamilial polarity is evident.

Coloration

African and American cichlids may be distinguished very conveniently, as the former have a black, metallic blotch dorsally on the hind edge of the operculum, missing in the American, with one, very interesting exception, viz. *Retroculus* which also has a tilapia mark, another African feature, plus various other ancestral or African traits. *Etoplus* also lacks an opercular spot.

The opercular spot pigment is on the medial side and on a slight rounded caudal projection of the gill-cover in African cichlids that I examined, except *Tylochromis*, which has a *Geophagus*-like gill-cover. The visibility is enhanced by the absence of scales from most or all of the lateral side of the operculum over the spot, except, again, in *Tylochromis*.

Retroculus differs in not having the caudad expansion, and the spot is slightly more removed from the opercular margin, featuring character state that may be identical with that of *Tylochromis*.

Baerends & Baerends-von Roon (1950) showed that the opercular spot in *Hemichromis* and a similar spot on the preoperculum in *Thorichthys meeki* are used in the same way during frontal display, whereby antagonizing individuals fold out the gill-covers and expose the gill-cover spot as a sort of eye-spot, giving an impression of increased head size.

The preopercular spot in *Thorichthys*, however, is formed by dense lateral surface pigment. Centrarchids (*Chaenobryttus* and *Pomotis* examined) have an opercular spot indistinguishable from that of the African cichlids except *Tylochromis*, on the medial side and not covered by scales on the lateral side. It may represent a parallel evolution instance that is quite remarkable.

The tilapia mark, a black spot at the base of the dorsal-fin in the transitional region between the spinous and soft parts is characteristic of young, and often adults, in the African genera *Tilapia*, *Sarotherodon*, and *Oreochromis* (Trewavas 1973), but occurs also in some other, west African, genera. The spot appears different in *Retroculus*, though it is in a similar position, and I would consider it just another ocellus, or eye spot, a kind of marking (dark, light-ringed spot) that is very common in South American cichlids, but rare among Africans.

Ocellated spots are found on the body, caudal-fin, or dorsal-fin of almost all larger South American cichlids. In some *Crenicichla* dorsal-fin ocelli are found only in a variable frequency (eg., *C. proteus*, *C. jupiaensis*). In *Acarabobo* it is occasionally a secondary female character. Flank ocelli are prominent in many species without caudal ocellus, but some *Crenicichla* have both.

Zaret (1977) investigated the significance of the caudal-fin ocellus in *Cichla* and found it to have an inhibitive effect on autopredation, and concluded that non-*Cichlas* may have an ocellus to escape predation from *Cichla* or *Astronotus*.

There is, however, a phylogenetic aspect to the spot also, otherwise one would expect at least one of the probably 3000+ species of South American non-cichlid fishes to have acquired a similar eye-spot as well. I suggest, with Lowe-McConnell (1969), that the ocellus primarily is a recognition signal of a more general nature, like contrasting marks in a great number of South American diurnal fishes. I also suggest that the marking on the caudal-fin base is homologous in *Cichla*, *Crenicichla*, *Batrachops*, *Astronotus*, *Chaetobranchoides*, and *Satanoperca*.

In these genera, the spot is slightly removed from the base of the fin, and although it starts as an axial marking its final position in adults is slightly apical. The spot is deep black and has a layer of dense light pigment around it. In *Crenicichla* species the spot usually remains at an earlier developmental stage as compared to *Cichla*, and in some species the spot is completely lacking.

In the *Cichlasoma*-*Aequidens* group, the spot lies close to the fin base and develops first by vertical pigment spreading, later concentrating to a spot on the bases of the dorsal rays; a pigment ring never develops, but the spot is ocellated by unpigmented (or little dark-pigmented) adjacent scales, occasionally also silvery dots. It is possible that spots of similar nature in *Australacara*, *Mesonauta*, and *Acaronia* are homologous, ocellated or not, but as a kind of central caudal-fin base marking is present at least in juveniles of all South American cichlids of which juveniles are known, and the alternative developmental ends are restricted in number and not identical in details, some convergence must be accounted for. Also, I think that the *Cichla*-*Crenicichla*-*Batrachops*-*Astronotus*-*Chaetobranchoides*-*Satanoperca* ocellus is an ancestral trait, although it would point to monophyly of this group (and an unknown assemblage of sister-taxa).

It is of some interest to note the slanting lateral band in various groups, evidently convergent, as details differ. A reverse slanting band is seen in some Lake Malawi cichlids (Trewavas 1935, Regan 1921; a band sloping from nape to caudal-fin base). A large midlateral blotch is common among American cichlids, and also seen in *Etoplus*, but I have not noted it in any African cichlids. Some African cichlids (*Thysia*, *Hemichromis*, some *Tilapia*) may have a series of blotches along the side. It is, not common in large American cichlids (eg., *Petenia*, *Batrachops*, *Cichla*, some *Crenicichla*).

It is, as in other fishes, characteristic that elongate forms are horizontally banded or horizontally blotchy, deep-bodied forms vertically barred, with some exceptions. The relatively elongate *Retroculus* are vertically barred, and juvenile *Batrachops* have a very striking contrasting pattern of vertical bars.

Many other markings are helpful in establishing relationships in particular cases, but mimicry is strongly suggested in at least in the case of *Geophagus harreri* and nominal *Guianacara*, and may be more widespread than now known or accounted for.

Sexual dichromatism rarely shows well in preserved material, and I have little to say about it. The South American cichlids are sex dimorphic, but for a few (eg., *Pterophyllum*, *Symphysodon*, *Acaronia*, *Astronotus*) sexual colour differences are slight or not (yet) found. Small species, especially *Apistogramma*, *Nannacara* and *Taeniacara* may show sex specific markings well in preservative, and also show considerable life colour sex differences.

Geophagine characters

Besides the *Cichlasoma*-like cichlids, there has hitherto been recognized only one more plurigeneric group of American cichlids. These I proposed should be called geophagines (Kullander 1980b, p. 45). Genera then recognized were *Apistogramma*, *Apistogrammoides*, *Taeniacara*, *Biotocetus*, *Acarichthys*, *Papiliochromis*, *Geophagus*, *Biotodoma*, *Gymnogeophagus* and *Retroculus*.

The uniting character is a lobe extending ventrad from the dorsal limb of the first gill-arch. *Acarichthys* was included although the provisionally incorporated *A. geayi* would lack the lobe. Later I have found that *A. heckelii* also lacks a typical lobe. Yet, these two species are very similar to other geophagines in most other respects and I have come to consider the lobe as not so important a character. A lobed or non-lobed condition, may be difficult to tell apart, and strictly defined the principal geophagine character is a ventral lamina on the first epibranchial, which is lined with a thick pad of connective tissue.

Such an epibranchial extension is present also in *Crenicicara*, herewith considered a geophagine, but not in *Acarichthys* or *Guianacara* (ex *Acarichthys*), or in any other cichlids. The shape of the first epibranchial is very variable among cichlids, however, and in *Claviforamnacara* there is a superficially similar ventral extension which, however, appears rather to be a broadened medial arm. The second epibranchial of all cichlids is of the form of the first as the latter is seen in the most typical geophagines, eg. *Geophagus* and *Satanoperca*.

Other pharyngognaths may have a wide first epibranchial but then not clearly with a ventral extension (embiotocids, pomacentrids, labroids; Nelson 1967, Stiassny 1981b; pers. obs.)

Characters other than the lobe that would unite geophagines are few. In fact, this is a very diverse group morphologically and with the recognition of primitive character states such as many procurrent caudal-fin rays, triradiate lateral line on caudal-fin, numerous gill-rakers, five dental lateralis pores, emarginate caudal-fin, parhypural spine, small scales, many vertebrae (c. 30) at least in the larger species, some doubt has suggested itself about the phylogenetic status of the lobe.

A special problem in finding additional character states, is posed by the many minute species, most in the genus *Apistogramma*, which do not conform in many respects that would otherwise distinguish the large forms. Osteological material of *Retroculus* and *Biotocetus* has not been available.

However, at least the large species are distinguished by having the supraoccipital crest grooved along the dorsal (rostral) edge, a particularly prominent character state in *Gymnogeophagus*. The supraoccipital crest form is very variable among cichlids, but in *Cichlasoma*-like forms at least, with a well developed crest, it is perfectly flat, save that in *Symphysodon* it is supported by lateral strengthened vertical zones.

The three ventral pectoral-fin radials are coalesced or sutured together. In this *Acarichthys*, *Satanoperca*, *Gymnogeophagus*, and *Geophagus* are best developed. Among other cichlids, I have verified the condition in *Pharyngotocacara* only, but the radials are variably approximated in different genera. In *Cichla*, *Crenicichla*, and *Cichlasoma* they are clearly independent, but in eg. *Mesonauta*, they are nearly as close as in larger geophagines.

A deep lachrymal is characteristic of larger geophagines, but there is no sharp limit to other cichlids, and the minute forms have only a moderately deep lachrymal. The character is correlated with a produced snout, which shows also in a long ethmo-vomerine region.

The geophagine shape is characteristically triangular in frontal aspect, with keeled nape, and flattened chest. It is different from the ovate outline of *Cichlasoma*, but a relatively depressed broad nape is featured by some *Satanoperca*, and the minute species have an elliptic frontal outline with rounded nape and chest.

The most interesting is the hemal canal formed by one to three posterior abdominal vertebrae. The one or the two anterior of these vertebrae, of course, have no hemal spine, but the arch is formed by a bridge extending between the ventrad directed basapophyses. A similar or identical condition is seen otherwise only in *Cichla* among large cichlids, but *Nannacara* parallels *Apistogramma* both in postabdominal ribs and abdominal hemal arch, and *Guianacara* lacks the hemal arch. Concerning the

last abdominal vertebra, there is a problem about its classification as it may possess basapophyses, a hemal fenestra, a hemal spine and ribs, besides that it articulates with the first anal-fin pterygiophore.

Characters listed do not unify the geophagines, especially as the minute species possess reduced states, but they motivate the inclusion of *Acarichthys* and *Guianacara*.

Many primitive character states put the group apart from *Cichlasoma*-like cichlids. There is no obvious connection to chaetobranchines, *Astronotus*, or *Acaronia*, but in some respects interesting similarities with *Cichla* and crenicichlines.

Crenicichlines and some geophagines are the only cichlids with fifth ceratobranchial gill-rakers; both groups include forms with serrate preoperculum.

Cichla has abdominal hemal arches, a cartilagenous connection between hypurals 2 and 3 like some geophagines, a keeled nape and many gill-rakers. Besides, the percid-like gradation of the dorsal-fin spines occurs also in *Satanoperca*, *Papiliochromis*, *Guianacara*, and *Crenicara* species, although less conspicuous. There is also a great overall resemblance especially to *Satanoperca* species.

Chromosomes

Few karyological studies have been made of American cichlids. Thompson's (1979) extensive study, with bibliography (but see also Scheel 1972) makes up for the otherwise small quantity, however. His results are fairly in agreement with the morphological. Thompson distinguished a plesiomorphic state with $2N=48$, all subtelocentric-telocentric (*Cichla* only), and two advanced, one with $2N \approx 48$, many metacentric (eg.

Nannacara, *Apistogramma*, *Pharyngotocacara*, *Crenicara*, *Uaru*, *Caquetaia*, *Symphysodon*), another with $N=48$, few metacentric, most subtelocentric (eg. *Acarichthys*, *Aequidens*, *Astronotus*, *Cichlasoma*, *Heros*, *Mesonotata*, *Coryphacara*, *Crenicichla*, *Margaritacara*, *Satanoperca*, *Geophagus*, *Pterophyllum*).

SUPRAGENERIC NAMES AND GROUPINGS

Nominomania

The name Cichlidae derives from Bleeker's (1859, p. XVII) Cychloidei, based on *Cychla*, a variant spelling of *Cichla*. Bleeker included all then known genera of cichlids, also *Chromis* Cuvier, then not yet considered restricted to a pomacentrid genus, *Ambiodon* Rafinesque (questionably; now in Sciaenidae), and *Pycnosterinx* Heckel (now in Polymixiidae in Beryciformes, v. Patterson (1964)) The following subfamilies and tribes have been proposed for groups to include South American cichlids.

Acharnina Günther 1861, p. 369.

Proposed as a 'group' of Nandidae, corresponding to subfamily. It includes *Acharnes*, actually a synonym of *Cichla*. Acharnina as a family group name is therefore a synonym of Cichlidae; and was proposed only following misleading information from the authors of *Acharnes*.

Geophaginae Haseman 1911b, p. 322.

Type-genus (not stated by Haseman) *Geophagus*; defined by 'a lobe on the upper branch of the first gill-arch.' Haseman's introduction of the name is not in any way formal, but on the succeeding page in his paper, Eigenmann uses it as a matter of course.

Chaetobranchinae Fernández Yépez, 1951, p. 11/.

Type-genus *Chaetobranchius*. Including originally also *Chaetobranchopsis*, and defined by the long gill-rakers.

Cichlinae Fernández Yépez, 1951, p. 12/.

Type-genus *Cichla*; defined by the short last dorsal-fin spine, evidently equal to *Cichla*.

Crenicichlinae Fernández Yépez, 1951, p. /2/.

Type-genus *Crenicichla*; defined by finely denticulated preoperculum, otherwise as Astronotinae (infra); other genera to be included not stated.

Astronotinae Fernández Yépez, 1951, p. /2/.

Type-genus *Astronotus*; defined by the last dorsal-fin spine being longer than 3/4 the length of the second dorsal spine and equal to or longer than the third dorsal spine, short and not numerous gill-rakers, and entire preoperculum. Evidently including all genera not included in other subfamilies proposed by Fernández Yépez, whichever those genera they may be.

Geophagi Cichocki, 1977b, p. 159.

A subtribe of assumedly a tribe Geophagini (never proposed), presumably including *Geophagus*; mentioned only in the passing, discussing relationships of *Bioto-doma*, with a reference to an unpublished paper (see Cichocki 1977a). A life colour and behaviour description may stand as diagnosis.

Hoedeman (1947) recognized the following groups (a scheme on page 13 of section X.60.76 in his book, gives an overview):

Haplochrominae

Subfamily; type-genus *Haplochromis* Hilgendorf; includes the tribe Cichlini in South America.

Cichlini.

Tribe; only for *Cichla*; defined by the upper pharyngeal jaw apophysis formed by both parasphenoid and basioccipital.

Tilapiinae

Subfamily; type-genus *Tilapia* Smith; includes the following four tribes in South America:

Chaetobranchini

Tribe; for *Chaetobranchus* at least; no diagnosis given.

Astronotini

Tribe; for *Astronotus* and *Aequidens* at least; no diagnosis given.

Cichlasomini

Tribe; for *Cichlasoma*, *Symphysodon*, *Pterophyllum*, and other genera not named; no diagnosis given.

Crenicarini

Tribe; for *Batrachops*, *Crenicichla*, and *Crenicara*; no diagnosis given.

Hoedeman's splitting, which includes also a subfamily Etroplinae and many African tribes besides those listed, is only based on ambitious reading of Regan's revisions of the Cichlidae and no new ideas or characters are presented, save for the formalisms. The classification has been cited, however, in a few later aquarium books (Frey 1959; Hoedeman 1969, 1974, 1980), but also by scientists (Wickler 1963). The -ini endings were changed to -idi in Hoedeman (1954, sections X.60.762.12, X.60.762.261; also in Hoedeman 1969, 1980).

There are thus directly available the following family group names based on South American cichlids:

Geophaginae Haseman, 1911; supersedes Geophagi Cichocki

Chaetobranchini Hoedeman, 1947; supersedes Chaetobranchinae Fernández Yépez

Astronotini Hoedeman, 1947; supersedes Astronotinae Fernández Yépez

Crenicarini Hoedeman, 1947

Crenicichlini Fernández Yépez, 1951

Cichlasomini Hoedeman, 1947

Tentative groupings

None of the names just listed finds recognition here, as it seems quite out of place to try formal divisions without a clear phylogeny encompassing the whole family. It may rather lead to confusion. Instead, groups of genera recognized are referred to by semivernaculars, like geophagines, in analogy with the use by eg., Greenwood (1974) of the collective terms haplochromines and tilapiines for larger assemblages of African cichlids, of which no formal suprageneric classification is available. Semivernaculars refer to two major assemblages of American cichlids, the characters of which are discussed elsewhere in this paper. I believe they are monophyletic, but problems in linking these groups at the base should be recognized. Also crenicichlines are well-defined, whereas 'chaetobranchines' is a just a convenient term.

Geophagines, referring to genera listed above under 'Geophagine characters'. With the inclusion of *Retroculus* this is a very distinct lineage. It is quite diverse with minute forms as well as some of the largest South American cichlids, mouth-brooders of various types, rheophiles, and long-snouted benthivores.

Cichlasomines, referring to the subjects of Part I, defined primarily by the dental lateralis foramina number. This is also a diverse group, but piscivores are more marked elements missing in the geophagine group; also, more evolved forms tend to generalization, whereas among geophagines adaptational trends may be more marked.

Crenicichlines, including *Crenicichla*, *Batrachops*, and *Teleocichla*. This group is defined on the characters of *Crenicichla*. All are elongate, but there is diversity in mouth structures. Many species among those undescribed are not particularly 'pike-like', even if a large mouth is basal. Also in this group, there are wide-spread comparatively generalized forms (the *saxatilis-lepidota* group), dwarfs (eg. *C. wallacii*), and rheophiles (*Teleocichla*); Luengo (1971) has an unverified report on mouth-brooding.

Chaetobranchines are the genera *Chaetobranchius*, *Chaetobranchopsis*, and *Chaetobranchoides*. These are identified by the long, numerous gill-rakers. There are connections to *Acaronia* (mouth structures, especially), and *Astronotus* (micro-gillraker form), two primitive genera that are maybe related, but not covered by the name.

Cichla, as an apart group, is referred to by its generic name, but its distinctness should be recognized.

Cichlid characters

This is not the adequate place for a discussion of familial characters or relationships. It should only be pointed out that the Cichlidae is actually a poorly defined family.

Liem & Greenwood (1981) defined cichlids as distinct from labroids, but not embiotocids, by having 'the lower pharyngeal jaw suspended in a muscular sling of which the fourth levator externus is dominant both morphologically and functionally', and from embiotocids by a single nostril on each side and quadripartite *m. transversus dorsalis anterior*. The Embiotocidae, as sister group, are defined by a loss of pharyngobranchial 2 teeth and 'viviparous mode of reproduction'.

As cichlids do have a posterior nostril, albeit very small and probably not functionally identical with that of other fishes, as a single nostril anyway is not that uncommon among fishes (eg. in blennioids, Gosline 1968; allotriognathids, Delschläger 1983), as there is also a cichlid (*Symphysodon*) without pharyngobranchial 2 teeth, and as the fourth levator externus is a composite in a cichlid species studied by Aerts (1982), their scheme is not convincing.

Stiassny (1981b) reported 'loss of a major structural association between pars A2 and A_{2c} of the adductor mandibulae muscle and the muscular insertion of a large ventral section of A2 onto the posterior border of the ascending process of the anguioar-

ticular', a ventral margin cartilage lining of the second epibranchial, expanded head of the fourth epibranchial, and 'characteristically shaped and distributed' microgillrakers.

I did not check the adductor mandibularis musculature, and assume that it is correctly stated. Microgillrakers vary in shape and position and besides being subject to a reductive trend among cichlids, are not at all unique. The shape of the fourth epibranchial is slightly variable with *Acaronia* and the African *Trematocara* (Stiassny 1981a) exceptional to the definition. On the whole, widening of the medial portion of the fourth epibranchial is not as evident in American as in African cichlids.

The second epibranchial cartilage is shared with embiotocids and while perhaps a synapomorphy of embiotocids and cichlids, it is not a unique cichlid character and also the relative amount of cartilage is variable among the Cichlidae.

Cichlids are thus as loosely defined as any other percoid family.

Internal classification attempts

Previous revisions, i.e. Heckel's (1840), Eigenmann & Bray's (1894), Regan's (1905-1906), Pellegrin's (1904), Eigenmann & Kennedy's (1903) of the American Cichlidae, have been sorting attempts in the first place. Little has been said about natural relationships or whatever the current adequate term. Neither is there much to extract from smaller papers. Two dendrograms depicting some kind of evolutionary relationships have been published however.

Regan's view of the relationships of the American Cichlidae is well illustrated by his (1906b) dendrogram, here reproduced as pre-text illustration. It is not an exact representation of the associated diagnostic key; I am not sure what made Regan place *Crenicara*+*Crenicichla*+*Batrachops* earlier than *Acara* in the key but as descendants of *Acara* in the diagram, but feel that there may be some evolutionary reasoning behind at least the dendrogram. As no discussion was ever presented on any character used, there is little to comment. More can be said about generic characters, however. To be sure, Regan did not pay much attention to polarities, and modern taxonomists may perhaps envy his time. Consideration of apomorphic characters has more explanative output, however, and makes taxonomy somewhat more interesting. Wherever possible, in the following text, Regan's generic characters are commented upon. There are no other classifications of such thoroughness, or they are not particularly different, so comments on, e.g., Pellegrin's (1904) or Eigenmann & Bray's (1894) groupings can be spared.

Ribeiro's (1915) reproduction of Regan's diagram is very far from the original, and his own (here Fig. 99) is apparently rather unfounded speculation, so there is little to do about it except noting its existence.

Neither diagram complies particularly well with the views presented below; but it should be noted that far fewer species were known to Regan.

THE FISHES

GENDERS OF GENERIC NAMES

Genders are given after protologue references, and are determined according to dictionaries or author's statement. There is only one interesting case in this regard within the group, viz. the *-cara* endings, which may be discussed at some length. New names proposed below, ending in *-cara*, all take feminine gender, conforming to the common situation. *Acará* is the Lingua geral word for cichlid, although other spinous fishes are also called *acará* in South America (e.g., the nandid *Monocirrhus polyacanthus* Heckel, otherwise *piracaá*, *pira-cará*, or *peixe-folha*), and some groups of cichlids are recognized by other names (e.g., *jacundá* for *Crenicichla*, and *tucunaré* for *Cichla*) (see also von Ihering 1940, Santos 1954, Pereira 1979).

Heckel (1840) established the genus *Acara* for 21 nominal species of cichlids, mostly South American. He explained the name thus: '*Acará* oder *Cara* sind die gewöhnlichen Namen, womit in der Brasilianischen Lingua geral, die meisten Chromis ähnliche Fische bezeichnet werden. *Natterer*.' The gender of *Acara* was not stated by Heckel, but it is apparently masculine as shown by the adjectival endings in the combinations *A. vittatus*, *A. pallidus*, *A. dorsiger*, *A. marginatus*, *A. cognatus*, *A. niloticus*, *A. punctatus*, and *A. ocellatus*. *Acara* later became a synonym

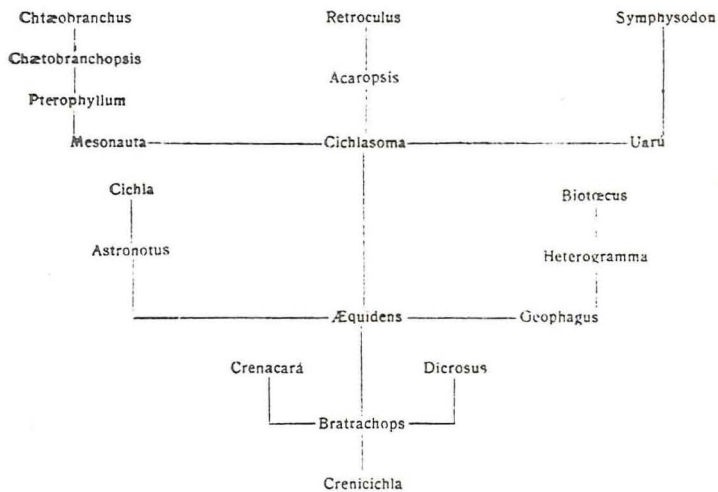


Fig. 99. Ribeiro's (1915) diagram of the relationships of Brazilian cichlids. *Chaetobranchius*, *Uaru*, *Crenacará*, *Dicrosus*, *Batrachops* misspelt.

of *Astronotus*. It has survived, however, in some compound names in the meaning of cichlid.

After Heckel, Acara has generally been treated as feminine, eg. by Steindachner (1875), Regan (1905c), and Pellegrin (1904; but, *Acara freniferus*). However, Acara is decidedly masculine, being based on a word of neither classical nor Indo-European origin, whereby the author's statement or indication determines the gender (International Code of Zoological Nomenclature, Art. 30(b)(i)). In Portuguese Brazilian it is treated as a masculine word (o acarã).

A few cichlid genera have names ending in *-acara* (or *-cara*), and these are, as a rule, treated as feminine. It is rarely recognized that two words have been used to form this ending. On the one hand, there are those names referring to Acara (or Acara), on the other hand those based on the Greek word *καρα* (or *καρη*), which becomes cara in Latin letters. The Greek word variants are both neuter and mean head or face (Menge 1957). Thus, Regan (1905a) 'corrected' Steindachner's (1875) *Crenicara* (serrate face) to *Crenacara* (serrate Acara), apparently unaware of the etymological basis for *Crenicara*.

Below, I give a list of the generic names within the Cichlidae ending in *-acara* or *-cara*, with the particular gender of each, as I have determined it. It should be noted that names ending in *-cara* occur also in other families, eg., in the Aspredinidae (*Petacara* Bohlke, treated as feminine), and the Loricariidae (*Xeno-cara* Regan, treated as feminine).

A. Acara and names ending in -acara

Acara Heckel (1840). Masculine. Based on an Amerindian word and treated as masculine by the author. Synonym of *Astronotus*.

Crenacara Regan (1905a). Feminine. Unjustified emendation of *Crenicara* (q.v.), feminine as used in the combination *C. punctulata*, and based on an Amerindian word, whether referring directly to Acará or to the latin form.

Macracara Woodward (1939). Feminine. The ending refers to *Taeniacara* and is based on an Amerindian word; implied to be feminine in the combination *M. prisca*.

Nannacara Regan (1905c). Feminine. The ending obviously refers to Acara, but is based on an Amerindian word and is treated as feminine by the author in the combination *N. anomala*.

Paracara Bleeker (1878). Masculine. Used originally with a noun only (*P. typus*), but the ending refers to Acara, and not Acará, as implied by analogous names created by Bleeker: *Paretroplus* (referring to *Etroplus*) and *Paratilapia* (referring to *Tilapia* Smith). Synonym of *Paratilapia* Bleeker.

Taeniacara Myers (1935). Feminine. Gender not stated and adjectival names not used, but since *-acara* here is from *Nannacara* rather than from Acara, the gender is implied to be as for *Nannacara*.

B. Names ending in -cara

The ending *-cara* is derived from either *καρα* or *καρη*. The former retains its gender (neuter) in Latin, but the latter becomes feminine if written cara. All cichlid generic names ending in *-cara* appear to be neuter.

Aulonocara Regan (1921). Neuter. The ending here is identical with that in *Trematocara*, as indicated by the comparison with that genus, and *-cara* in *Trematocara* is from *καρα*, neuter. But Regan otherwise (eg., 1921, *Cyrtocara*) treated Acara, *-acara*, and *-cara* as feminine.

Crenicara Steindachner (1875). Neuter. Used originally with the adjectival epithet *elegans* only. The name alludes to the prepercular serrations, so it is apparently based on *-cara*. Article 30 (a) (i) (1) of the International Code of Zoological Nomenclature says: 'A name is to be regarded as a Greek or Latin word of the same spelling, unless its original author states otherwise'. 'Same spelling' must be cara (actually *kara*), and not care (*kare*).

Cyrtocara Boulenger (1902). Neuter. See *Crenicara*. The name refers to the head shape.

Trematocara Boulenger (1899b). Neuter. Determined from the adjectival ending in the combination *T. marginatum*; thus, *-cara* here is obviously from *καρα*.

INCERTAE SEDIS

Forms not to be discussed below are the Central American groups, like *Theraps*, reaching south of the Panama canal; in fact the limit here is the Andes and Caribbean coast cordillera, as I know very little about trans-Andean cichlids. Thus are excluded 'Cichlasoma' species of which Eigenmann (1922) has the basic descriptions and figures, see also Meek & Hildebrand (1916) and Dahl (1960). Full species lists of *Coeruleacara*, *Caquetaia* and *Gallochromis* are given, however.

Remaining *incertae sedis* forms, include some unidentifiable because of poor descriptions and missing type-material, as well as some known from insufficient material.

Acaropsis rondoni A. Ribeiro, 1918. *Comissão Linhas. telegr. estrat. Matto Grosso Amazonas Publ.* (46), p. 11, Pl. IV, fig. /1/ (Rio do Sangue).

This species shows not even a superficial resemblance to *Acaronia*. It is certainly a cichlasomine, with four dental pores, but I am not sure of the predorsal scale pattern (of about 9 median scales). Chest and prepelvic scales are cycloid; the preoperculum and the vertical fins are naked. The dorsal-fin is very low, the penultimate spine 12.8 % of SL (the last broken). The shape is elongate, the snout produced.

Centrarchus? vittatus Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 161, Pl. 14 (-).

This species is based on a drawing. It could possibly be a *Cichlasoma* as Jardine's figure shows four anal-fin spines; but the description says '3/7' about the anal-fin count.

Hoplarchus planifrons Kaup, 1860. *Arch. Natges.* 26, p. 131 (-).

Kaup based this species on a specimen in the Munich Museum, but the type is not preserved there (Terofal, *in litt.*). Unfortunately, there is no figure, and the yet very long description, would seem to fit a large number of cichlids. The geographical origin of the type is unknown, but it is possible that it represents part of the residue from the Spix & von Martius' collection not described by Agassiz or Spix. With flat forehead, light and dark spots in soft dorsal- and caudal-fins, D. XV.10, A. III.8, ten large opercular scales, and 22 scales along the side, it is possible that *Ae. tetramerus*, or a similar *Aequidens* species is intended, but further speculation on the precise identity of the fish appears futile.

Labrus filamentosus La Cépède, 1802. *Hist. nat. Poissons* 3, pp. 430, 479, Pl. 18, fig. 2 (le grand golfe de l'Inde).

Labrus filamentosus is now and then cited as a South American cichlid. There is no existing type-material (listed neither by Blanc 1962, or Bauchot 1963) and it cannot be identified even to genus on basis of La Cépède's meagre description and poor figure, and the family is not clear.

Günther (1862) listed it as an *Acara*, and most recently Fowler (1954) catalogued it as an *Aequidens*. Bauchot (1963), however, thought that it looked like a *Glyphisodon*; she seemed unaware of its occasional appearance in catalogues of cichlids. There is little point in future listing of the name.

Perca bimaculata Bloch, 1792. *Natges. ausländ. Fische* 6, p. 82, Pl. CCCX, fig. 1 (Flüssen von Brasilien).

Acara margarita Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 338 (nom. nov. subst. *Perca bimaculata* Bloch).

See Part I for discussion.

Pomotis? bono Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 171, /Pl. 18; not seen/ (all the rivers of Guiana, and in pools and marshes).

The drawing referred to by Jardine is missing from both copies of the book that I examined. There is nothing in the description to identify the species.

'*Cichlasoma*' sp.

A single 65.8 mm, deep-bodied specimen from the R. Payamino in Ecuador is not referable to any South American cichlasomine genus, but the species may be related to Central American forms.

D. XVII.12; A. VII.11; unpaired soft fins extensively scaly. Gill-rakers short, one epibranchial, seven ceratobranchial externally on first arch. Long lateral line sequences on caudal-fin, six scales between rays D2-3, nine scales between rays V4-5. Outer series teeth slightly enlarged, especially the median pair in the upper and one next to the median in each lower jaw half. The snout is somewhat pointed, but jaw bones short, the premaxillary ascending processes reaching to the orbit. I cannot make out the colour pattern as the fish is badly faded; but there is a narrow vertically extended spot slightly behind the center of the flank, and traces of vertical bars. New collections will be interesting.

FOSSILS

INCERTAE SEDIS

Acaronia longirostrum Bardack, 1961. *Amer. Mus. Novit.* (2041), p. 16, Fig. 6 (Tertiary Subandino, la Yesera Creek, Salta Province, Argentina).

Aequidens pauloensis Schaeffer, 1947. *Bull. Amer. Mus. nat. Hist.* 89, p. 29, Pl. 4, fig. 3 (?Pliocene beds at Tremembé, São Paulo).

Aequidens saltensis Bardack, 1961. *Amer. Mus. Novit.* (2041), p. 13, Fig. 5 (Tertiary Subandino, La Yesera Creek, Salta Province, Argentina).

MACRACARA

Macracara Woodward, 1939. *Ann. Mag. nat. Hist.* (11) 3, p. 451 (type by monotypy *M. prisca* Woodward).

Macracara prisca Woodward, 1939. *Anni. Mag. nat. Hist.* (11) 3, p. 451, Pl. XVI, fig. 3 (Tertiary formation exposed in the left bank of the river Parnahyba at Nova York, Municipio of Pastos Bons, in the State of Maranhão, Brazil).

The fossil record of South American cichlids is surprisingly meagre. That is probably a measure of collecting intensity (even if Brazilian fossil fish can be purchased in gift shops in Stockholm). Of the four or five species none is older than Miocene, possibly they are all Pliocene. Generic assignments are uncertain, and no apomorphic character states have been described that would link the fossils to any particular lineage known from Recent material. So for the present, the information content of the Tertiary cichlids is chiefly potential. They should be re-examined when the osteology of Recent forms, both of the Old and New World, is better known.

Woodward (1898) gave notice of an *Acara* sp. with pterygiophores of 14 spines and 8 or 9 rays in the dorsal-fin, the anal-fin with A. III.8 or 9, from bituminous shales at Taubaté, state of São Paulo, Brazil, age uncertain (Arratia 1982: ?Upper Tertiary; de Oliveira 1956: Pliocene possibly). From the same locality, Woodward (1898) also described *Percichthys antiquus*, which H. von Inering (1898) speculated might be rather an *Acara* or *Chaetobranchus*. Arratia (1982), however, confirms the percichthyid status of *P. antiquus* and places the species in the monotypic

genus *Santosius* Arratia. Schaeffer (1947) identified the *Acara* sp. as possibly the same species as his *Aequidens pauloensis* from a nearby locality.

The association of a cichlid and a percichthyid is remarkable as at present freshwater percichthyids are restricted to Patagonia and not found together with cichlids.

Macracara prisca Woodward is based on two specimens from supposed lower Tertiary deposits at Nova York, in the state of Maranhão, Brazil. Although the larger syntype must be over 150 mm, Woodward compared it specifically with the minute *Taeniacara*. As it appears from Woodward's photograph, and the vertebral count (16+20) *M. prisca* could be a *Geophagus* or *Retroculus*, or of a related extinct lineage.

Re-examination of the *Macracara* types, considering critical characters (other than those used by Woodward) likely will show the form to be related to some Recent group. There is a Recent species of *Geophagus* in the Parnaíba basin.

The dating is doubtful, resting on the association with the clupeid *Knightia* Jordan, which may be characteristically lower Tertiary (cf. Schaeffer 1947), and the Eocene dating of the North American supposed cichlid *Priscacara* (cf. below). Pace the *Knightia*, the *Macracara* horizon may be of younger date than Paleogene; it was considered questioned Pliocene by Schaeffer (1947).

Aequidens pauloensis is known from a single specimen, 143.9 mm, chiefly an impression, with smashed head, probably Pliocene, at Tremembé, in the state of São Paulo, Brazil (R. Paraiba system). I have re-examined it but have little to add to Schaeffer's (1947) description - the generic assignation is clearly incorrect, however. It had small scales, squ. long, probably more than 25, perhaps about 30; vertebrae 10-12 (estimated) +16; D. XV.11 (uncertain; lepidotrichia missing), A. III. (short; 8-10 rays according to Schaeffer). There were five foramina along the free edge of the preoperculum, suggesting a total count of seven foramina for that bone.

The species is not assignable to any Recent genus, particularly not *Aequidens* (small scales, seven preopercular lateralis foramina; 16 caudal vertebrae). The abdominal vertebral count is uncertain and may have been higher than the estimate (upon which I agree with Schaeffer). Also *Ae. pauloensis* has been found with *Santosius antiquus*.

The best known fossil cichlid locality in South America, described by Bardack (1961), is a freshwater upper Tertiary (Miocene-Pliocene) siltstone bed, at La Yesera Creek, Salta, Argentina (upper R. Salado system). It contains two cichlid species:

Aequidens saltensis, by virtue of the dorsal-fin count (XIII.13) and vertebral count (11-12+16) cannot be an *Aequidens*. Bardack's (1961) photo of the holotype is not distinct, and his description includes no further details allowing referral to any particular Recent genus, but it is most likely a geophagine, possibly *Gymnogeophagus australis sensu Gosse*.

Acaronia longirostrum, up to 19 cm total length, has 13-14+16-17 vertebrae, D. XIII.13 (count uncertain though), A. III.7, a long snout and long ascending premaxillary processes. The vertebral count is too high for an *Acaronia*; the premaxillary ascending processes too long for *Cichla*; the two supraneurals (on Bardack's Fig. 6) exclude *Crenicichla*; the dorsal-fin count excludes *Astronotus* (the spines also appear somewhat slender and long on Bardack's Fig. 6); the anal-fin count excludes *Caquetaia*. So, the species may represent an extinct lineage. Bardack's photos are somewhat obscure, but give the impression that much of the skull is preserved and thus some optimism may be expressed about the informativeness of the material.

Another neotropical fossil cichlid is *Cichlasoma woodringi* Cockerell, from the Miocene of Haiti, revised by Myers (in Tee-Van 1935). It seems to be like the Recent *Nandopsis haitiensis* (Tee-Van) in all respects except for a slightly higher vertebral count (14+16 or 18, vs. 13+15).

Priscacara Cope (1877, 1883) from the Eocene of the state of Wyoming, U.S.A., was originally proposed as related to cichlids or pomacentrids. Pellegrin (1904) accepted the genus as cichlid, and Haseman (1912b) went at length to show that it is nearer to cichlids than to pomacentrids or labrids. Regan (1906-1908, 1916) and Myers (1938) suggested that *Priscacara* is a centrarchid group. The alternative is a seranid-percichthyid relation (cf. Schaeffer & Mangus 1965), a possibility that I would favour after examination of two specimens of *P. pealei* Cope (NRM P868). Another North American fossil cichlid, *Kindleia fragosa* Jordan (1927), from the Cretaceous of Alberta, Canada, is an amiid (Grande 1980).

RECENT GENERA

ACARABOBO n. gen.

Type-species: *Acara dorsiger* Heckel.

Nannacara bimaculata Eigenmann, 1912. *Mem. Carneg. Mus.* 5, p. 488, Pl. LXVI, fig. 1 (Erukin).

Acara curviceps Ahl, 1924. *Mitt. zool. Mus. Berl.* 11, p. 44, Fig. 5 (Amazonenstrom).

Acara dorsiger Heckel, 1840. *Annl. wien. Mus. Natges.* 2, p. 348 (Sümpfe in der Nähe des Paraguay-Flusses bei Villa-Maria).

Acara flavilabris Cope, 1870. *Proc. Amer. philos. Soc.* 11, p. 570 (near Pebas, Ecuador).

Acara freniferus Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 255 (Ambyiacu).

Acara (Acara) Thayeri Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 71, p. 68, Pl. I, fig. 2 (im Amazonenstrom und dessen Ausständen bei Cudajas, in den See Hyuanuary bei Manaos und im Lago Maximo bei Alemquer).

This is the *dorsiger* group already discussed in Part I. The name derives from the local denomination (according to Natterer, in Heckel 1840) of *A. dorsiger* in the type-locality area. *Acará bobo* means something like 'stupid cichlid', but only in allusion to the ease of catching the fish with the bare hands. I have observed myself that *A. curviceps* and the Aveiro species are not shy for motion around them - but that may be, I feel, because they already located the escape hole in the seine. The gender is masculine. Whitley (1951) has complicated nomenclatural matters with this group, by designating *A. dorsiger* type-species of *Nannacara* A. Ribeiro, and re-naming the latter *Parvacara* for reason of homonymy with *Nannacara* Regan. However, as it is completely clear that Ribeiro (1918d) was not proposing a new name but referring to *Nannacara* Regan, there is actually no genus for the name *Parvacara*. That name is therefore still available if someone wishes to use it for some other group. The gender of *Acarabobo* is masculine.

The genus includes two groups separated by body lengths, and one species tentatively assigned to *Acarabobo* pending further work.

The small species, none over 40 mm SL in the wild, are *A. dorsiger* in the Paraguary and Guaporé systems; *A. curviceps* taken at Santarém, Monte Alegre, Parintins, Itacoatiara, and Óbidos; an undescribed form taken at Aveiro and in the nearby R. Cupari, and another undescribed form in the middle R. Xingu. These differ chiefly in lower meristics from the larger forms, but all have two supraneurals unlike *A. bimaculatus*.

Acarabobo thayeri reaching at least 78 mm, is a common fish along the lower Ucayali-Solimoes, sympatric with *A. flavilabris*, but never taken in the same places. It is the only species with scaly dorsal- and anal-fins, but is more stout-bodied than the other large forms, and has therefore lower meristics (eg., squ. long. 22; 24 in *A. flavilabris*, 23-24 in the Orinoco-Negro species). *Acarabobo flavilabris* is restricted to the upper Amazonas basin, taken in the Napo at Santa Cecilia, along the Ucayali-Amazonas at Jenaro Herrera, Iquitos, Pebas. It reaches at most c. 80 mm SL. An undescribed species from the rivers Inírida and Guarrojo in Colombia and R. Preto da Eva in Brazil, reaches 75 mm SL. Hongslo observed a pair at Caranacoa guarding eggs on a leaf so this may be a leaf-litter spawner like *Krobia*, *Pharyngotocacara*, and *Coeruleacara* species.

Acarabobo bimaculatus, finally, is a small species restricted to the Potaro and adjacent Essequibo in Guyana. It has only a single supraneural, and departs from other *Acarabobo* as well as *Nannacara* in the contrasting dark vertical bars on light ground. It lacks the many reductive specializations of *Nannacara*, but may prove to

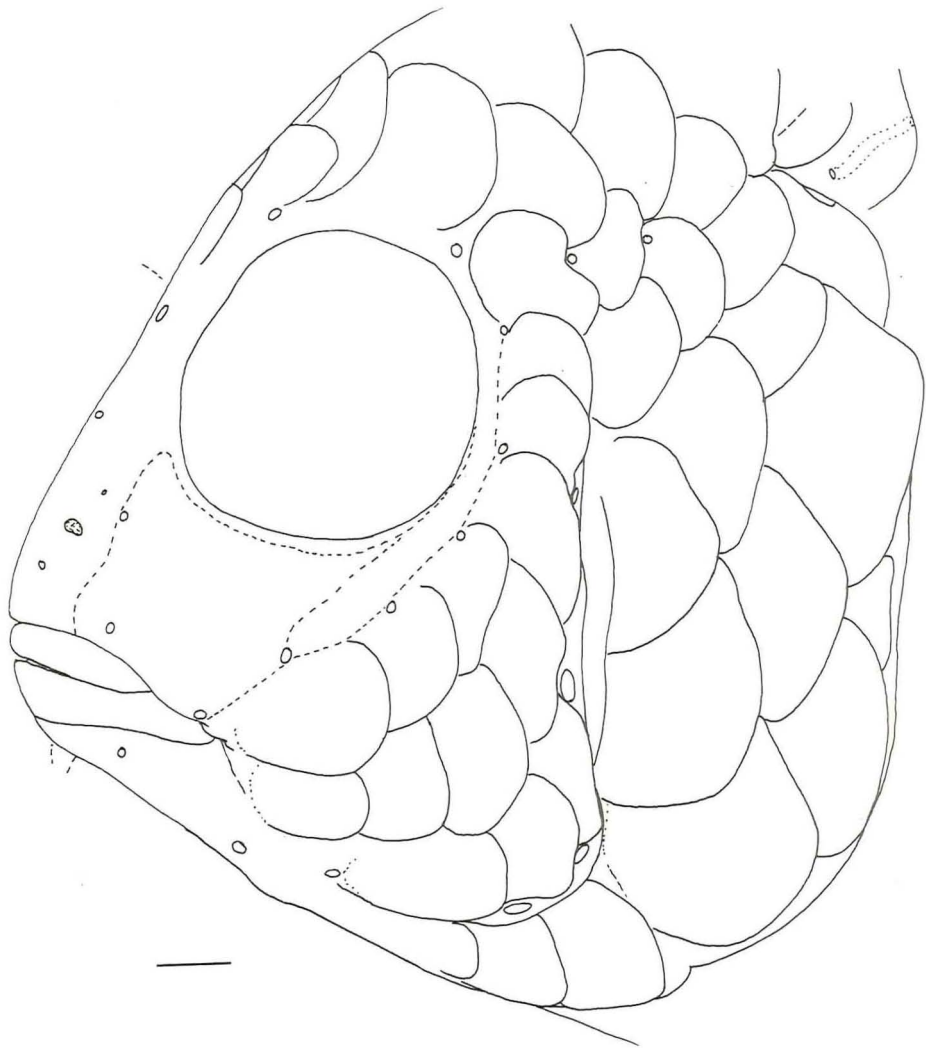


Fig. 100. *Acarabobo thayeri*. Lateral view of head, to show scale pattern of cheek and gill-cover. Scale 1 mm. From a syntype, NMW 33740, 70 mm SL.

be generically distinct from *dorsiger*-like forms as well.

These fishes are distinguished on the reduced cheek squamation (two series of large scales) and three interopercular scales (Fig. 100). Preopercular scales are likely plesiomorphic at least among cichlasomines, and biserial squamation at least is not unique with these fishes. The rare occurrence of the combination biserial cheek squamation and three preopercular scales might be taken as a synapomorphy of *Nannacara* and *Acarabobo*, but still *Acarabobo* must be a rather primitive group. *Acarabobo* does not show any of the striking osteological specializations of *Nannacara*. From *Cichlasoma* they are distinguished osteologically chiefly by lack of parhypurapophysis and fourth ceratobranchial teeth.

ACARICHTHYS

Acarichthys Eigenmann, 1912. *Mem. Carneg. Mus.* 5, p. 500 (type by original designation *Acara heckelii* Müller & Troschel). - Masculine.

Acara Heckelii Müller & Troschel in Schomburgk, 1849. *Reisen Brit. Guiana* 3: 624 (Sümpfen der Savanne).

Geophagus (Mesops) Thayeri Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 71, p. 108, Pl. III, Fig. 2 (Amazonenstrom bei Teffé, Villa bella, Obidos, Cudajas, Tonantins, Jatuarana, Ueranduba, Serpa, Rio Tapajos, R. Trombetas, R. negro, R. Xingu, See Hyanuary, José Assú, Saraca, Alexo und Lago maximo etc.)

Acara subocularis Cope, 1878. *Proc. Amer. philos. Soc.* 17, p. 696 (/Amazonien Peru/).

Acarichthys is not considered by Regan, partly because the genus was not yet named, partly because the absence of an epibranchial lobe made him include the only species in *Acara* (= *Aequidens*). Regan (1905d) described *A. heckelii* as *A. subocularis* Cope, believing that *A. heckelii* might be identical with *Acara geayi* (Regan 1905c).

The types of *A. heckelii* and *A. subocularis* are apparently lost. The latter is, from the description, close to or identical with *Geophagus thayeri*, of which a large syntype series is preserved. The identity of the former is questionable, as the description is not detailed; but by selection of a Guianan neotype of the same species as *G. thayeri*, the nomenclature of the group would be stabilized.

Acarichthys heckelii occurs along the Ucayali-Solimões, upper Brazilian Amazonas, lower R. Negro, R. Branco, and R. Essequibo. It is found in black, clear and white waters and limiting ecologically is maybe only the preference for open bottoms.

The outwards appearance is clearly geophagine, both in shape and colour pattern. However, the first epibranchial is short and not expanded ventrally; the thick soft skin may remind of a lobe, but hardly more than in many non-geophagines.

Aside from the missing lobe, the characters of *Acarichthys* agree largely with those of *Geophagus*. The cranial osteology is similar to that of *Geophagus* especially in the supraoccipital crest, jaws, and dentition, deep lachrymal and operculars. But the snout is not produced, but rather rounded, with deep ventral portion. The gill-rakers externally the first gill arch are small, edentulous and few, 4-5 epibranchial, 6-7 ceratobranchial. A single supraneural with antrorse distal spinous process. Microgillrakers externally on three posterior arches. Interarcual cartilage very little elongated; first pharyngobranchial expanded ventrally. Median frontal crest moderately elevated; coronalis foramen dorsad-rostrad directed. No rakers on lower pharyngeal tooth-plate, but four tooth-plates on fourth ceratobranchial. Broad blunt proximal process on distal postcleithrum. Vertebrae 14+15; swimbladder abdominal, no caudal ribs. Supracleithrum occasionally serrated. Long parhypural spine, six procurrent caudal-fin rays in each lobe; cartilage plate between hypurals 2 and 3 not verified. Lower lip fold interrupted (continuous according to Regan 1905d).

The cheek is scaly, except a very small rostroventral area. Nape and thoracic scales are not much smaller than flank scales. Squ. long. 28-29. There is no dorsal lobe lateral line on the caudal-fin but frequently one or two tubed scales between rays V4 and V5.

The pelvic-fin shape is unique among cichlids; the inner branch of the first ray is a trifle longer than the outer and the second ray branches nearly as long, the two outer rays thus forming a very broad tip. Also the caudal-fin shape is unusual in that the corners are slightly prolonged, not only the marginal ray as in other large geophagines.

While defining the geophagines, I (Kullander 1980b) provisionally placed *Acara geayi* in *Acarichthys*, but similarities are rather superficial.

ACARONIA

Acaronia Myers, 1940. *Stanf. Ichthyol. Bull.* 1, p. 170 (nom. nov. pro *Acaropsis* Steindachner). - Feminine.

Acara (*Acaropsis*) Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 71, p. 80 (type by monotypy *Acara nassa* Heckel). - Masculine.

Acaronia nassa Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 353 (... Mottogrosso...Rio-Guaporé).

Centrarchus ?? *rostratus* Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 163, Pl. 15 (Rio Negro).

Acara cognatus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 356 (Barra do Rio-negro).

Acara unicolor Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 357, Pl. XXX, fig. 25 (Barra do Rio-negro).

Apistogramma ambloplitoides Fowler, 1940. *Proc. Acad. nat. Sci. Philad.* 91, p. 281, Fig. 63 (Ucayali River basin, Contamana, Peru).

Acaronia is considered by most authors as *Aequidens* with long ascending premaxillary processes. '*Aequidens*' then can only be a cichlid with three anal-fin spines lacking epibranchial lobe, for there is little in superficial morphology common to these genera. Pellegrin (1904) was original, and perhaps most correct in comparing with *Chaetobranchius*. The gill-rakers of *Acaronia* are short and few, however (7-12 on lower limb of first arch in *A. nassa*).

Acaronia nassa is relatively large, reaching at least c. 150 mm SL, with piscivore physiognomy, especially in a relatively large mouth. Lowe-McConnell (1969) found them solitary fish in Guyana and they are usually in small numbers or singly in other collections. Guyanan *A. nassa* stomachs contained chiefly fish, shrimps and insects remains (Lowe-McConnell 1969).

The geographical distribution includes the Rupununi, Demerara, Branco, Trombetas, Madeira, Guaporé, Ucayali-Amazonas-Solimões, and Orinoco.

Counts are low, D. XIII-XIV. 9-10, A. III.8-9, squ. long. 22, rarely 23; cheek scales large, in 2 or 3 series. All scales are large, also the nape and prepelvic scales; the former are about 6 to 9, and cycloid, either median or overlapping pairs. The irregular arrangement is unlike that in cichlasomines, and also the median predorsal squamation is reduced by the fossa for the premaxillary process intruding into the scaly nape rostrally.

The colour pattern consists in a narrow band back from the orbit obliquely to the end of the dorsal-fin base, containing a midlateral spot in the rostralmost of five vertical indistinct bars. On the head there is a dark spot close above the posterior part of the orbit. In juveniles a strongly caudad inclined suborbital stripe which in adults separates into two spots, one close to the eye, the other on the preopercular corner. The unpaired fins are vividly dotted with dark squarish dots separated by light interspaces. The caudal spot is light-margined but very narrow, rather like a bar, positioned ventrally on the dorsal caudal-fin lobe base.

The cephalic lateralis system is like in cichlasomines, but preoperculo- and mandibular series foramina and all skin pores are enlarged compared to other South American cichlids. The tubes of the flank lateral lines are also prominent. Caudal-fin lateral line scales are rare on dorsal and ventral lobes, but a scale may be present between ray D3-4 and V4-5. The coronalis canal is distinct in that the transverse canals run

slightly caudad and end raised with slightly elevated median frontal crests; this feature is correlated with the long premaxillary processes.

Acaronia is very different from cichlasomines, however, in jaw and gill-raker structure, and no closer relationship is indicated.

The ascending process of the premaxilla are long, reaching beyond the middle of the orbit; a rostral foramen is not present; the alveolar process is slightly shorter than the ascending, yet long and slender, and features a narrow median maxillad process. The lower jaw projects slightly before the upper and is characterized by a ventral anguloarticular process that is slightly longer than deep. Jaw teeth are fixed, minute, recurved unicuspid, arranged in several series, all teeth of about the same size. The maxilla is long and slender, with light head and comparatively small dorsal process; it is distally well exposed in intact fish, partly because the lachrymal is very narrow, reaching caudad to below middle of orbit.

The branchial skeleton is relatively compact, nearly as in cichlasomines, and the first epibranchial relatively short. The gill-rakers are as in *Cichla*, but much shorter; 3 epibranchial and hypobranchial rakers externally on the first arch, also a hypobranchial on succeeding arches.

Tooth-plates are missing from the fourth ceratobranchial. Uniquely among South American cichlids, the fourth epibranchial is not particularly widened medially. All four gill-arches carry cichlasomine-like microgillrakers externally, there may also be some internally on the fourth arch. Interarcual cartilage of modal form.

The lips both have continuous folds, and resemble most closely those of chaetobranchines.

The fins are naked except the basal third of the caudal-fin.

The rostral process on the distal postcleithrum is prominent though short and blunt.

The branchial skeleton is relatively light and the absence of fourth ceratobranchial tooth-plates, and the few epibranchial rakers are notable. Whereas the lower pharyngeal tooth-plate is wide, about as in cichlasomines, the ventral (fifth ceratobranchial elements) ridges are weakly developed. Hypobranchial gill-rakers and the microgillraker set, probably also the gill-raker shape are best interpreted as ancestral.

The axial skeleton is regressed with only 12+12 or 11+13 vertebrae. A parhypurapophysis is lacking, but there are two supraneurals. The dorsal urohyal apophysis is spine-like and dorsad pointing.

Travassos & Pinto (1959) re-described *A. nassa*, also considering jaw and branchial osteology, with figures. They show the dental with five ventral foramina, and the jaw teeth very large, otherwise their fish conform reasonably with mine.

The relationships of *Acaronia* cannot be pinpointed, but appear to be with chaetobranchines. Jaw structures, teeth and lips are similar, but the branchial skeleton, microgillrakers, gill-rakers, and lateralis system are drastically different. The regressed axial skeleton, absence of parhypurapophysis, only three procurrent caudal-fin rays, raised coronalis foramen, absence of fourth ceratobranchial tooth-plates, and, in part, naked fins, are shared, but not unique derived states. The several primitive traits such as the long slender jaws, continuous lip folds, hypobranchial gill-rakers, the light ceratobranchial support of the lower pharyngeal tooth plate and unequally distributed states such as first gill-arch microgillrakers, many epibranchial gill-rakers, relatively slender fourth epibranchial and postcleithral process provide some reason for giving weight to not unique character states. The elevated coronalis canal, albeit related to the long premaxillary fossa, and the maxillad premaxillary processes, albeit a stronger found in *Caquetaia*, are proposed as synapomorphies of *Acaronia* + chaetobranchines.

Although it is possible that the widely distributed *A. nassa* is a group of similar geographical species, there is no evidence supporting recognition of more than one form in the Amazonas and Guianas. However, a single sample from a caño between the rivers Tauca and Tiquira on the Maripa-Ciudad Bolívar carretera evidently represents an undescribed species, easily distinguished from *A. nassa* by immaculate caudal-fin, large midlateral spot, and continuous suborbital stripe.

Acaronia in many ways resembles cichlasomines, yet I think that the jaw and branchial structures exclude the possibility of closer relationship. The preopercular lateralis foramina are very large, and whereas in *Cichlasoma* loss of clpop 2 is

likely, the rostral preopercular foramen in *Acaronia* may be the result of fusion of clpop1 and 2. As the predorsal scale pattern is irregular and the number of predorsal midline scales is variable, I do not consider the yet low number as anything but a convergence tied to an increased scale size. Squamation features of *Acaronia* are autapomorphic as this is the only large cichlid that has such reduced squ. long. count; in all other cichlid low squ. long. counts (ie. large scales) are correlated with small size; the same may be said of vertebral number.

AEQUIDENS

Astronotus (Aequidens) Eigenmann & Bray, 1894. *Ann. N.Y. Acad. Sci.* 7: 616 (type by original designation *Acara tetramerus* Heckel). - Masculine.

Aequidens chimantanus Inger, 1956. *Field. Zool.* 34, p. 437, Fig. 94 (Rio Abacapa on the west side of Chimantá-tepui; 1,300 feet altitude).

Acara diadema Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 344 (einem Ygarapé oder Waldbache bei Marabitanos).

Aequidens metae Eigenmann 1922. *Mem. Carneg. Mus.* 9, p. 241, pl. XXX, fig. 2 (Barrigón); Eigenmann 1922. *Boln Soc. colomb. Cienc. nat.* 9, p. 198 (Barrigona, Río Meta).

Acara pallidus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 347 (Rio-negro).

Aequidens duopunctata Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 338, Pl. LVI (Manaos).

Aequidens stollei Ribeiro, 1918. *Commissão Linhas telegr. estrat. Matto Grosso Amazonas Publ.* (46) p. 13, Pl. V, fig. /3/ (Rio Jamary).

Acara tetramerus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 341 (Rio-branco).

Chromys uniozellata Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 15, Pl. 6, fig. 1 (Rio Ucayale, mission de Sarayacu).

Acaronia trimaculata Allen in Eigenmann & Allen, 1942. *Fish. West. South Amer.*, p. 389, Pl. XXII, fig. 8 (Iquitos).

Acara viridis Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 343 (in den durch das Anschwellen der Flüsse gebildeten Waldlachen.....in einer derselben bei der Stadt Matogrosso liegenden und Juquiã...genannten).

Aequidens awani Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 335, Pl. LV (São Antonio de Guaporé, Rio Guaporé).

Aequidens guaporensis Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 335, Pl. LIV (São Antonio de Guaporé).

Aequidens, as restricted in Part I, is virtually what older authors called *Acara tetramerus*. *Aequidens tetramerus*-like forms are still a problem, forming probably a geographical species complex. But other species are very distinctive.

Aequidens metae is endemic to the upper R. Meta system. *Aequidens pallidus* is a lower R. Negro form. Travassos & Pinto's (1958b) study of *Ae. tetramerus*, is apparently based on *Ae. pallidus*. *Aequidens diadema* is taken in the upper R. Negro and Orinoco. *Aequidens tetramerus* (Pl. XV, fig. 1) occurs at least in the R. Branco and Guianas, but Central Amazonian material is doubtful. *Aequidens uniozellatus* is endemic to Peruvian Amazonia. *Aequidens stollei* needs fresh material to be checked against *Ae. tetramerus*. Of undescribed species there is a strikingly barred species in the upper Paraguay system, a metallic green species in the R. Nanay, a colourful endemic in the Carahuayte at Jenaro Herrera on the Ucayali, and the species figured by Lüling (1980c), which is endemic to the Aguaytia and Pachitea.

The aberrant form *Ae. viridis* is endemic to the R. Guaporé. *Aequidens chimantanus* appears restricted to the type-locality area.

APISTOGRAMMA

Apistogramma Regan, 1913. *Ann. Mag. nat. Hist. (B)* 12, p. 382 (nom. nov. pro *Heterogramma* Regan). - Feminine.

Heterogramma Regan, 1906. *Ann. Mag. nat. Hist. (7)* 17, p. 60 (type by subsequent designation by Eigenmann (1910) *Mesops taeniatus* Günther). - Feminine.
Pintoichthys Fowler, 1954. *Archos Zool. S. Paulo* 9, p. 316, 386-387 (type by original designation *Biotodoma trifasciatus* Eigenmann & Kennedy). - Masculine.

Geophagus (Mesops) Agassizii Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 71, p. 111, Pl. VIII, fig. 2 (Curupira..., Cudajas..., Rio Puty..., Lago Maximo...See Manacapuru).

Geophagus amoenus Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 250 (River Ambyacu).

Apistogramma pertense var. *bitaeniata* Pellegrin, 1936. *Bull. Soc. natl. Acc-lim. Fr.* 83, p. 56 (Rio Madeira (Brésil)).

Apistogramma klausewitzii Meinken, 1962. *Senckenberg. biol.* 43, p. 138, Abb. 1 (Brasilien, oberer Rio Solimões, Igarapé Preto).

Apistogramma kleei Meinken, 1964. *Aquar. Terrar. Z.* 17, p. 293, fig. p. 295 (unbekannt).

Heterogramma Borellii Regan, 1906. *Ann. Mag. nat. Hist. (7)* 17, p. 63 (Carandasiño, Matto Grosso).

Heterogramma rondoni Ribeiro, 1918. *Comissão Linhas telegr. estrat. Matto Grosso Amazonas. Publ.* (46), p. 16, Pl. XI (Caceres, na Caiçara (Campina)).

Apistogramma reitzigi Mitsch, 1938. *Aquarium, Berl.* 1938, p. 181 (Wahrscheinlich mittleres Südamerika).

Heterogramma ritense Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 62, Pl. LXX (Santa Rita, Rio Santa Rita of the Paraguay basin).

Apistogramma aequipinnis Ahl, 1938. *Zool. Anz. Leipz.* 123, p. 246 (vermutlich Argentinien).

Apistogramma brevis Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 107, Fig. 13 (Petit Igarapé du Lago Peneda, rive droite du Uaupès, État d'Amazonas, Brésil. (0°01'N 67°21'W)).

Apistogramma cacatuoides Hoedeman, 1951. *Beaufortia* (4), p. 1, fig. p. 3 (near Paramaribo, Dutch Guiana).

Apistogramma caetei Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 76 (Igarapé in Bragança (Estado do Pará, Brazil; 1°45'S 46°47'W)).

Heterogramma commbrae Regan, 1906. *Ann. Mag. nat. Hist. (7)* 17, p. 64 (Carandasiño, Matto Grosso; Colonia Rizzo).

Heterogramma corumbae Eigenmann & Ward, in Eigenmann, McAtee & Ward, 1907. *Ann. Carneg. Mus.* 4, p. 146, Pl. XLV, fig. 3 (Corumba).

Heterogramma commbrae /Regan/, 1906. *Ann. Mag. nat. Hist. (7)* 17, p. viii (unjustified emendation of spelling).

Heterogramma corumbae A. Ribeiro, 1918. *Archos Mus. nacl Rio de J.* 21, p. 132 (unjustified emendation of spelling).

Apistogramma elizabethae Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 103, Fig. 12 (Igarapé affluent de la rive droite du Uaupès à Trovaó (environ 20 km en amont de

l'embouchure de Uaupés), État d'Amazonas, Brésil. (0°02'N 67°26'W.)).

Apistogramma eunotus Kullander, 1981. *Bonn. zool. Beitr.* 32, p. 184, Fig. 1 (Peru, Depto. Loreto, R. Ucayali system, near Pucallpa, on road to Aguaytia, "Dunkelwasser bei 'Campo Verde'").

Apistogramma geisleri Meinken, 1971. *Senckenberg. biol.* 52, p. 35, Abb. 1 (Amazonas-Gebiet, Rio Curuçamba bei Obidos).

Apistogramma gephyra Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 131, Fig. 17 (Igarapé affluent de la rive gauche du Rio Negro, dans l'Archipel des Anavilhanas, État d'Amazonas, Brésil. (3°00'S 60°45'W.)).

Apistogramma gibbiceps Meinken, 1969. *Senckenberg. biol.* 50, p. 91, Abb. 1 (Brasilien, wahrscheinlich Gebiet des Rio Negro).

Apistogramma gossei Kullander, 1982. *Cybium* (3) 6: 65, Fig. 1 (Brasil, terr. Amapá, R. Oyapock system, Martinique).

Apistogramma hippolytae Kullander, 1982. *DCG-Informn* 13, p. 182, Fig. 1 (Brasil, est. Amazonas, Rio Solimoes System, Igarapé des Lago Manacapuru).

Apistogramma hoignei Meinken, 1965. *Senckenberg. biol.* 46, p. 258 Abb. 1 (Zufüsse der Sümpfe am Unterlauf des Rio Portuguesa westlich der Orte Sta. Rosa und Camaguan, an der Autostrasse von Calabozo am Südende der seenartigen Erweiterung 'Embalse del Guárico' des Rio Guárico nach San Fernando am Mittellauf des Rio Apurè, im Staat Guárico, Venezuela).

Apistogramma hongsloui Kullander, 1979. *Zool. Scr.* 8, p. 74, Fig. 5 (Finca Boca de Guarrojo (small laguna closest to the houses of the finca), R. Guarrojo, Vichada, Colombia (4°07'N 70°45'W)).

Apistogramma inconspicua Kullander, 1983. *Zool. Scr.* 11, p. 307, Fig. 1 (Bolivia, depto. Santa Cruz, R. Paraguay system, small pool of the R. Candelaria, above bridge on road Carmen-Santa Rosa (16°00'S 61°40'W)).

Apistogramma iniridae Kullander, 1979. *Zool. Scr.* 8, p. 76, Fig. 7 (Pueblo Bretania (Yuri Bajo), Caño (Río) Bocón, depto. Guainía, Colombia (3°39'N 68°05'W)).

Apistogramma luelingi Kullander, 1976. *Bonn. zool. Beitr.* 27, p. 259, Fig. 1 (Kleine Quebrada unterhalb Todos Santos (Bolivien)).

Apistogramma macmasteri Kullander, 1979. *Zool. Scr.* 6, p. 70, Fig. 1 (Finca La Ponderosa (on the road to Restrepo), Villavicencio, depto Meta, Colombia. Stream... at the foot of the Cordillera (4°15'N 73°35'W)).

Apistogramma meinkeni Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 119, Fig. 15 (Igarapé affluent de la rive droite des Uaupés (environ 20 km en amont de l'embouchure des Uaupés), Trovao, État d'Amazonas, Brésil. (0°02'N 67°26'W.)).

Apistogramma moae Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 61, Fig. 9 (Igarapé São Salvador, affluent rive gauche du Rio Moa, Cruzeiro-do-Sul. État de Acre. Brésil. (7°38'S 72°36'W.)).

Apistogramma nijsseni Kullander, 1979. *Revue suisse Zool.* 86, p. 938, Fig. 1 (Peru (Loreto), R. Ucayali system, Jenaro Herrera, R. Copal, "marigots des Tupacs").

Heterogramma ortmanni Eigenmann, 1912. *Mem. Carneg. Mus.* 5, p. 506, Pl. LXVIII, fig. 1 (Erukin).

- Apistogramma parva* Ahl, 1931. *Sber. Ges. naturf. Fr. Berl.* 1931, p. 210 (Rio Capim).
- Apistogramma personata* Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 111, Fig. 14 (Rio Uaupès à Assai, État d'Amazonas, Brésil (0°02' N 67°27'W)).
- Heterogramma taeniatum pertense* Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 359, Pl. LXVI (Manaos).
- Apistogramma piauiensis* Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 79, Fig. 11 (Brésil: Piauí, Lagoa Seca, about 1 km from camp on Rio Parnaíba at Barra do Longa (near Buriti dos Lopes). (3°08'S 41°54'W)).
- Heterogramma pleurotaenia* Regan, 1909. *Ann. Mag. nat. Hist. (8)* 3, p. 270 (La Plata).
- Apistogramma pulchra* Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 135, Fig. 18 (Rio Preto, affluent de la rive gauche du Rio Candeias a 25 km de Porto-Velho, Territoire du Rondonia, Brésil. (8°46'S 63°45'W)).
- Apistogramma regani* Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 65, Fig. 10 (Igarapé affluent de la rive gauche du Rio Negro, dans l'Archipel des Anavilhanas, État d'Amazonas, Brésil. (3°00'S 60°45'W)).
- Apistogramma reticulosa* Kullander, 1980. *Bull. zool. Mus. Univ. Amsterd.* 7, p. 158, Fig. 1 (Brasil, Estado do Amazonas, R. Madeira drainage system, Igarapé Xicanga, about 5 km W of Humaitá (07°31'S 63°04'W)).
- Apistogramma roraimae* Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 138, Fig. 19 (Igarapé Uazinho a environ 20 km de Boa Vista sur la route Boa Vista-Cacarai, Territoire du Rio Branco, Brésil. (2°49'N 60°40'W)).
- Apistogramma ortmanni rupununi* Fowler, 1914. *Proc. Acad. nat. Sci. Philad.* 66, p. 277, Fig. 19 (Rupununi River, British Guiana).
- Heterogramma steindachneri* Regan, 1908. *Ann. Mag. nat. Hist. (8)* 1, p. 370, fig. p. 371 (Georgetown, Demerara).
- Apistogramma ornatipinnis* Ahl, 1936. *Sber. Ges. naturf. Fr. Berl.* 1936, p. 141 (Britisch-Guiana).
- Apistogramma wickleri* Meinken, 1960. *Intl. Revue ges. Hydrobiol.* 45, p. 655, Abb. 1 (Anzunehmen ist, dass die Tiere aus den Guayana-Ländern eingeführt wurden).
- Apistogramma sweglesi* Meinken, 1961. *Aquar. Terrar. Z.* 14, p. 136, fig. p. 137 (...Wasserläufen bei Letitia in Peru).
- Mesops taeniatus* Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 312 (River Cupai (800 miles from the sea)).
- Biotodoma trifasciatus* Eigenmann & Kennedy, 1903. *Proc. Acad. nat. Sci. Philad.* 1903, p. 536 (Arroyo Chagalalina).
- Apistogramma trifasciatum harald schultzi* Meinken, 1960. *Aquar. Terrar.* 7, p. 291, Abb. 1 (Oberer Guaporé, auch Itenes genannt, im Norden des Staates Matto Grosso).
- Heterogramma trifasciatum macillense* Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 360, Pl. LXII, fig. 2 (São Antonio de Guaporé).
- Apistogramma uaupesi* Kullander, 1980. *Bonn. zool. Monogr.* 14, p. 122, Fig. 16 (Igarapé affluent de la rive droite des Uaupès (environ 20 km en amont de l'embouchure des Uaupès), Trovao, État d'Amazonas, Brésil. (0°02'N 67°26'W)).

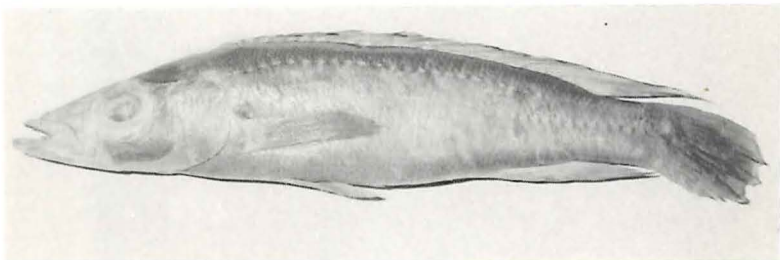
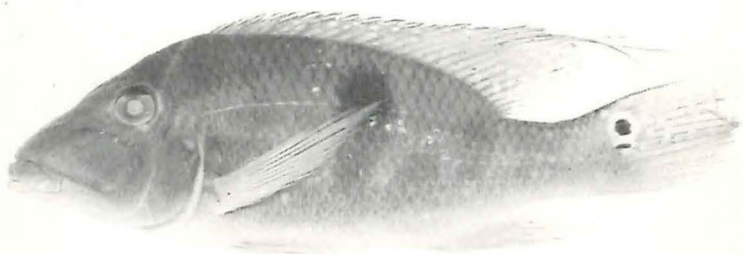
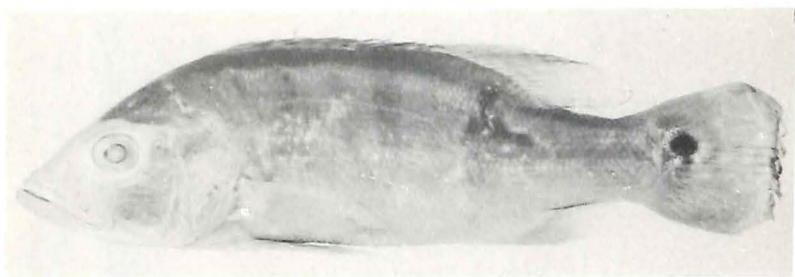
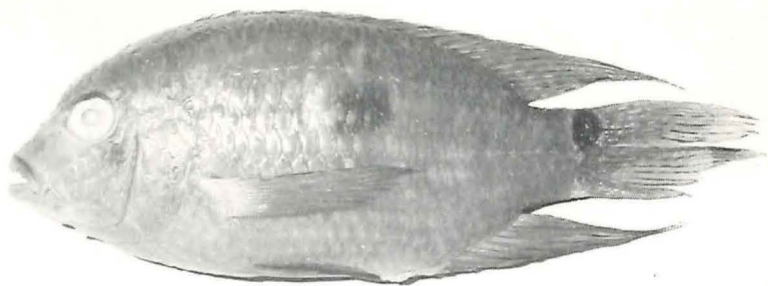
Plate XV

Fig. 1. *Aequidens tetramerus*. Holotype, NMW 33757-33758t., 125.7 mm SL.

Fig. 2. *Cichla ocellaris*. Holotype, ZMB 2839, 183.4 mm. Photo Anita Hogeborn.

Fig. 3. *Satanoperca* sp. aff. *daemon*, from the R. Trombetas system. IRSNB unreg. (SOK 20), 193.2 mm SL.

Fig. 4. *Crenicichla macrophthalma*. Syntype, NMW 33082. 198.3 mm SL.



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Apistogramma viejita Kullander, 1979. Zool. Scr. 8, p. 73, Fig. 3 (Caño, affluent of Rio Yucao, depto Meta, Colombia. About 500 m westwards along the road Puerto Gaitán-Puerto López from a laguna midway between Rio Yucao and Rio Manacacías, 300 m from the road (4° 20' N 72° 09' W)).

This group was recognized by Pellegrin (1904; *Biotodoma*) and Regan (1906a; *Heterogramma*) on the closer approximation of the upper lateral line to the dorsal-fin origin as compared to *Geophagus*. That character state apparently is only an expression of small size, which was probably the real but not so sophisticated-sounding defining character state, and few, relatively large trunk scales. Geophagines of intermediate size (*Papiliochromis*) have also an intermediate lateral line position.

Recently (Kullander 1980b) I proposed instead the characterization: 1) gill-rakers on the fifth ceratobranchials; 2) first epibranchial lobe, with marginal rakers; 3) three, rarely four or six anal-fin spines, 4) 14-18 dorsal-fin spines.

These character states help to distinguish from all other geophagines except, as I found, *Gymnogeophagus*, *Margaritacara* and *Gallochromis*. But none of them is unique and none decidedly advanced.

Apistogramma species are distinguished from most other geophagines by low counts, eg. 12+12-13 vertebrae (cf. c. 30 in large forms), but they likely follow with small size; the largest species, *A. steindachneri* grows to 65 mm SL (ZMA 107.008; many hundred specimens of the species examined).

Other reductions, eg. the many or almost exclusively pored lateral line scales, absence of dorsal and ventral caudal-fin lateral lines, absence of microgillrakers, parhypural spine, only three procurrent caudal-fin rays in each lobe, in several species naked anterior chest and ventral cheek, also likely relate to size. The infraorbitals show much variation with regard to loss and coalescence, but at least two canal-bearing bones are present and they frequently have narrow ventral laminar extension.

Gill-rakers are few or absent externally on the first ceratobranchial, but I am not sure whether this is merely a reduction dependent on size, as many other small cichlids have gill-rakers all along the edge of the first ceratobranchial. Absence of fourth ceratobranchial teeth, and the single supraneural are shared with many larger cichlids, eg. *Satanoperca* among geophagines. The rostral process of the distal postcleithrum is small, but comparable to that of larger geophagines. Also the anguloarticular has a long pointed rostrad directed ventral process, and there are five dental lateralis foramina. Like *Taeniacara* and *Nannacara*, *Apistogramma* species have the alveolar premaxillary process toothed along its length, whereas larger geophagines have reduced jaw dentition.

Fifth ceratobranchial rakers are poorly developed.

The axial skeleton is particular for the absence of hypapophyses and the one or two epipleural ribs over the anterior caudal vertebrae.

The primary synapomorphy, however, appears to be the independent skin opening of the caudal anguloarticular foramen. Compared to other cichlids, it has a more central position, but there is among geophagines a tendency for this foramen to open laterad rather than caudad. Two species, viz *A. borellii* and *A. trifasciata*, depart in lacking completely an anguloarticular lateralis canal.

As these two species, both in the Paraguay system, also otherwise tend to be more reduced, they likely represent a further development. *A. borellii*, however has rather elevated median frontal crests, which I would consider plesiomorphic. *Taeniacara* also lacks the anguloarticular canal, but in addition lacks also the caudal--most dental foramen.

External characters of some interest include the continuous lower lip fold shared with *Satanoperca acuticeps* among larger geophagines and the frequent caudal spot. Along with the edentulous fourth ceratobranchial, single supraneural, fifth ceratobranchial rakers, isospondyly, absence of pleural ribs from hemal spines, relatively larger scales, they suggest that *Apistogramma* may be closer to *Satanoperca*, *Margaritacara* or *Gallochromis* than to remaining larger geophagines.

Most species listed above have been described or re-described recently. Meanwhile I also collected topotypes of *A. taeniata* and find it very little different from

species like *A. geisleri* or *A. regani*. I also made an attempt to collect *A. amoena* at Pebas. Of the three species of *Apistogramma* obtained, *A. agassizii*, *A. eunotus*, and *A. cacatuoides*, the first mentioned is the only one close to Cope's description of *A. amoena*, by its dark dorsal-fin base. It seems therefore likely that *A. amoena* is a senior synonym of the well-known *A. agassizii*. This probability should be recognized but there is no point in using *amoena* as a senior synonym of *agassizii*, both because *A. agassizii* as a wide-spread form eventually may be shown to consist of distinct populations requiring names whereby both names might become valid, and because the proper action if positive evidence of the identity of *agassizii* and *amoena* were available, would be to suppress *amoena* in favour of *agassizii* as a well-known name.

Further work with *Apistogramma* has been limited to species descriptions (Kullander 1979b, 1980a, 1981b, 1982a,b,d, 1983a). There are still many species to be described, among them several aberrant forms.

In my 1980b paper I divided the genus into species groups. Later work (especially 1982a, 1983a) has led to some reorganization, and I am not satisfied with polarities in the few characters used. Contrary to what I once suggested, I think now that lyrate caudal-fin shape in males, as closer to the general geophagine condition, is more likely ancestral, despite the more spectacular condition on such small fishes. Finding *A. cacatuoides* and *A. luelingi* females with truncate-emarginate caudal-fin supports a revised view that modest finnage among *Apistogramma* species is a more advanced condition than the several instances of elongated marginal caudal-fin rays or dorsal-fin lappets. Most other characters used to define groups are reductive and may be expected to appear in parallel in minute cichlids. Alone some chromatic and dental traits would seem still to hold.

The group is morphologically diverse enough to invite to splitting. Recognition of the merely more reduced *Taeniacara* is questionable in view of the variation amongst *Apistogramma*. There is a shortage of reliable characters, however, and no more extensive phylogeny is in sight.

Re-examination of the types of *A. rupununi* shows these to be adult males, and with rounded caudal-fin they cannot be *A. steindachneri* (cf. Kullander 1980b); with more restricted flank spot than *A. hippolytae*, they represent a third named species in the *A. steindachneri* group.

Schmettkamp (1982) recently summarized, for popular use, taxonomic and behavioral data on *Apistogramma* and figured several undescribed species. No wild material is available of species described by Schmettkamp as Blutkehl, Rotkehl, Glanzbinden, Orangeflossiger, Schwarzaum, and Segelflossen, but Glanzbinden shows great resemblance to Meinken's *A. sweglesi*, the types of which are lost. Schmettkamp's Doppelbinden has been collected in the middle R. Negro, the Rotpunkt, a *macmasteri* group species without produced dorsal-fin lappets is collected in the Ariari in Colombia; Breitbinden comes from the R. Inírida system. Collections in new areas continue to yield new *Apistogramma* species. One from the Araguaia, similar to *A. caetei*, and a minute species from the upper Xingu, are the first to be reported for the Brazilian highland rivers. The La Plata basin (Kullander 1982c) and Guianas (*A. steindachneri*, *A. ortmanni*, *A. rupununi*, *A. gossei*) are unlikely to yield more species, but some *regani*-like forms remain to be described from Central Amazônia, one more *macmasteri* group form has been taken in the lower Orinoco system, and there are at least three more species in Bolivia, and one common to the Putumayo and middle Napo. Several undescribed species come from the R. Negro, which seems to be particularly rich in these small fishes.

APISTOGRAMMOIDES

Apistogrammoides Meinken, 1965. *Senckenberg. biol.* 46, p. 48 (type by original designation *Apistogrammoides pucallpaensis* Meinken). - Masculine.

Apistogrammoides pucallpaensis Meinken, 1965. *Senckenberg. biol.* 46, p. 48, Fig. 1 (Bach kurz ausserhalb der Vorstadt von Pucallpa, Peru, der in den Ucayali mündet).

The single species of the genus reaches c. 30 mm in the wild, i.e. in still waters along the Ucayali from Pucallpa northwards and Peruvian R. Amazonas downstream to Isla Santa Sofia. There are several unique colour traits, notably the three spots on the caudal-fin base, forming sort of an ocellus, dark caudal peduncle end, very thin lateral band and a second faint band along the back. The head is much wider than in any *Apistogramma*, and with the blunt front, the head shape is unique among geophagines. The most striking characteristic is, however, the long anal-fin, reaching much further forward on the body than in other geophagines.

Although Meinken counted eight anal fin-spines in his four specimens, I find seven in three and eight in only one. Seven is actually the modal number, eight occasional, six or nine exceptional. There are many other errors in Meinken's description that give a very wrong impression of the species and its characters. Many of the teeth on his Abb. 2 are only papillae; there is also a lobe, albeit small, on the first epibranchial; and of course *Apistogrammoides* like all cichlids have only five pelvic-fin rays, not six. I have not studied the osteology of this form, but place it anyway tentatively closest to *Apistogramma*, as it has the same anguloarticular pore arrangement. The long anal-fin is not a synapomorphy shared with *Cichlasoma*, but may be an autapomorphy among geophagines. *Apistogramma luelingi* has, however, usually four anal-fin spines (Kullander 1976) and *A. commbrae* frequently four instead of three (Kullander 1982a). The wide head and unique caudal-fin pattern do as *ad hoc* autapomorphies. Interestingly a similar caudal peduncle marking, and a relatively narrow lateral band are also shown by *commbrae*-like species (Kullander 1983).

ASTRONOTUS

Crenilabrus (Astronotus) Swainson, 1839. *Nat. Hist. Fish.* 2, pp. 173, 229 (type by monotypy *Lobotes ocellatus* Agassiz). - Masculine.

Acara Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 338 (type by subsequent designation by Gill (1858), *A. crassipinnis* Heckel). - Masculine.

Hyrogonus Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 303 (type by monotypy *Lobotes ocellatus* Agassiz). - Masculine.

Lobotes ocellatus Agassiz, 1831, in de Martius, *Sel. Gen. Sp. Pisc. Bras.* p. 129, Pl. LXVIII (Oceano Atlantico).

Acara crassipinnis Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 357 (... Rio-Paraguay... in Buchten bei Villa Maria und Caiçara...Rio-Guaporê bei Matogrosso, im Rio negro und im Rio-branco).

Cychla? rubro-ocellata Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 153, Pl. 10 (Rio Negro and its tributaries).

Acara compressus Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 256 (Ambyiacu).

Acara hyposticta Cope, 1878. *Proc. Amer. philos. Soc.* 17, p. 697 (/Amazonian Peru/).

Astronotus ocellatus var. *zebra* Pellegrin, 1904. *Mém Soc. zool. Fr.* 16, p. 183 (Santarem).

Astronotus orbiculatus Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 331, Pl. LIII (Santarem).

This is evidently a relatively primitive form, differing from chaetobranchines and *Cichla*, however, in more compacted branchial skeleton and strong, fixed teeth.

Upper and lower lips folds interrupted medially; lower lip attachment as in *Cichla*. Gill-raker counts 2-4+1+8-10 externally on first arch, the upper ceratobranchials villiform, the lower knob-like, like the other rakers, in large adults short, blunt, with numerous small teeth apically. No teeth on fourth ceratobranchial. First epibranchial short, rather stout, without ventral lamina, second with wide ventral laminal expansion. First pharyngobranchial slender, little widened ventrally; interarcual cartilage minute. Second pharyngobranchial rostral to third, with lateromedial orientation, toothed. Fourth upper tooth-plate separate from pharyngobranchial 3. Pharyngobranchial 3 with well developed dorsal apophysis. Jaw and pharyngeal jaw

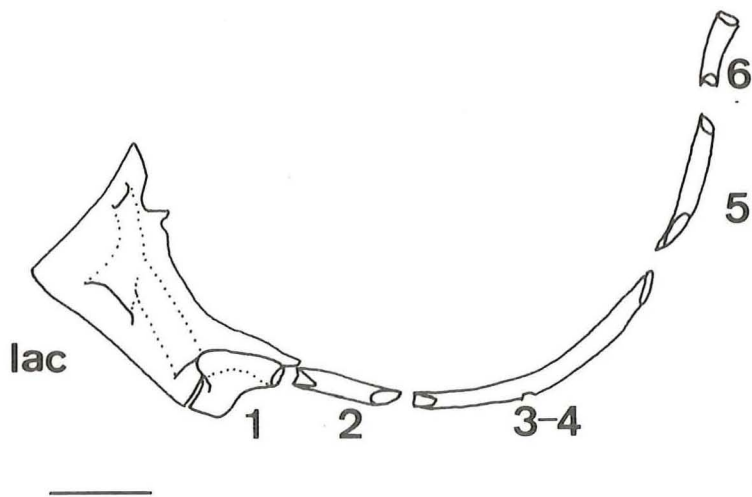


Fig. 101. *Astronotus ocellatus*. Lateral aspect of left side suborbital series of a 38 mm specimen (NRM 11311, Alizarin 46). In large specimens the ends of infraorbitals make contact. Scale 1 mm; infraorbitals numbered.

teeth strong, fixed; lower pharyngeal jaw with about six cross-series of teeth. Pre-maxilla and dental each externally with a series of strong pointed teeth and a narrow inner band of very small, otherwise similar teeth; all teeth, also those of the pharyngeal jaw (which similar in shape to those of *Cichlasoma*) fixed; already formed teeth submerged in tooth-bearing bones near toothed surfaces. There are five dental, two anguloarticular, seven preopercular foramina in the preoperculo-mandibular lateralis series. The suborbital series (Fig. 101) consists in a strong, narrow lacrimal with only three lateralis canal foramina, the posterior with a joint ventrad opening with that of the curved dorsal canal of the contiguous otherwise laminar first infraorbital; posterior to these run four tubiform infraorbitals, the second of these with a median opening. The coronalis foramen is simple and not elevated; of the rostral frontal foramina the posterior lies slightly lateral and caudal on the canal leading to the adnasal.

The skull is relatively wide with low supraoccipital and frontoparietal crests. The sphenotic has a wide (triangular as seen in lateral view) lateral surface, flattened, but cupped centrally, where the 6th infraorbital is positioned.

No rostral directed spinous process on distal postcleithrum. Urohyal with moderate rostrocaudal directed anterior truncated process. Ascending and alveolar processes of premaxilla of equal length; large rostral foramen medially between medial and articular ascending processes.

15+16 vertebrae; hypapophyses on fourth (paired), and fifth (dextral) contacting each other apically. Two supraneurals. Caudal-fin with three procurrent, eight principal rays in each lobe. Two epurals, five hypurals; parhypural spine only a small nipple. Pectoral-fin broad, with 15 rays, fifth longest in juveniles, fourth in adults, never scaly. First pelvic-fin ray longest; both sides scaly anteriorly in large specimens. Soft dorsal-, anal-, and caudal-fin with very dense layer of scales, to near ray tips in adults. D. XI-XIV.18-21; A. III.15-17.

Lateral lines well separated, by three horizontal scale series. Triradiate caudal-fin lateral line, with short axial branch; dorsal branch between rays D 3-4, ventral between rays V4-5, neither beyond middle of fin. Cheek squamation divided by a narrow naked stripe back from mouth angle, not reaching preopercle. Gill-cover scales small; preoperculum naked. Predorsal scale-pattern stochastic. Prepelvic scales small. About 30 scales around caudal peduncle. Scales cycloid on head, anterior sides, back, chest and preventrally. Squ. long. 34-39.

A prominent ocellus on caudal-fin base just above lower lateral line. A dark stripe on naked cheek line.

Astronotus is decidedly a more primitive cichlid than *Cichlasoma*, but it has several interesting missing link characters, is, for instant, intermediate in the lacrymal-first infraorbital relation. Whereas clearly advanced over *Cichla*, there is some difficulty finding an apomorphy for *Astronotus* in relation to cichlasomines. But in any case, the specific association with *Aequidens*, to be learned from Regan, is not verified by the character states listed above.

I recently (Kullander 1981d) described juveniles and discussed the synonymy and distribution. Local variation is confirmed by later material, so that the monotypy of the genus is questionable.

AUSTRALACARA n. gen.

Type species: *Chromis facetus* Jenyns.

Chromis facetus Jenyns, 1842, in Darwin, Zool. Voy. *Beagle* 4, p. 104 (Maldonado, Rio Plata).

Chromys oblonga Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 14 (le Tocantins (Province de Goyaz)).

Heros autochthon Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 299 (Brazil).

Heros Jenynsii Steindachner, 1869. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 60, p. 292, Pl. II (Umgebung von Montevideo).

Heros acaroides Hensel, 1870. *Arch. Natges.* 36, p. 54 (Bei Porto Alegre in stagnirenden Gewässern).

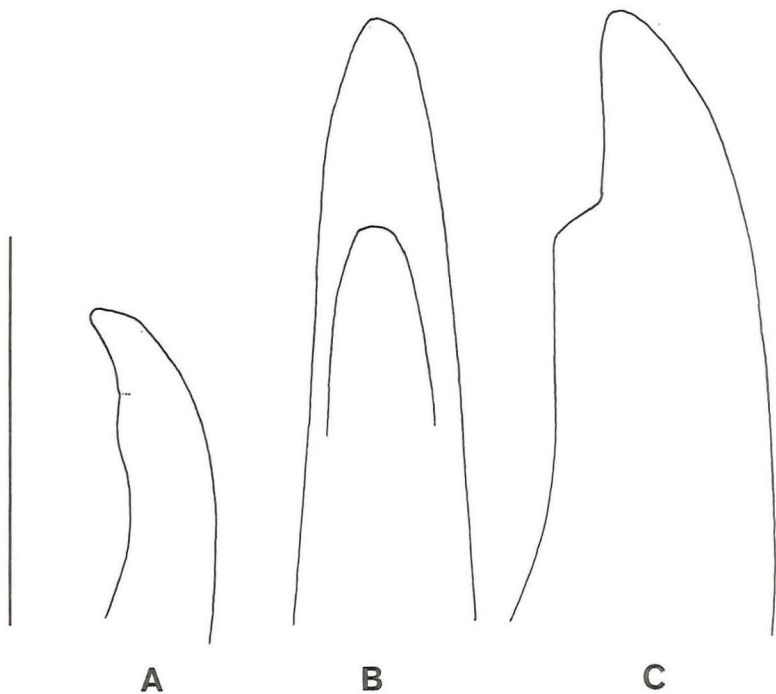


Fig. 102. *Australacara faceta*. Lower jaw teeth. A, inner anterior in lateral aspect (retrorse); B, adsymphyseal labiad series tooth in lingual aspect; C, tooth in B in lateral aspect. Scale 1 mm. From ZFMK unreg., 124 mm SL.

This species has already been discussed in Part I, where the genus is referred to as 'Section 3'. The gender of the generic name, which refers to the distribution, is feminine. The characteristic teeth are figured in Fig. 102. I have not seen the type of *C. facetus*, which may be in Cambridge, U.K. Regan's (1905e) *C. oblongum*, and MNHN material of the same origin, are oblong chiefly because they are starved aquarium specimens. The type of *C. oblonga* is in an extremely bad condition, but agrees in verifiable characters with Brazilian-Uruguayan coast *Australacara*. The distribution suggests, however, that geographical species may be distinguished (coastal rivers of Brazil and Uruguay from the Paraíba do Sul to Rio de la Plata; also the Paraná inferior, medio, superior, and Alto Paraná; the type of *oblonga* is said to come from the Tocantins).

Werner (1981) and Stawikowski (1982) have descriptions of breeding in aquaria, with colour photos. Unlike *Cichlasoma*, *A. faceta* hang the larvae to surface-close substrates, possibly an adaptation to breeding in oxygen-poor waters; reversely to other cichlids, free-swimming juvenile *A. faceta* assemble close to the surface when the light is out. *Herotilapia multispinosa* occasionally place their larvae on vertical surfaces (Baylis 1974); it is normal to *Symphysodon* and *Pterophyllum* which also spawn on elevated surfaces.

Heros oblongus Günther (1869) from R. Motagua, was re-named *Cichlasoma Güntneri* by Pellegrin (1904). The latter name should stand, as *guentheri*.

BATRACHOPS

Batrachops Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 432 (type by subsequent designation by Eigenmann & Bray (1894), *B. reticulatus* Heckel). - Masculine.

Boggiana Perugia, 1897. *Ann. Mus. civ. Stor. nat. Genova* (2) 18, p. 148 (type by original designation *B. ocellata* Perugia). - Feminine.

Crenicichla cyanonotus Cope, 1870. *Proc. Amer. philos. Soc. Philad.* 11, p. 569 (Upper Marañon, near Pebas).

Crenicichla elegans Steindachner, 1882. *Denkschr. k. Akad. Wiss. Wien Math-natw. Cl.* 44, p. 15 (Hoch-Peru).

Batrachops reticulatus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 433 (Rio-negro).

Batrachops punctulatus Regan, 1905. *Proc. zool. Soc. Lond.* 1905, p. 156, Pl. XIV, fig. 1 (R. Essequibo).

Batrachops semifasciatus Heckel, 1840. *Annln wien. Mus. Natges.* p. 436 (Flusse Paraguay bei Caiçara).

Crenicichla simoni Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 345, Pl. LIX (Rio Paraguay at São Luiz de Cáceres).

Boggiana ocellata Perugia, 1897. *Ann. Mus. civ. Stor. nat. Genova* (2) 18, p. 148 (Puerto 14 de Mayo, dipartimento di Bahia Negra, nel Chaco boreale).

Acharnes Chacoënsis Holmberg, 1891. *Revta Argent. Hist. nat.* 1, p. 182 (Formosa).

The status of *Batrachops*, which stands presently unchanged since Regan, depends on the inclusiveness of *Crenicichla*. With the current understanding of the latter, there is little justification for *Batrachops*.

The teeth are in fewer series than in the majority of the *Crenicichla*, and are also all fixed and those of the outer series are stronger. The head is also considerably wider and the snout very short. Lips and nostril position are as in *Crenicichla* of the *johanna* group, but *Batrachops* have much fewer and more extremely ctenoid scales; like *johanna* group species they are also large (to about 200 mm). Until the taxonomy of *Crenicichla* is resolved the group may be provisionally recognized, and will probably remain relatively intact.

The three species are allopatric, *B. semifasciatus* found in the Paraguay and Bolivian Amazonas drainages, *B. reticulatus* in the R. Negro and Essequibo, *B.*

cyanotus in Peru. The two northern forms are more similar to each other, but the species have not been subject to phylogenetic analysis.

Batrachops semifasciatus has an impressive synonymy, with nominal species in four different genera. Whereas *C. simoni* are clearly young *B. semifasciatus*, the status of *A. chacoensis* is not definite as there are no types available. The type of *B. semifasciatus* could not be found in the NMW so I have not examined the type of *B. ocellata* either. Regan considered the latter two distinct on the basis of the extension of the maxilla, to 'beyond middle of eye' in *ocellata*, 'to below anterior margin of eye' in *semifasciatus*. He knew *semifasciatus* only through Heckel's description, and *ocellata* from personal experience. However, Heckel wrote about the mouth shape in *semifasciatus*: 'Die breite Mundspalte öffnet sich etwas über die Achse, der hintere Rand des Oberkiefers liegt vertikal unter dem vorderen, die Einlenkung des breiten wenig vorstehenden Unterkiefers beinahe unter dem hinteren Augenrand.' The 'Oberkiefer', in my interpretation is apparently not the maxilla, but the upper lip, which actually disappears under the lower lip before (in young) or about below (in adults) the anterior margin of the orbit. So there would seem to be no known difference between *B. ocellata* and *B. semifasciatus*.

BIOTODOMA

Biotodoma Eigenmann & Kennedy 1903. *Proc. Acad. nat. Sci. Philad.* 1903, p. 533 (nom. nov. pro *Mesops* Günther). - Feminine.

Mesops Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 311 (type by subsequent designation by Eigenmann & Bray (1894) *Geophagus cupido* Heckel). - Masculine.

Geophagus Cupido Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 399 (Rio-negro...Rio-Guaporè und dessen Morästen in der Umgegend von Matogrosso).

Geophagus wavrini Gosse, 1963. *Bull. Inst. r. Sci. nat. Belg.* 39 (35), p. 2, Pl. I, fig. 1 (Haut Orénoque, entre San Fernando de Atabapo et le Casiquiare).

Biotodoma species resemble *Papiliochromis*, *Acarichthys* and *Guianacara* in shape, ie. elongately ovate, but are similar to *Satanoperca* in the only three infraorbitals. Branchial skeletal features, and the median distal interhypural cartilage, are rather as in *Geophagus*, however. There are two tooth-plates on the fourth ceratobranchial and the lower pharyngeal tooth-plate is wide, with strong teeth; the first pharyngobranchial is widened ventrally; medial arms of the first epibranchial are closely approximated; microgillrakers externally on second to fourth arches. The median frontal crests are high; unusual among larger geophagines is the fifth branchiostegal ray position ventral to the anterior ceratohyal. A plesiomorphic character state emphasized by Gosse (1976) is the two supraneurals. Vertebrae 14+14. The jaw dentition forms a band. The lobe is wide, resembling that of *Margaritacara*, with short ventral marginal rakers. Ceratobranchial rakers weak, relatively few; totals 5-6+1+3-6; transverse folds moderately developed; no rakers on lower pharyngeal tooth-plate. No accessory lateral lines on caudal-fin; fins naked except caudal-fin. Opercular and pectoral girdles bones smooth. The coloration is diagnostic, plain (bluish-greyish) with a black white-margined spot posterodorsally on the side. Variation in position of the spots allows easy distinction of three species, which also of slightly different body shape. There is also a contrasting stripe from the nape interrupted by the eye, to the preopercular corner, similar to the head stripe in *Acarichthys*. Characters point to generalization, but give no clear indication of relationships.

The elongate *B. wavrini* with the flank spot below the upper lateral line, is known from a few collections in the R. Negro, R. Preto da Eva, and the Casiquiare canal. *Biotodoma cupido* is the most deep-bodied, with the spot on and above the upper lateral line, margined by a light stripe anteriorly and posteriorly. It occurs in Bolivian Amazonia and in the Ucayali-Solimões. The Guianan (Essequibo drainage) endemic has the spot on the lateral line, bordered at its best by four small light spots. It is of intermediate depth.

Cichocki (1977b) has a detailed account of the reproductive behaviour of the Guyana form.

Biotodoma nomenclature is somewhat messy. As Günther proposed the name *Me-sops* it was preoccupied by *Mesops* Audinet-Serville (1831; as *Mésops*). *Me-sops* Günther was, however, replaced for reason of homonymy with *Mesops* Billberg (1820). That name is a *nomen nudum*, but was referred to also for replacing *Me-sops* Audinet-Serville with *Mesopsis* Bolívar (1906).

BIOTOECUS

Biotocus Eigenmann & Kennedy, 1903. *Proc. Acad. nat. Sci. Philad.* 1903, p. 533 (nom. nov. pro *Saraca* Steindachner). - Masculine.

Saraca Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71*, p. 125 (type by monotypy *S. opercularis* Steindachner). - Feminine.

Saraca opercularis Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71*, p. 125 (See *Saraca* und Ausstände des Amazonenstromes bei Villa bella).

These small geophagines (to 38 mm SL) are known chiefly from Steindachner's (1875) description based on Lago Saracá and Parintins material. Later collections, from along the upper Brazilian R. Amazonas, R. Negro, R. Branco, and R. Orinoco (Bolívar State) indicate that the species is not rare, but the material is usually in bad condition.

Fernández-Yépez (1969, Fig. 5) has a habitus sketch; Goldstein (1973, p. 112) and Axelrod (1976, p. 88, lower right) colour photos of living specimens.

No study has yet been made of material from different regions, hence the monotypy of the genus is provisional.

External features include many striking reductions, but give only vague hints as to closer relationships. The shape is elongate with long, slender caudal peduncle. The fins are naked except for the base of the caudal-fin. The flank lateral lines are absent or only pored. The lacrymal has only three lateralis foramina, the dental only four, suborbitals and the distal extrascapular are lacking. Flank scales are ctenoid and small (squ. long. 28); head, belly, and thoracic scales cycloid or lacking (posterior nape, lower cheek, all or anterior prepelvic chest naked).

The dorsal-fin has seven to nine spines of subequal length, and 11 to 15 rays; A. III.7. The caudal-fin, with 16 principal rays, has a deeply emarginate hind margin, and the 8-10 procurrent rays support strong keeled basal edges. The pelvic-fin has the first ray longest.

Gill-cover and pectoral girdle bones are smooth. Vertebrae still unstudied; a single supraneural. The lobe on the first epibranchial is well-developed, but without gill-rakers; only a blunt raker between the lobe and the epi-/ceratobranchial angle, and another in the angle externally on the first arch; no rakers on the lower pharyngeal tooth-plate, and no microgillrakers. Both lip folds are discontinuous.

Preserved specimens are opaque, probably transparent in life, with a series of dark spots along the side, of which that covering most of the operculum (medial side pigmented) is most prominent; also a midlateral spot relatively strong, like a midbasal caudal spot and a spot over anterior dorsal-fin edge.

The genus is recognized on the reduced lateralis system of the head, the reduced head and chest squamation and the dorsal-fin shape. Although these character states may correlate with the small size, they may also reflect a cryptic mode of life that is suggested by the coloration.

CAQUETAIA

Caquetaia Fowler, 1945. *Proc. Acad. nat. Sci. Philad.* 97, p. 133 (type by original designation *C. amplioris* Fowler). - Feminine.

Petenia Kraussii Steindachner, 1878. *Denkschr. k. Akad. Wiss. Wien Math.-natw. Cl.* 39, p. 28, Pl. II (grossen, seeartig ausgebreiteten Cienega, welche der Magdalenen-Strom mit einem seiner ostlich gelegenen Hauptarme kurz vor seiner Mündung in das Meer bildet).

Petenia myersi Schultz, 1944. *J. Wash. Acad. Sci.* 34, p. 410, Fig. 1 (Río Dedo, tributary of the Río Ortegúaza, near Florencia (Amazon system, Colombia)).

Caquetaia amploris Fowler, 1945. *Proc. Acad. nat. Sci. Philad.* 97, p. 133, Fig. 47 (Morelia, Río Caquetá drainage, Colombia).

Acara (Petenia) spectabilis Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 71, p. 96, Pl. IV (Amazonenstrome bei Gurupa und Obidos).

? *Cichlasoma umbriferum* Meek & Hildebrand, 1913. *Field Mus. nat. Hist. Publ. (Zool.)* 10, p. 88 (Río Cupe, Cituro, Panama)

This genus consists of three moderately deep, strongly compressed, rather large species, characterized by moderately large, ctenoid scales (squ. long. 28-30), relatively small predorsal scales in a stochastic pattern, extensively scaly soft vertical fins (almost all of caudal-fin in *C. spectabilis*); scaly pectoral-fin base and pelvic-fin margin; 5 or 6, occasionally 7 anal-fin spines; rounded caudal fin; long caudal-fin lateral line sequences between rays D2 and D3, and V4 and V5 (occasionally V3 and V4); externally on first gill-arch 8-11 ceratobranchial, two epibranchial rakers, all short, denticulate, but upper ceratobranchial with lateral point; coronalis pore lacking; lips thick, wide, folds continuous; but above all the very large mouth, with extremely long ascending premaxillary processes, ventrad produced maxilla, and enlarged anterior teeth:

In a 95 mm *C. spectabilis*, head length 36.2 mm, predorsal length 40.1 mm, the ascending premaxillary processes are 24.5 mm, the alveolar 11.9 mm long; the lower jaw is 21.5 mm, the maxilla 16.9 mm long. In *C. myersi*, the ascending premaxillary processes are even longer, reaching almost to the dorsal-fin origin. The jaw dentition consists in an outer series of strong fixed, canini-form teeth, about 10 in the upper jaw, behind a few minute, about 10-15 in the lower jaw, and an inner band of extremely small teeth, some depressible. The anteriormost pair in the upper jaw is greatly enlarged and the teeth almost touch with their tips, being slightly mediad inclined; they close in the flesh of the lower lip. The teeth of the outer series of the lower jaw are stronger anteriorly than posteriorly, but the symphyseal area opposite the enlarged premaxillary teeth has only minute teeth; there are no particularly enlarged teeth in the lower jaw. The alveolar process of the premaxilla has a very well-developed blunt maxillad process. The maxilla is extended ventrad by a flattened elongated paddle-blade emerging in its full extent below a ventrorostral curved expansion of the lachrymal; reaching caudad to or almost to the posterior margin of the orbit. As the long lower jaw is not accompanied by a strong dorsal orientation and by only moderately produced snout, the interoperculum and lower limb of preoperculum are correspondingly pushed into near vertical positions.

Regan (1905e) put *C. kraussii* and *C. spectabilis* in his subgenus *Parapetenia* of *Cichlasoma*, along with Central American *Cichlasoma* with enlarged anterior teeth. Schultz (1944), revising *C. kraussii* and *C. spectabilis*, and describing *C. myersi*, placed these species in *Petenia* along with the Central American *P. splendida* Günther, and most authors apparently agree with him (also Steindachner, 1875, describing *C. spectabilis*; 1878, describing *C. kraussii*; Pellegrin 1904). Fowler (1945a) noted the 'peculiar physiognomy' of his *Caquetaia*, but did not compare with other genera.

I have compared *C. myersi*, *C. kraussii*, and *C. spectabilis* with especially *Nandopsis* species of the guapote group, and find them quite different. The latter (*N. motaguensis* (Günther), *N. cf. friedrichsthalii* (Heckel)) are elongate fishes with chiefly the lower jaw enlarged; the maxillary tip is well exposed, but only little exposed, not reaching much below the labial mouth parts; no premaxillary maxillad process, moderately long ascending premaxillary processes (to behind middle of orbit, but then snout somewhat produced), coronalis pore opening through skin just

caudal to premaxillary ascending processes; no ventrorostral projection of lachrymal, a pair of enlarged canine teeth in upper jaw and also two teeth in lower jaw enlarged, one on each side of the enlarged premaxillary teeth when mouth closed (see also Regan 1906-1908). Although the caudal-fin is rounded, the lip folds continuous, and the mouth shape superficially similar, the two groups appear distinct.

The only other American cichlid anywhere near to *Caquetaia* in jaw morphology is *Petenia splendida*. From figures and descriptions (Günther 1862, 1869; Pellegrin 1904; Eaton 1943; Regan 1905e, 1924) it would approach *Caquetaia* in having a maxillad premaxillary process, a long exposed maxilla, and long ascending premaxillary processes. It apparently lacks enlarged jaw teeth and vertical-fin scales, and has (Schultz 1944:) 38-41 scales along the side.

I therefore tentatively recognize *Caquetaia* as a valid genus for *myersi*, *spectabilis* and *kraussii*, but *P. splendida* may be a very close relative.

Of the *Caquetaia*, *C. myersi* is evidently the most specialized form, with longer ascending premaxillary processes than the other two species, reaching to almost the dorsal-fin origin instead of only to the extrascapular region, and five instead of six anal-fin spines. It is collected only in the upper Napo (Santa Cecilia; Missahuellia; R. Punina near Coca; Limoncocha (Loiselle 1982)) and Caquetá (Florençia; R. Dedo) systems. Schultz' (1944) and Fowler's (1945a, of *C. amplioris*) descriptions and figures give a reasonable picture of the species. Loiselle (1982) provided a photo of a young specimen, life colour notes and aquaristic information. It differs from the other two also in lacking a caudal base spot, and in the dark stripe from the nape obliquely forwards curved through the orbit to the lower jaw base.

Caquetaia spectabilis has been adequately figured and described by Steindachner (1875). It differs from the other two in larger scales (squ. long. 28, rather than 30) and in having a dark blotch on the middle of the side but none over the lateral line origin and no dark stripe on the head. I have seen material from Manari Creek, Bem Querer, Gurupá, Óbidos, Porto do Moz, Cametá, mouth of R. Negro, 'R. Madeira', Monte Alegre, Cachoeira Porteira (R. Trombetas), Santarém. The species appears restricted to the R. Branco and R. Amazonas system downstream to Cametá.

Caquetaia kraussii is restricted to the Atrato, Cauca, Magdalena, Maracaibo, and Unare basins, but introduced in the Apure and Lago Valencia (Mago 1978; Regan 1905e; Pellegrin 1904; Schultz 1944, 1949; Steindachner 1878, 1880b; Eigenmann 1922; pers. obs.). Aside from a large dark spot over the lateral line origin, the size decrease of the scales dorsad from the lateral line is more marked than in the other two species. Steindachner (1878) has a fine description and good figures.

The three species are well differentiated and apparently well separated geographically.

'*Cichlasoma umbriferum*, from the Magdalena, Atrato and Tuirá systems (Miller 1976) may belong in this group, as it lacks a coronalis pore and has a maxillad premaxillary process (albeit small), but its jaw bones are not as long as in *Petenia* and *Caquetaia* and the dentition is more like in guapotes.

Caquetaia appear to be relatively generalized fishes, despite the pronounced jaws. The most interesting feature of these fishes, and *Petenia*, is the premaxillad process of the alveolar premaxillary process. Among South American cichlids, chaetobranchines and *Acaronia* have an indication of such a process, but it is lacking in all others. It is rare among African cichlids (but Stiassny (1981a) figures it in *Trematocara* and *Hemibates*, Liem (1978) in *Hemibates*). Nandids (Liem 1970), centropomids (Greenwood 1976) and percids (pers. obs.) have it well-developed. It may nevertheless have some claim for a synapomorphy of *Caquetaia-Petenia*, especially as it is associated with uniquely long ascending premaxillary processes and long exposed maxilla. Other features do point to a relatively ancestral group, however, such as the small scales, stochastic predorsal squamation and scaly fins.

The dentition is similar to that of the African *Hemichromis*, which also apparently lacks a coronalis pore.

CHAETOBANCHOIDES n. gen.

Type-species: *Chaetobranchus semifasciatus* Steindachner.

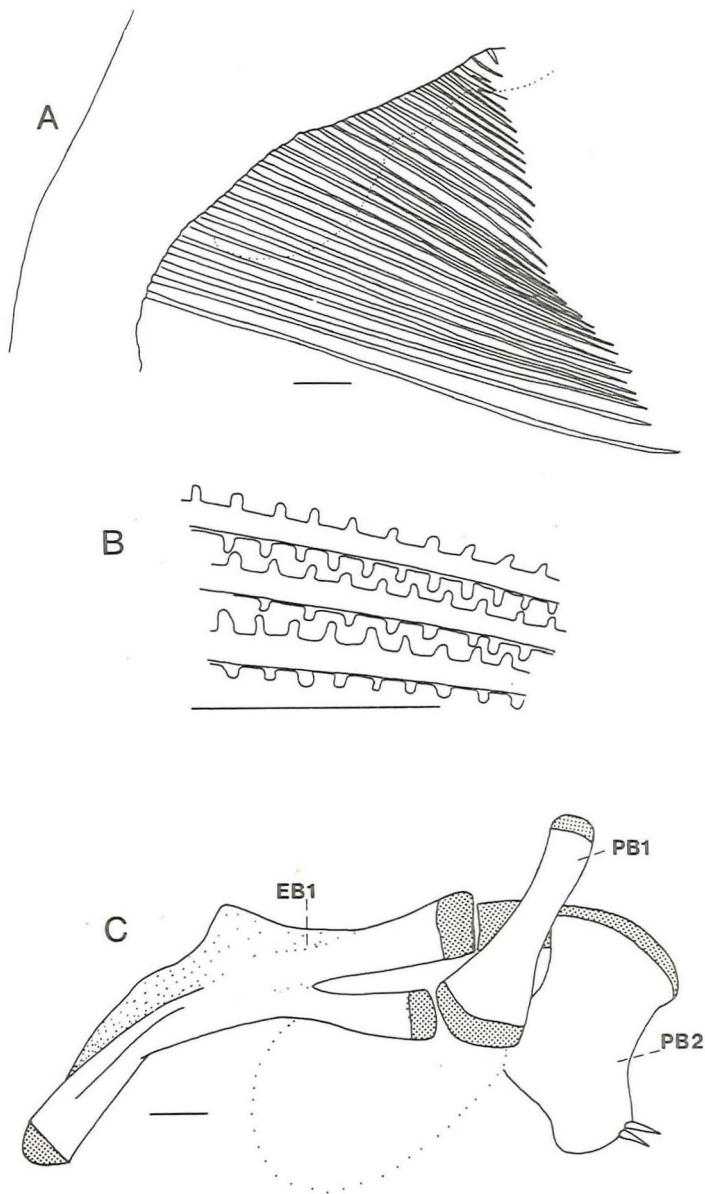


Fig. 103. *Chaetobranchoides semifasciatus*. Details of first gill-arch. A, dorsal portion of epibranchial, with long gill-rakers; B, sections of middle of three upper ceratobranchial rakers, in lateral aspect, to show interdigitating marginal projections; C, dorsal part of arch in rostral aspect, EB1 first epibranchial, PB1-2, pharyngobranchials, cartilage stippled, outline of pharyngeal pad a dotted line. Scales 1 mm. From NRM 11155, 132 mm SL.

Chaetobranchus (*Chaetobranchus*) *semifasciatus* Steindachner, 1875. Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71, p. 130, Pl. VII (Amazonenstrom bei Obidos, Cudajas, Teffê; Rio Içá; Lago Hyuanary und Saraca bei Silva).

Chaetobranchoides is basically like *Chaetobranchopsis* and *Chaetobranchus* (q.v.). Its osteology is still unstudied, but several characters indicate generic separation although no definite autapomorphy has been found.

A basic description and figure of *Ch. semifasciatus* is provided by Steindachner (1875). The species reaches a length of c. 200 mm, and has been collected only along the Solimões and Brazilian R. Amazonas, from Tefê to Óbidos (also R. Içá according to Steindachner).

Chaetobranchoides semifasciatus is high-backed and distinguished in coloration as brassy with four dark cross-bars on the back below the dorsal-fin and a silver-ringed superior caudal spot slightly removed from the caudal-fin base. A dark stripe runs along the naked zone of the cheek (only in females according to Steindachner).

Mouth features are similar to those of *Chaetobranchus*, but the lower jaw is distinctly prognathous. The suboperculum has the free edge serrated. Squ. long. 28; circumpeduncular scale series 20. The cheek squamation is divided by a naked line continuing the lachrymal margin to the preoperculum. The soft dorsal- and anal-fin bases are narrowly scaly basally; pectoral- and pelvic-fins naked. The caudal-fin is densely scaly, with long lateral line sequences between rays D1 and D2, V1 and V2, V2 and V3, V3 and V4. The caudal peduncle is moderately long.

The first gill-arch has about 35 epi-, about 85 cerato-, and about 5 hypobranchial gill-rakers externally, the terminal ones small, but most very long, slender, flattened, with marginal interlocking projections (Fig. 103); inner rakers and those on inner arches shorter, but still long and numerous. Two teeth on pharyngobranchial 2; a small tooth-plate on basibranchial 2. Microgillrakers externally on the second to fourth gill-arches and internally on the fourth.

All of the above listed features appear plesiomorphic where different from other chaetobranchines. *Chaetobranchoides* further differs from *Chaetobranchopsis* in the anal-fin count (A. III.13-15), and the vertical-fin squamation is much narrower than in that genus. The contiguous bilateral elements and strongly curved horns of the lower pharyngeal jaw, as figured by Pellegrin (1904, Fig. 7) is possibly an apomorphy relative to other chaetobranchines.

The name *Chaetobranchoides* (gender masculine) has already been used by A. Ribeiro (1918a, p. 133), but clearly as an error for *Chaetobranchus*.

CHAETOBANCHOPSIS

Chaetobranchus (*Chaetobranchopsis*) Steindachner, 1875. Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71, p. 133 (type by monotypy *Chaetobranchus orbicularis* Steindachner). - Masculine.

Chaetobranchopsis australe Eigenmann & Ward, 1907, in Eigenmann, McAtee & Ward. Ann. Carneg. Mus. 4, p. 144, Pl. XLIV, fig. 1 (Bahia Negra).

Chaetobranchus (*Chaetobranchopsis*) *orbicularis* Steindachner, 1875. Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71, p. 133, Taf. VIII, fig. 1 (Amazonenstrom bei Pará, Santarem, Gurupa, Rio Xingu bei Porto do Moz, Rio negro und R. Hyavary).

Chaetobranchopsis bitaeniatus Ahl, 1936. Sber. Ges. naturf. Freunde Berl. 1936, p. 139, fig. p. 140 (Amazonas).

Chaetobranchopsis species are compressed, deep-bodied fishes with long anal-fin (A. IV-VI.16-18), very short caudal peduncle, and more obtuse front than other chaetobranchines, also not as large as these, reaching only 115 mm SL.

The coloration is similar to that of *Chaetobranchus*. A wide dark band obliquely from the gill-cleft to the dorsal-fin base end, including a midlateral spot; often another, hypaxial band, between pectoral-fin and caudal-fin bases. No caudal spot. No cheek stripe; but a dark transverse intermandibular stripe is characteristic.

The soft dorsal- and anal-fins are extensively scaly; the caudal-fin densely scaly, with long lateral line sequences between rays D1 and D2, V1 and V2, D3 and V4. Squ. long. 26; 16 circumpeduncular scale series; cheek completely scaly. Opercular bones entire.

In *Ch. australis*, of which alizarin material is available, there are 13+14 vertebrae; 2 supraneurals; paired long, ventrally co-ossified hypapophyses on third vertebra. Parhypurapophysis and median internypural cartilage absent; three procurent rays in each caudal-fin lobe.

The posterior myodome fossa is wide, margined by well-developed ledges on which Baudelot's ligament attach. The neurocranial pharyngeal apophysis forms from the parasphenoid, and has separate articulation facets for the third pharyngobranchials.

The gill-rakers are long and slender as in *Chaetobranchoides*, but fewer (c. 20 epi-, c. 60 cerato-, c. 5 hypobranchial externally on first arch). Basibranchial and fourth ceratobranchial teeth absent. No microgillrakers internally on fourth gill-arch, but present externally on second to fourth arches.

The branchial skeleton is elongated, with especially the lower pharyngeal tooth-plate with long rostral process; slender bilateral elements of tooth-plate loosely connected medianly and posteriorly widely separated. Third pharyngobranchials widely separated, oblong, relatively compressed dorsoventrally, with small, low parasphenoid apophysis. Fourth upper tooth-plate elongate, loosely connected with third pharyngobranchial. Pharyngeal teeth small, in moderate number (only 1-2 on the second pharyngobranchial, however), and socketed. Interarcual cartilage strong, but not elongated. First epibranchial moderately long, without ventral lamina, but with high dorso-caudal wing.

Jaw bones moderately elongate; minute maxillad process on alveolar ramus of premaxilla, but no rostral premaxillary foramen. Teeth conical, minute, in narrow bands. Lower jaw slightly prognathous. Urohyal spine short, dorsad-rostrad pointing. Fifth branchiostegal ray base medial to anterior ceratohyal.

Five dental, seven preopercular, four lachrymal lateralis foramina; infraorbitals slender (io2, io3+4 with median foramen, long io5, io6). Coronalis canal transversely slightly caudad running, uplifted to dorsad-rostrad opening by well-elevated median frontal crests.

Chaetobranchopsis has been recognized on the higher anal-fin count as compared to other chaetobranchines. This character state may be disputed, but the absence of a basibranchial tooth-plate, absence of inner microgillrakers on the fourth gill-arch and the head markings put the group apart.

The species level taxonomy requires more work. Two species are tentatively recognized:

Chaetobranchopsis orbicularis includes *Ch. bitaeniatus*. The latter is based on starved aquarium specimens showing a colour phase at the time not recorded but shown more or less well by at least some specimens in larger series of both *Ch. orbicularis* and *Ch. australis*. The species is collected in the Oyapock, Madeira, and the Solimões-Brazilian R. Amazonas from L. Janauacá to Isla Marajó (also R. Javari according to Steindachner). It has modally six, occasionally five anal-fin spines and modally 15 dorsal-fin spines.

Chaetobranchopsis australis is collected in the Paraguay and Guaporé systems. It has modally five, occasionally four or six anal-fin spines and modally 14 dorsal-fin spines.

CHAETOBANCHUS

Chaetobranchus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 401 (type by subsequent designation by Eigenmann (1910a) *Chaetobranchus flavescens* Heckel). - Masculine.

Chaetobranchus flavescens Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 402 (Fluss Guaporé und die in der Nahe seiner Ufer gelegenen Moraste, auch am Ausflusse des Rio-negro).

Chaetobranchus bruneus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 405

(Rio-negro, unweit von seiner Mündung).

Centrarchus? cyanopterus Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 165, Pl. 16 (Essequibo).

Chaetobranchus robustus Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 310 (Guiana).

Chaetobranchus ucayalensis Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 15, Pl. 6, fig. 2 (Sarayacu (Pérou)).

Geophagus badipinnis Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 251, Pl. XI, fig. 1 (R. Ambyacu).

Chaetobranchus species are large (to c. 250 mm SL), moderately deep cichlids with naked dorsal- and anal-fin. They have the pharyngeal structures of other chaetobranchines, but internal fourth gill-arch microgillrakers and basibranchial 2 tooth-plate unlike *Chaetobranchopsis* and fewer gill-rakers than *Chaetobranchoides* (c. 25 epi-, c. 55 cerato-, c. 5 hypobranchial externally on first arch).

The snout is long as in *Chaetobranchoides*, but the jaws about equal anteriorly.

Squ. long. 26; 16 circumpeduncular scale series; cheek squamation divided only rostrally; caudal-fin lateral lines as in *Chaetobranchopsis*. Opercular bones entire. Vertebrae 13+13; 2 supraneurals; no parhypural spine; lateralis system as in *Chaetobranchopsis*. D. XII-XIII, 13-14; A. III, 11-12; three procurrent caudal-fin rays in each lobe.

The coloration includes a dark band from head to end of dorsal-fin base with a prominent midlateral spot; a ventral side band as in *Chaetobranchopsis* is occasionally indicated; no caudal spot; dark cheek stripe faint, a stripe along lower jaw sides strong.

The genus is widely distributed. *Chaetobranchus ucayalensis* is recognized from Ucayali and Peruvian R. Amazonas material. Material with slightly more posterior midlateral spot from Guyana, western Surinam, R. Guaporé, upper R. Madeira, lower R. Solimões, lower R. Negro, R. Branco, R. Oyapock, R. Approuague, Brazilian R. Amazonas, is identified as *Ch. flavescens*; Fernández Yépez (1951) has an Orinoco drainage record.

Chaetobranchoides, *Chaetobranchopsis*, and *Chaetobranchus* are relatively ancestral cichlids to judge from the five dental and seven preopercular lateralis foramina, medial base of the fifth branchiostegal ray, continuous lip folds, two supraneurals, stochastic predorsal squamation, numerous gill-rakers (also on hypobranchials), and long caudal-fin lateral lines.

They are nevertheless not to be associated with *Cichla* or other plesiomorphic cichlids, eg., in featuring American type lower lip attachment, cichlasomine-like finnage, lacking parhypurapophysis and median interarcual cartilage, having only three procurrent caudal-fin rays, lackings separate infraorbital 2 and with four lacrymal lateralis foramina, and having relatively few vertebrae (13+13 or 13+14).

Mouth and pharyngeal structures suggest planktivores but no positive stomach analysis data have been published (cf. Knöppel 1970; Lowe-McConnell 1969). The mouth is wide and large, especially the lower jaw shallow and wide, the upper jaw well protrusible. Jaw teeth are very small, in narrow bands. The gill-rakers are long, slender, close-set and numerous, especially externally on the first arch; with bilateral skin fold along the roof of the pharynx they form a closed chamber effective for filtering; also the floor of the pharynx is longitudinally folded, assisting in distributing water and food toward gill-arches. Two genera have a small tooth-plate on the second basibranchial unique to them among cichlids.

The lower pharyngeal tooth-plate is long and slender, and the bilateral elements well-separated posteriorly; also the upper pharyngeals are wide apart; the second pharyngobranchial is nearly edentulous, with only one or two teeth.

The numerous gill-rakers and loosely connected pharyngeal jaw might be regarded as extreme specializations, but not necessarily from, eg. the cichlasomine type. The basibranchial tooth-plate contrasts with the otherwise weak dentition, and whether primitive or advanced may serve chiefly as support for the median ventral pharyngeal skin-fold.

Chaetobranchines and *Astronotus* have a unique microgillraker type, but differ otherwise saliently, especially in jaw and pharyngeal structures. *Acaronia*, with similar jaws, has very different lateralis system and gill-arch skeleton.

Characteristic of chaetobranchines are also the long pointed pectoral-fin, reaching to near the end of the anal-fin base, and the three or four long caudal-fin lateral lines. The latter may represent an ancestral condition, but as none lies between rays V4 and V5, positions may be modified compared to the modal cichlid.

The three genera recognized here differ greatly from each other. *Chaetobranchoides* may be the most primitive, with more gill-rakers, *Cichla*-like caudal-fin ocellus, basibranchial tooth-plate, divided cheek squamation, long caudal peduncle, four caudal-fin lateral lines, smaller scales, serrated suboperculum.

Chaetobranchius is advanced in its naked dorsal- and anal-fins, absence of caudal spot, reduced gill-raker number, only partly divided cheek squamation, larger scales, three caudal-fin lateral lines, entire operculars, as compared to *Chaetobranchoides*.

Chaetobranchopsis has well-scaled fins, but lacks inner fourth gill-arch microgillrakers and basibranchial tooth-plate. It has more anal-fin spines than the other two genera and a correlated very short caudal peduncle. The coloration is similar to that of *Chaetobranchius*, with which closer relationship is also otherwise suggested.

CICHLA

Cichla Schneider, 1801. *Bloch. Syst. Ichthyol.*, p. 336 (type by subsequent designation by Eigenmann & Bray (1894), *C. ocellaris* Schneider). - Feminine.
Acharnes Müller & Troschel, 1849, in Schomburgk. *Reisen Brit. Guiana* 3, p. 622 (type by monotypy *A. speciosus* Müller & Troschel). - Masculine.

Cichla intermedia Machado-Allison, 1971. *Acta Biol. Venez.* 7, p. 473, Fig. 7 (río Casiquiare, Territorio Federal Amazonas).

?*Cichla nigro-maculata* Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 147, Pl. 7 (R. Negro and Padauri!).

Cichla Monoculus Spix, 1831, in de Martius. *Sel. Gen. Sp. Pisc. Bras.*, p. 100, Pl. LXIII (as *Cichla Monoculus*) (marí Brasiliae).

?*Cichla Tucunare* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 409 (Rio-branco).

?*Cichla toucouarai* Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 17, Pl. 10, fig. 1 (le lac des Perles de la province de Goyaz; le Tocantins; l'Amazone).

?*Cichla bilineatus* Nakashima, 1941. *Boln Mus. Hist. nat. Javier Prado* 5, p. 73, Fig. 13/ (los lagos y rios de Sudamérica tropical /cercanias del Puerto de Iquitos!).

Cichla ocellaris Schneider, 1801. *Bloch. Syst. Ichthyol.*, p. 340, Pl. 66 (India Orientali).

Acharnes speciosus Müller & Troschel, 1849, in Schomburgk. *Reisen Brit. Guiana* 3, p. 622 (Kuste; Mündung des Essequibo).

Cichla orinocensis Humboldt, 1833, in Humboldt & Valenciennes. *Voy. Humb. Bonpl.* 2, p. 167, Pl. XLV, fig. 3 (les rives de l'Orénoque et du Guania ou Rio Negro).

Cichla argus Valenciennes, 1833, in Humboldt & Valenciennes. *Voy. Humb. Bonpl.* 2, p. 169 (-).

Cichla atabapensis Humboldt, 1833, in Humboldt & Valenciennes. *Voy. Humb. Bonpl.* 2, p. 168 (l'Orénoque; Rio Atabapo).

?*Cichla trifasciata* Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 151, Pl. 9 (Rio Negro; Padauri!).

Cichla temensis Humboldt, in Humboldt & Valenciennes, 1833. *Voy Humb. Bonpl.* 2, p. 169 (Temi).

Cychla flavo-maculata Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 145, Pl. 6 (Rio Negro and Padauriri).

?*Cichla unitaeniatus* Magalhães, 1931. *Monogr. Braz. Peixes*, p. 225 (Rio Negro e do Purus).

Cichla are easily distinguished from all other South American cichlids on the shape of the dorsal-fin: the spines increase in length to about the fifth, then there is a gradual decrease to a very short penultimate spine, and the soft fin is again about as high as the anterior spinous part. Mouth large, with prominent jaws, lower jaw prognathous and maxilla well exposed. Anal-fin small and densely scaled in adults. From about 100 mm SL a prominent ocellus on caudal-fin base; otherwise coloration very variable ontogenetically and between individuals although at least at larger sizes species-specific. Bilateral elements of lower pharyngeal jaw separate posteriorly and extensively covered by fine teeth. On first gill arch seven or eight epibranchial, one in the angle, and 14 to 19 cerato- and hypobranchial rakers, those caudally on ceratobranchial long, gradually smaller towards arch articulations, strongly denticulate. Lateral line commonly discontinuous; triradiate on caudal-fin. Anal-fin with three spines. Lip folds discontinuous symphysially, upper and lower lips narrowly connected ventrally on maxilla (African type lips, Fig. 106). Preoperculum entire.

The genus *Cichla* was established by Schneider (1801) for Heptapterygii (fish with seven fins) with head naked (scaleless) anteriorly, small teeth, and neither spines nor serrations on the gill-cover. Of the 24 species, most are now placed in other families, but what are now called *Geophagus surinamensis*, *Crenicichla brasiliensis*, *Cichla ocellaris*, and the enigmatic *Perca bimaculata* Bloch, were included. Heckel (1840) restricted the genus to *C. ocellaris* and similar forms, but a formal type-designation was not made until Eigenmann & Bray (1894).

The authorship of *Cichla*, *C. ocellaris* and other names proposed in Schneider (1801) is not quite clear. The work is a catalogue, with descriptions of the world's fishes, compiled by M.E. Bloch (1723-1799). The work must have been in quite an advanced state at the time of Bloch's death, supposed to appear after the Easter of 1799 (Bloch in Karrer 1978, p. 148). Yet Schneider 'concluded, corrected, and edited' it. Remarks inserted by Schneider are signed 'Schn.', but he is likely responsible for some of the remaining text and some of the organization of the book.

Even though the major part of the book likely was written by Bloch, I favor Schneider as author of the names published therein, as he is responsible for their publication. It is nowhere said that the book would be a cooperative project and it matters in no way in zoological nomenclature who constructed a particular name or who provided the descriptive basis, but only responsibility for publication (International Code of Zoological Nomenclature, Art. 50).

The genus has been extensively treated in recent papers by Machado (1971, species revision), Stiassny (1982, relationships), and Zaret (1977, 1980, life history).

Five species are formally recognized here, but there is much uncertainty concerning the number of species and species names in the current literature, and a revision of the genus will probably show the existence of a few more species.

Of the 15 nominal species, eight (*temensis*, *atabapensis*, *orinocensis*, *flavomaculata*, *nigromaculata*, *trifasciata*, *bilineatus*, *unitaeniatus*) were described from specimens not preserved or hear-say; four (*ocellaris*, *argus*, *toucounarai*, *monoculus*) type-specimens lack or have erroneous locality-data, one (*tucunare*) cannot be found for the moment, and one (*speciosus*) with approximate locality-data is a young specimen in very bad condition. Only for *C. intermedia* is there an extensive description with good figures, locality data and types. (A putative type-specimen of *C. monoculus* was only recently discovered by Maurice Kotteiat.)

Three species are recognized in the current literature: *C. ocellaris*, *C. temensis* and *C. intermedia*, and these names were employed by Machado in his recent revision (1971) for three Venezuelan forms. *Cichla ocellaris* is generally regarded as a very variable species with wide distribution; *C. temensis* is less variable and should be easily recognized by its small scales and the colour pattern (cf. Machado 1971); *C. intermedia* also has a distinctive coloration (cf. Machado 1971).

A revision of Surinamese *Cichla*, shows these to be *C. ocellaris*. I have seen no *C. ocellaris* from outside the Guianas. Two *Cichla* specimens from the Oyapock system are *C. monoculus* (see below). The large-scaled *Cichla* in Guyana, described by Eigenmann (1912) and Lowe-McConnell (1969) as *C. ocellaris*, appears to be true *C. ocellaris*. *Cichla temensis* was reported by Lowe-McConnell (1969) from the R. Branco drainage in Guyana. It does not seem to occur naturally in the Guianas, but two species of *Cichla*, imported from Brazil, were tried in fish culture in Guyana (Lowe-McConnell 1969) and if released into the open waters there may now be more than one *Cichla* species in Guyanan Atlantic rivers.

Cichla occurs in the Marowijne drainage, but the two specimens available (IRSNB 19707, Saut Bali; IRSNB 17569pt., downstreams of Epoia (in mouth of *Geophagus harreri*) are too small to allow a definite identification, although they certainly agree well with *C. ocellaris*. Puyo (1949) reported "*C. ocellaris*" from the upper Mana, the Oyapock at Saut Cafésoca, and the upper Maroni, and Pellegrin (1904) listed material from Cayenne and Maroni.

Cichla temensis appears to be restricted to clear and black water drainages, found in the Orinoco, Negro and Tapajós systems. It differs from *C. ocellaris* in the much smaller scales (100-120 in the lateral line according to Machado 1971) and the colour pattern: adults with four to six horizontal series of yellow spots along the sides. Good figures in Machado (1971). NRM material from Taracará, R. Uaupés (NRM 11308).

Cichla monoculus is found at least near Manaus and in the R. Oyapock, but the distribution is probably wider in the central Amazonia. It has three vertical bars, much wider than in *C. ocellaris*, and reduced in adults to three spots on the back, chiefly located between the dorsal-fin and the upper lateral line section. It is figured by Zaret (1977, Figs. 1 and 2), and Goulding (1981, Fig. 5.41.). NRM material from Manaus (NRM 64954) and Manacapuru (NRM 11309), ZMA material from the Oyapock (ZMA 107.761, Igarapé Jumina).

Cichla orinocensis is known from the Orinoco basin and the upper R. Negro. In this species there are vertical bars that are strongest below the upper lateral line in specimens 150-160 mm, and large adults have three ocelli along the side, the anterior two below the upper lateral line section. Although there is an existing holotype of *C. argus*, but no known type-material of *C. orinocensis*, Günther (1862), as first reviser, chose the latter name. Good figures in Machado (1971; called *C. ocellaris*). NRM material comes from the mouth of the R. Guarrojo in Colombia (NRM THO/1972103.4152).

Cichla intermedia, from the Casiquiare and middle Orinoco, has a continuous flank band and eight to nine faint vertical stripes when young; adults a series of more or less continuous and ocellated spot-series along the side. Good figures in Machado (1971), no other preserved material known.

The generic distribution includes all of Amazônia, Guianas and Orinoquia, but for reason of lack of large series, no attempt was made at (forced) identification of Peruvian and Bolivian material available - Amazonian white-water *C. ocellaris* auctt. agree well with *C. monoculus*, however. Limited series from the Jurueña and Xingu may represent additional species.

I have worked especially with the Surinamese form of *Cichla*, in particular with the aim of re-defining the type-species, *C. ocellaris*, the name of which is currently applied on several species, but also took the opportunity of revising some of the characters emphasized by Stiassny (1982) in a study of *Cichla* relationships (see discussion).

My conclusion is that *Cichla* is probably the most plesiomorphic cichlid existing, with potential rivals only among the Madagascar-India. This means that *Cichla* is highly useful as a reference species for plesiomorphic character states.

Below, I present a description of the Surinamese *Cichla*, with osteological notes (not intended to be complete; consult Stiassny 1982 and Machado 1973 for additional detail) from a single cleared and stained specimen. A complete material list is available on request.

Cichla ocellaris Schneider, 1801
(Plate XV, fig. 2)

Holotype. ZMB 2839. 183.4 mm SL. Coll. M. E. Bloch.

Diagnosis. A relatively deep-bodied *Cichla* (depth 24.8-34.1 % of SL in size range 50-414 mm), with relatively large scales (squ. long. 70-79). Lateral line usually continuous at all sizes. Vertical bars narrow, in large adults spots in the first two bars lie above lateral line, ocellus of third vertical bar prominent; no horizontal series of yellow spots along sides; no dark bar on caudal peduncle.

Material. Descriptive data below from 101 ZMA specimens, 45-414 mm SL, from Nickerie, Saramacca and Suriname R. systems; available have been also USNM, RMNH, and NRM specimens to a total of 244 specimens from the Corantijn, Nickerie, Saramacca, and Suriname R. systems, as well as the holotype, of unknown provenance.

Description. From ZMA 107.238, 298.6 mm, an adult male, followed by notes on variation in the Surinam material, and on the holotype.

Body moderately deep and laterally compressed; little broader anteriorly than posteriorly. In facial aspect with flat chest, relatively vertical sides and narrow nape; over trunk compression gradually stronger dorsad on back, but abdominal region flattened anteriorly, posteriorly ventral midline rounded off. Caudal peduncle tapering caudad, with convex dorsal and ventral edges. Dorsal-fin base contour straight horizontal or feebly rising caudad along spinous portion; gradually descending posteriorly. Chest contour straight, nearly horizontal; abdominal contour about straight horizontal; anal base about straight, upwards slanting.

Head moderately long, little compressed, with long snout. Predorsal contour ascending, straight save for minor convexity above nostril and a compressed hard elevation in front of dorsal-fin. Eye slightly elliptic horizontally, below forehead contour, all in upper, most in anterior halves of head. Nostril closer to orbit than to snout tip. Interorbital area convex. Mouth large, terminal, low in position, caudally wider than rest of head. Ascending processes of premaxilla extending to behind nostril but not reaching anterior margin of orbit. Caudal part of maxilla well-exposed, extending to nearly middle of orbit. Lower jaw slightly prognathous; articulation below little behind middle of orbit.

Upper lip fold interrupted symphysially, where, however, a thickened connection with opposite side fold, caudad a simple fold, not inwards-curved. Lower lip fold bilaterally from near symphysis, widest medially, much reduced before attachment caudally to maxilla and dorsally to premaxillary tip. Postlabial skin fold with short incision just before preorbital.

Operculars entire. Preoperculum with uneven straight vertical free margin, rounded ventral margin. Operculum short, not reaching ventrad to interoperculum, which extends little caudal of preoperculum; length about 1.5 times the depth, exposed surface similar in area to that of suboperculum; a wide skin flap along caudodorsal edge, continued around weak caudodorsal blunt subopercular projection.

Scales ctenoid except where otherwise noted. Cheek naked below line continuing labian margin of preorbital caudad; above several irregular series of scales, those dorsally and rostrally of about flank scale size, ventrally smaller; a patch of cycloid scales ventrally; dorsal cheek scale series continued onto first infraorbital to level of anterior margin of orbit; four vertical series behind orbit; behind upper margin of orbit a narrow naked zone caudad to preoperculum. Preoperculum naked. Operculum, suboperculum save for narrow naked free margin, and interoperculum posteriorly, densely scaled.

Body scales rather small; slightly larger on flanks and abdomen than along dorsal trunk margins and anterior preventral scales. Wide naked area above orbits; predorsal squamation reaching rostrad to not quite anterior margin of orbit; nuchal protuberance naked medially. Prepelvic scales very small save for posteromedial which of about flank scale size. Pectoral axilla and pectoral-fin naked. About 32 circumpeduncular scale series.

Spinous dorsal-fin naked. Along bases of nine anterior rays a series of ctenoid

scales, larger than those on fin proper. From behind last spine to behind 11th ray small cycloid scales in series close behind preceding spine or ray (not filling up space to next ray), double series behind last spine and first ray, otherwise simple series; commencing slightly distad to fin base, anterior series reaching to near tips of rays, posteriorly successively shorter, last to one-fourth of ray length; interradial scales also on membranes between major ray branches, to near fin edge.

Anal-fin with heavy basal sheath of ctenoid scales; interradial scales cycloid, proximally in dense layer, distad narrower; no scales between ray branches; medially scaly layer a little wider than half length of longest rays.

Caudal-fin middle membrane and that above naked medianly from fin tip proximad to ocellus; otherwise a wide convex proximal layer of larger scales and densely packed series of small interradial scales that obscure fin rays; distally a narrow zone of cycloid scales and a narrow naked fin edge.

Pelvic-fin on medial side with basal layer of scales and double series of cycloid interradial scales, anteriorly to spine tip, posteriorly shorter; on lateral side double interradial series of cycloid scales on first two membranes to level of spine tips.

Lateral line continuous; anteriorly uneven, but more or less horizontal, strongly downturned over three horizontal scale series little caudal to origin of soft dorsal-fin, caudad nearly horizontal, to caudal-fin base; continued on caudal-fin base by four canals in downwards sloping series and a long sequence on dorsal lobe and a short sequence on ventral lobe (which distally regenerated). On body lateral line scales feebly smaller than those adjacent.

Dorsal-fin origin little posterior to vertical from hind margin of operculum; first spine of about length of last; some of longer spines apparently with broken tips, but shape otherwise conforming to that described from intact specimens below. Soft fin with narrowly rounded tip, 12th and 13th rays longest, not reaching caudal-fin base. Anal-fin short, spines increasing in length to third; soft fin rounded, not extending to caudal-fin base. Caudal-fin apparently with regenerated lower lobe; dorsal lobe truncate, ventral rounded; ray count impossible without removing dense squamation. Pectoral-fin subacuminate, with fourth ray longest, not extending to vent, but halfway to anal-fin base end. Pelvic-fin short, broad, second ray longest, distal edge straight.

Teeth small, little recurved, in narrow bands in both jaws, symphyses naked. Mouth and gill-cover cannot be much opened without risking damage to specimen, so for details of dentition and gill-arches, see notes below from other specimens.

Variation: A representative young specimen (ZMA 105.083, 47.6 mm SL) elongate with strikingly large head and mouth; outline tapering caudad from head. In facial view nape broadly rounded, head sides vertical, chest medially flat but narrower than in large adults. Head elongate, deeper than wide, with slowly ascending evenly curved dorsal contour and little sloping pre-ventral contour. Interorbital area flattened medially, eye nearly tangent by forehead contour. Large, oblique, ventrally placed mouth posteriorly wider than interorbital but narrower than occipital region. Tip of maxilla well exposed, reaching to nearly middle of orbit; ascending processes of pre-maxilla reaching to just short of orbit; lower jaw hardly at all prognathous, its articulation below middle of orbit. Lips like in adults; opercularia like in adults but that suboperculum not so deep.

Major shape changes correlated with increasing size include a rise of dorsum, straightening of predorsal outline, lowering of eyes relative to predorsal contour and lower jaw prognathy.

A 138.6 mm young specimen (ZMA 105.058) mostly like adults. Elongate, with entire dorsum elevated, spinous dorsal-fin base horizontal. Frontal outline rising straightly to dorsal-fin origin save for minor elevation just before orbit. In frontal view nape keeled, chest flat. Lower jaw distinctly prognathous, articulation below about posterior margin of orbit.

Five males besides 299 mm specimen have a nuchal hump. One of these has appearance of a stunted fish and is only 200 mm SL (ZMA 107.598). The others are 236, 268, 268, and 414 mm SL (ZMA 105.085, two; 105.194; 105.054).

Scales in horizontal series above that containing lower lateral line section from end of caudal peduncle forwards to head 70 (1), 71 (1), 72 (5), 73 (1), 74 (3), 75

(3), 76 (5), 77 (5), 79 (1), no apparent size correlation.

Side scales ctenoid at all sizes available. In 47.6 mm specimen cheek and gill-cover squamation like in 299 mm specimen except that scales very thin and cycloid, also only very buccal margin of first infraorbital scaled. In 138.6 mm specimen as in 299 mm specimen but only posterosuperior opercular and subopercular scales ctenoid; a 160.7 mm specimen with posterior/superior half of cheek with ctenoid scales. Predorsal scales cycloid in 47.6 mm specimen; predorsal midline naked medially. Extension of naked midline reduced in larger specimens, and most predorsal scales ctenoid in 138.6 mm specimen. Abdominal scales ctenoid in all specimens; chest and prepelvic scales thin, cycloid in 47.6 mm specimen, which also naked opposite tip of cleithrum; in 138.6 mm specimen prepelvic squamation complete and but a few cycloid scales remaining rostrally.

Lateral line either continuous or in two sections. When continuous course as in 299 mm specimen, of 71 (1), 73 (3), 74 (1), 75 (4), 76 (8), 77 (1), 78 (2), 79 (1), scales, all with canals. In measured specimens line discontinuous on right side in four specimens with 42/33, 44/31, 45/33, and 46/32 scales. In ZMA material of 101 specimens line continuous except in four (including 47.6 mm specimen) which have a discontinuous left side line, in 12 specimens with right side line discontinuous, and in three with bilaterally discontinuous lateral line. When line discontinuous downwards running section missing; however, either of horizontal sections may proceed a few scales caudad or ventrad respectively of that connection, occasionally also scales preceding connecting section may overlie it and obscure canals so that the lateral line may appear discontinuous more often than it actually is; it also happens that terminal curvatures of anterior and posterior sections are horizontally displaced, resulting in discontinuity.

Lateral line continued on caudal-fin by three or four scales but these canals not easily perceived in very large specimens. In smallest specimens, about 5 cm, four to six canals, in those 6-7 cm, 10-15 canals in a separate section running between rays V4 and V5, in still larger specimens a long series of canals all the way out to near end of caudal-fin; a dorsal lobe section from at least 55 mm SL, then of 2-4 canals, still only of about ten scales in specimens 80-90 mm, in larger fish extending all the way to near end of fin between rays D3 and D4; usually those sections continue across basal caudal-fin squamation towards median continuation of lateral line of body, and it is then usually reached by ventral section but not by dorsal. These sections also become obsolete in very large specimens; occasionally additional sequences of lateral line scales on caudal-fin.

Fins except caudal-fin naked in 47.6 mm specimen; dorsal-fin remaining naked save for basal scales in 160.7 mm specimen (ZMA 105.058); in next larger (170 mm, ZMA 105.066) almost fully scaled like in 299 mm and other larger specimens, though only to behind 9th ray. Basal anal-fin squamation developing from 50 mm, interradiated squamation present proximally on anterior part at 55 mm, 138.6 mm specimen has anal-fin only little less densely scaled than reference specimen and other large specimens.

Pectoral axilla and pectoral-fin remain scaleless at all sizes. 138.6 mm specimen has a basal squamation but few interradiated scales on medial side of pelvic-fin and interradiated scales proximally on lateral side; in still larger fish pelvic-fin squamation gradually approaches condition in 299 mm specimen.

Caudal-fin scales cycloid in 47.6 mm specimen; basally a convex layer of larger scales, beyond marginally thin interradiated scales to almost half length of fin; hind margin of scaled area concave. In 138.6 mm specimen caudal-fin squamation like in 299 mm specimen, only not quite as dense, and membranes between rays D3 to V3 naked along middle, more rostral on median membranes; squamation symmetrical in intact specimens but a regenerated lower lobe is frequent and then scaling irregular on it.

D. XIV.17 (1), XV.17 (20), XV.18 (4); last ray may be actually two, but when base of last major branch/ray could not be distinguished from that of preceding ray/branch it was not counted as a separate ray. In smallest specimens available first spine inserted behind a vertical from hind edge of operculum, but relative position becomes more forward with increasing size. First spine about as long as last and relative length increasing to fourth to about sixth which subequal in length, then decreasing gradually to penultimate, which about half length of fifth and shorter than ultimate; rays much longer than posterior spines. Soft fin rounded off posteriorly, extending to

Table 38. Morphometry of *Cichla ocellaris* in Surinam. Variation and mean of measurements from 25 specimens in ZMA 105.002, 105.007, 105.054, 105.058, 105.059, 105.086, 105.161, 105.194, 105.572, 105.669, 107.238, 50.0-414.0 mm SL, in per cent of SL and, separate holotype (183.4 mm SL) measurements in mm and per cent of SL.

Measurement	Range	in % of SL		Holotype	
		$\bar{x} \pm s(x)$	mm	% of SL	
Head length	32.1-35.8	33.8 \pm 0.18	60.5	33.0	
Head depth	21.4-28.4	23.9 \pm 0.33	44.5	24.3	
Body depth	24.8-34.1	29.9 \pm 0.57	58.1	31.7	
Snout length	10.8-13.1	11.6 \pm 0.14	20.4	11.1	
Orbit diameter	6.5-11.8	9.2 \pm 0.26	15.1	8.2	
Interorbital width	7.2- 9.7	8.2 \pm 0.15	15.4	8.4	
Pectoral fin length	20.3-25.1	22.6 \pm 0.32	45.1	24.6	
Upper jaw length	14.0-16.9	15.0 \pm 0.16	27.8	15.2	
Lower jaw length	18.2-20.4	19.0 \pm 0.13	36.3	19.8	
Caudal peduncle depth	10.6-13.2	11.0 \pm 0.16	23.6	12.9	
Caudal peduncle length	15.8-18.6	17.4 \pm 0.14	29.1	15.9	
Fifth D spine length (n=24)	11.3-14.4	13.2 \pm 0.15	24.4	13.3	

middle of caudal peduncle in smallest, little longer in large specimens, but not reaching to caudal-fin base.

A. III.10 (6), III.11 (19). Insertion of the first, minute spine opposite about fifth to sixth dorsal-fin ray; spine length increasing caudad; in large specimens dense squamation prevents individual erection of spines, but also unlike in dorsal-fin, spines follow very closely upon each other, so that upon cursorily inspection at least the first is not easily located. Soft fin has a feebly rounded hind edge in 47.6 mm specimen, with second ray the longest, though median rays reach further caudad; in 138.6 mm specimen fin with a rounded-off tip with rays 5-6 longest; in smallest specimens reaching backwards to middle of caudal peduncle, in large fish further, but never to caudal-fin base.

Caudal-fin with 16 principal rays in young; rays obscured by scales and terminally excessively branched in fish over 100 mm. Hind margin slightly emarginate in smallest specimens; shape often indeterminable due to damage in large specimens but when determinable truncate with squared upper corner and rounded lower corner.

P. 13 (1), 14 (16), 15 (8). Short, shape rounded in young, becoming rather acuminate in large specimens; asymmetrical, with fourth ray longest.

V. I.5, spine inserted in advance of a vertical from pectoral axilla; tip rounded; hind edge straight in young, becoming slightly concave in large specimens; first and second rays subequal in extension.

Jaw teeth in a specimen c. 245 mm SL (ZMA 105.133, with wide open mouth) small recurved, simple, pointed, densely in well-defined bands that widen symphysiad, symphysis naked, upper jaw band anteriorly wider than lower jaw band. Anteriorly teeth less than 1 mm long, posteriorly gradual size decrease. On first gill-arch in that specimen, and a 92.4 mm specimen (NRM ZISP593) figured (Fig. 104, 105), externally seven epibranchial, one in angle (or rather epibranchial) and 15-16 ceratobranchial rakers; rostrally (on first hypobranchial) three weakly denticulated dermal plates. Length of rakers increasing to the uppermost ceratobranchial, which c. 8 mm long in the larger fish, then again decreasing, last three epibranchial rakers small to rudimentary. Longer rakers rostrocaudally compressed and gradually slenderer distad; all strongly denticulated along medial edge. Inner rakers short, denticulated apically. A soft dorsal ridge along ceratobranchial, but no transverse soft ridges.

Seven or eight epibranchial rakers, one in epi/ceratobranchial joint; 14 (1), 15 (5), 17 (4), 18 (10), 19 (4) - (1) rakers on lower limb in measured specimens - number decreases with increasing SL apparently because lower rakers, especially anterior three, which lie on first hypobranchial, tend to become plate-like and are not easily seen or felt on well-preserved specimens. Actual number therefore is apparently 18 or 19, including three hypobranchial.

A single specimen (NRM 11310) radiographed has 19+16 vertebrae and 2 supraneurals.

Coloration: Coloration extremely variable, but this variation due, as it appears, mostly to ontogenetic changes and state of preservation. Brightly coloured large specimens presumably present a special breeding coloration. Bar numbering is from young specimens (q.v.).

299 mm male (right side): Underside yellowish white from caudal-fin base to throat and in a zone along ventral sides. Back dark grey, with narrow black scale edges, flanks lighter, brownish. Nape in advance of a line from the gill-cleft obliquely forwards and upwards across nuchal hump, blackish. Forehead, snout dark grey to blackish. Preorbital brown-grey. Cheek brownish, dirty grey-whitish on naked ventral part. Preoperculum brown-grey, except interopercular edge, which grey-white, and dull silvery vertical margin. Operculum grey-brown, suboperculum lighter ventrad. Interoperculum whitish save for brownish scaled area. Lower jaw end white. Upper lip grey, darker symphysiad, lighter caudad; maxillary skin ablabially blackish. Tip of maxilla and lower edge of lower lip whitish; upper edge and tip of lower lip grey. Lower jaw whitish, greyish adlabially. Branchiostegal membrane and intermandibular area greyish white.

Scale centers on back and sides light; on back tending to opalescent; on sides faint opalescent spot basally on most scales, especially below upper lateral line section. Scattered silvery spots on caudal peduncle sides.

Markings: Small black spots irregularly behind orbit, two on cheek, one preopercular, one anterior and two faint posterior opercular, one on subopercular posterior

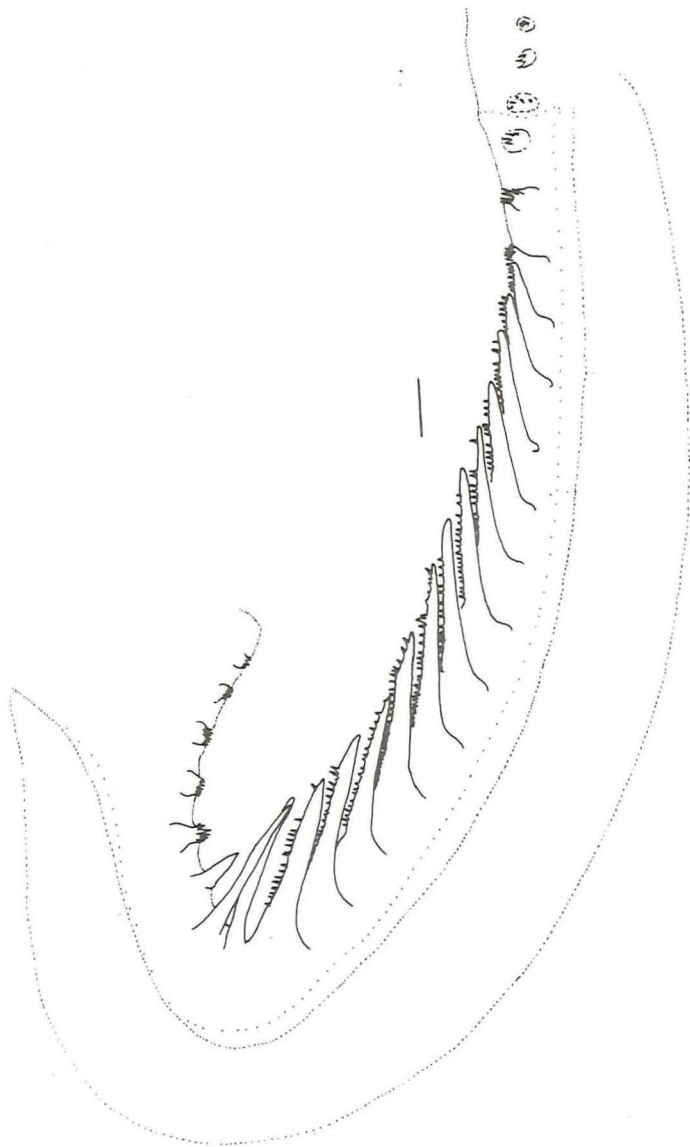


Fig. 104. *Cichla ocellaris*. First gill-arch in external aspect. Scale 1 mm. From NRM ZISP593, 92 mm SL.

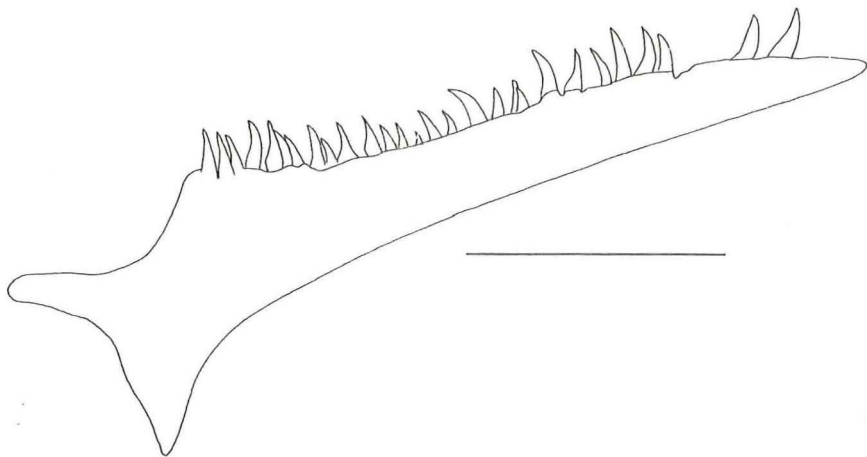


Fig. 105. *Cichla ocellaris*. Lateral aspect of second from posteriormost external gill-raker on first ceratobranchial. Scale 1 mm. From NRM ZISP593, 92 mm SL.

process; more or less ocellated by opalescence. A blackish stripe over mouth angle to preoperculum. On flanks shadows of Bars 1a and 2a; Bars 1, 2 and 3 expressed chiefly as large irregularly shaped blotches dorsally (extended vertically to level of lower lateral line section); ringed with white to silvery or opalescent bright spots, most prominent around Bar 3 spot. Inside of pectoral axilla brown; just anterior to axilla a blackish brown spot with light to silvery hind margin. Under addressed pectoral-fin a large uneven blackish brown spot ringed with silvery white spots, and succeeded caudad and slightly dorsad by three similar, minute spots, one chiefly in Bar 2, the last, in Bar 2a. Shape and precise position of postorbital head spots, dorsal blotches and those before and behind the pectoral axilla slightly different on the both sides of the fish.

Dorsal-fin with the anterior eight membranes blackish brown, every second membrane base with a pale to opalescent spot; posteriorly mottled dark brown and light. Soft fin brownish, paler towards distal margin, covered by large light spots, especially prominent posteriorly. Anal-fin mottled brownish, edge narrowly dark. Caudal-fin light brownish with large, indistinct light spots on dorsal lobe and along middle; close to base, above lower lateral line section level a black spot with white to silvery spots contained in a pale ring around, diameter little less than that of eye. Pelvic fin brownish outwardly, lighter inwardly.

299 mm specimen is the only specimen available with three large dorsal flank ocelli.

Young fish (from ZMA 105.083, 47.6 mm SL) are yellowish white on underside and lower part of head, trunk and caudal peduncle, up to pectoral axilla level. Dorsum brown grey, sides lighter. Nape and forehead brown-grey. Lower lip white posteriorly, grey anteriorly. Upper lip grey dorsally and along margin, white caudally and ventrally. Preorbital greyish. Cheek silvery dorsally; operculum, preoperculum and suboperculum greyish with some silver especially anteriorly on operculum and suboperculum. No pre- or postorbital dark stripes. A pale narrow stripe obliquely dorsad-rostrad across nape from gill-cleft.

Along middle of sides three dark spots, (1) dark-brown, roundish just posterior to pectoral axilla level, below upper lateral line section, with faint narrow dorsal extension; (2) faint, brown, above vent, with fainter extensions dorsad and ventrad; (3) dark-brown, horizontally extended, above soft anal-fin, with fainter extension along caudal peduncle middle to caudal base spot.

Spinous dorsal-fin smoky, soft fin clear with dark spot on each ray base. Anal-fin clear, base narrowly dusky. Pelvic-fin clear. Caudal-fin faintly smoky, especially medianly; midbasally a roundish spot, slightly extended caudad; large whitish spot dorsocaudal and ventrocaudal to base spot.

This colour pattern is found in specimens up to about 55 mm; then short vertical bars develop, the first (Bar 1) with the first spot in center, the second (Bar 2) absorbing the second spot. Specimens c. 60-70 mm develop large light spots on the back, two horizontal dark bands outwardly in the soft dorsal-fin; occasionally narrow dark vertical shades behind Bar 1 (=Bar 1a), and behind Bar 2 (=Bar 2a); a bar (Bar 3) may also show through the anterior part of the third flank spot; light spots preceding caudal spot still indistinct. Specimens c. 70-80 mm have light spots also on sides (or only on the sides), well-developed vertical bars (1, 1a, 2, 2a, 3; but a-bars not always apparent); the third flank spot tends to become absorbed by Bar 3, the caudal base spot tends to be isolated from caudal peduncle pigment, and lighter spots around brighten. At 90-100 mm, no flank spots remain, the soft dorsal-fin becomes light-spotted and the isolated caudal base spot tends to take a more dorsal position than in smaller fish. Specimens c. 130 mm have light spots on the back, side spots whitish or silvery, the caudal base ocellus is ocellated and lies dorsal to the lateral line, a-bars always distinguishable. Specimens 161 mm and larger develop an ocellated spot dorsally in Bar 3 and spots behind pectoral axilla appear. Specimens over 200 mm have lost the light back spots and on the sides they also disappear, Bar 3 is lost at larger sizes, but Bars 1 and 2 have dark spots dorsally and all have more or less of spots behind the pectoral axilla.

Large adults (>200 mm) are more or less brownish with light underside. The vertical bars are pointed ventrally. The Bar 3 ocellus usually is roughly boomerang-shaped with apex directed rostroventrad. There is commonly a second caudal ocellus below the lower

lateral line level, contiguous or not with the major ocellus. A spot or bar is more or less evident from the gill-cleft, obliquely forwards and upwards to the nape sides (in very young, the posterior light margin is more conspicuous, in the 299 specimen contiguous with dark anterior nape). Small silvery scale-center spots are found in about half of the specimens over 200 mm, more or less neatly arranged in horizontal series on flanks and caudal peduncle; in those without, the sides are indistinctly light/dark marbled.

Holotype. Schneider (1801) afforded *Cichla ocellaris* a very fine plate (no. 66) besides the description: 'Cichla with large gape, oblique, lower jaw long, pointed, with small teeth in single series, two dark transverse stripes, large black spot at end of dorsal-fin, black ocellus bright white at base of rounded and scaly caudal-fin, lateral line descending towards anal-fin, whereafter straight, dorsal-fin with middle hollowed, basally scaly, scales small, vent far back. Branchiostegal rays 5. P. 15. V. 1/6, A. 3/14, C. 20, D. 15/32. Habitat as the preceding /India orientali/.' (Translation from the Latin). That part is probably by Bloch; a note appended by Schneider is open to various interpretations: 'Branchia spura nulla, nec maxillae branchiales, sed ossa duo aspera in palato extremo. Schn.'

The specimen has since been studied only by Müller & Troschel (in Schomburgk 1849) who merely remarked on the dextrally interrupted, sinistrally continuous lateral line.

The stated type-locality, 'India orientali', is certainly an error, either from incorrect original locality data, or a lapse in the compilation of the manuscript of Schneider (1801). It is very likely that the fish came from Surinam as this country is a common source of 18th century South American natural history objects.

The holotype is preserved in relatively fine condition, somewhat soft and slightly discolored. It has 7 or 8 series of teeth in the upper jaw, about five in the lower jaw, not a single series as stated in the original description, apparently an observation lapse (already subjected to Heckel's (1840) sarcasm).

The specimen is a female 183.4 mm SL, 219.7 mm TL, agreeing excellently with Surinamese *Cichla* of the same size. The shape and remains of colour pattern are apparent from Plate XV, fig. 2; measurements are given in Table 38. It departs from Surinamese *Cichla* only in the scaly pectoral-fin base, and is notable for having the right side lateral line interrupted (as pointed out by Müller & Troschel).

In shape it departs from the specimen described above chiefly in lacking a nuchal protuberance. Squ. long. 71. First infraorbital scaly abduccally; most of predorsal midline naked. Pectoral-fin base, on left side also adjacent pectoral axilla, scaly between rays 1 to 10. Pelvic-fin scaly anteriorly on both sides. Dorsal-fin scales running in single series on soft fin membranes except last four; series gradually shorter posteriorly on fin. Anal-fin heavily scaly anteriorly, to edge of fin, squamation gradually restricted to base posteriorly, last membrane naked. Left side lateral line smoothly continuous, on right side interrupted, with two horizontal scale series separating the sections (41/34); four tubed scales on caudal-fin base, continuing lower lateral line, and long tube series, to distal edge of fin squamation, on membranes D3-D4, V4-V5 on right side, D3-D4, V3-V4, V4-V5 on left side. D. XV.18, A. III.11, P. 14. Soft dorsal- and anal-fins with rounded tips, not reaching to base of caudal-fin. Caudal-fin lower lobe regenerated, hind edge damaged, otherwise appearing truncate. Rakers 7+1+18.

Back olivaceous, middle sides somewhat lighter, below pectoral-fin base level yellowish, abdomen greyish. Traces of narrow, ventrally narrowed dark Bars 1 and 2 from halfway between lateral line and dorsal-fin down to lower lateral line level. Angled but irregular brown blotch above lower lateral line anteriormost portion with a few silvery dots around it; scattered silvery dots also anteriorly on flanks associated with Bars 1 and 2. Soft dorsal-fin dusky with large round pale yellowish spots. Anal-fin immaculate. Caudal-fin with dorsal dark brown ocellus, with bright white semicircle anteriorly, paler white semicircle posteriorly, trace of another, contiguous spot on lower lateral line level; large light spots on soft portion.

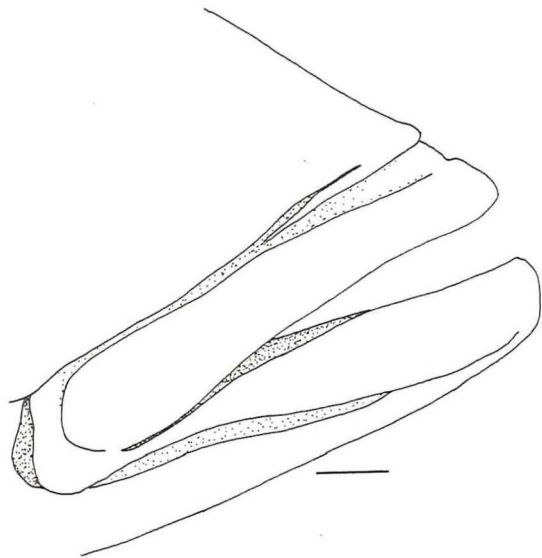


Fig. 106. *Cichla ocellaris*. Snout tip in lateral aspect, to show interrupted lip folds and African type lower lip attachment to maxilla. Scale 1 mm. From NRM A82/3425, 50 mm SL.

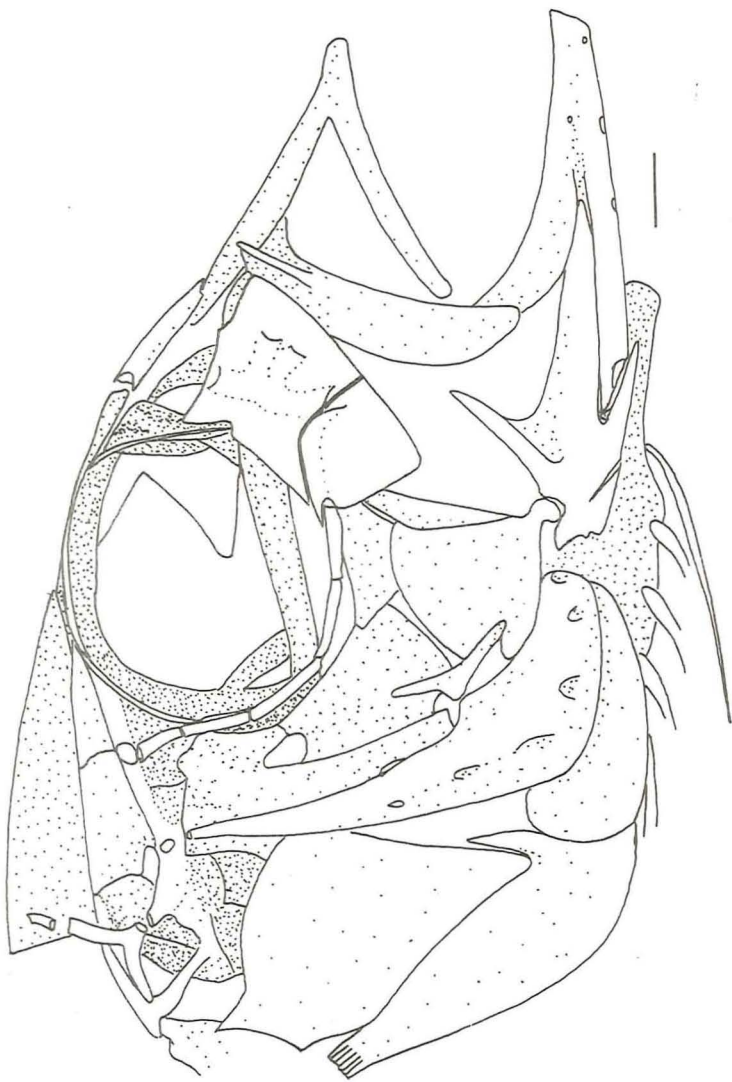


Fig. 107. *Cichla ocellaris*. Cranium, lateral aspect. Scale 2 mm. From NRM A82/3426, 71 mm SL.

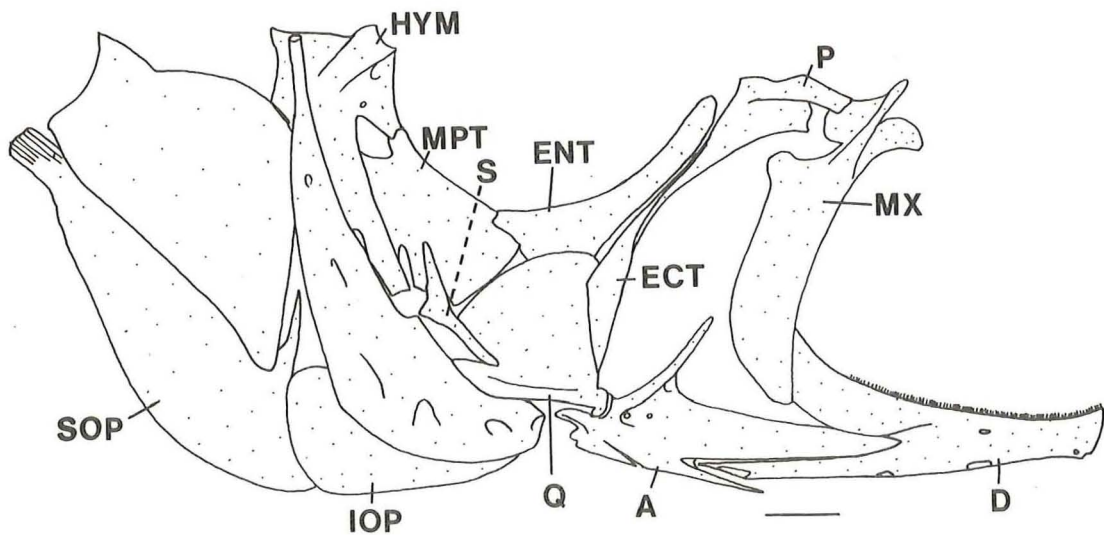


Fig. 108. *Cichla ocellaris*. Lateral aspect of suspensorium. Scale 2 mm. A anguloarticular, D dental, ECT ectopterygoid, ENT entopterygoid, HYM hyomandibula, IOP interoperculum, MPT metapterygoid, MX maxilla, P palatine, Q quadrate, S symplectic, SOP suboperculum. From NRM A82/3426, 71 mm SL.

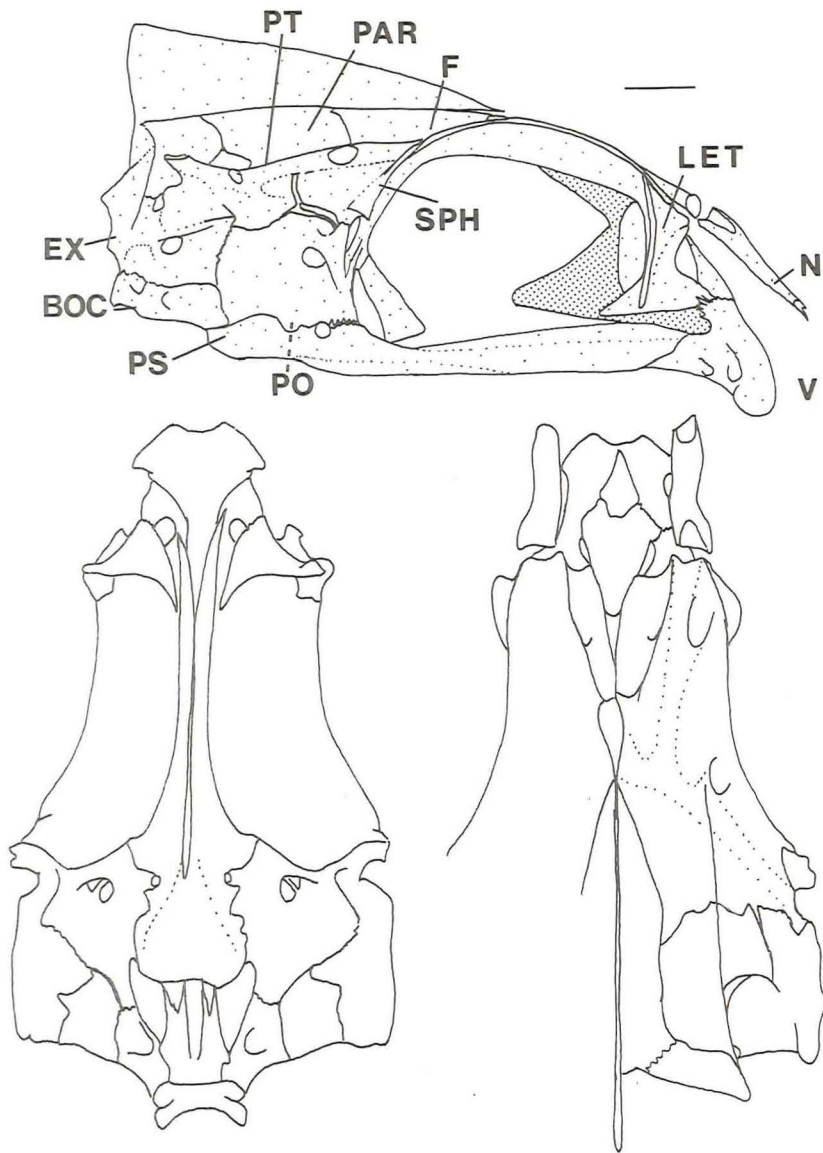


Fig. 109. *Cichla ocellaris*. Neurocranium in lateral (top; cartilage stippled), ventral (left lower), and dorsal (right half chiefly, lower right) aspect. Scale 2 mm. BOC basioccipital, EX exoccipital, F frontal, N nasal, PAR parietal, PO prootic, PS parasphenoid, PT pterotic, SPH sphenotic, V vomer. From NRM A82/3426, 71 mm.

Osteology. Notes taken from a 71 mm specimen, cleared and stained with alizarin and alcian blue (Figs. 107-114. NRM A82/3426 - Alizarin 44, Brokopondomeer, 31 Aug. 1966). Branchiocranial structures are as described by Machado (1973) and Stiassny (1982).

Notable cranial features include the relative elongation of the skull as well as many skeletal elements. The supraoccipital crest is relatively low (Figs. 107-109).

The dorsal skull lateralis canal has foramina at the ends of a the long tubiform nasals, five frontal foramina of which the rostralmost faces the posterior nasal foramen, another caudal and lateral to it, one opening forming a joint coronalis opening with that of the opposite sides (medial frontal ridge very low), one lateral to the anterior end of the narrow frontoparietal crest, and one opening jointly with the rostral of three pterotic foramina. Deep narrow fossa anterolateral to the median canal opening, end blind close to the divide of the transverse canal.

The parasphenoid has a feebly developed articular apophysis and surface just anterior to the parallel projections forming a symphysis with the basioccipital. The basioccipital has marked bilateral ridge-like ventral processes for the attachment of Baudelot's ligament. Rostrally, the basioccipital contributes marginally to the support for the apophysis otherwise formed by the parasphenoid, but do not seem to enter the articulating area.

The palatine has a long ventral spine tightly fused along the rostral margin of the ectopterygoid, reaching to the level of the quadrate. The ectopterygoid ends narrowly near the palatine head. A strand of cartilage lies along the long adjacent margins of ecto- and entopterygoid. A narrow laminar expansion of the ectopterygoid overlaps the rostral margin of the quadrate, but does not extend to the articular head of the quadrate. A laminar narrow expansion of the quadrate overlies the dorsal margin of the rostral portion of the preopercle. The symplectic has a laminar dorsal projection up between the cartilage-filled laminar ventral expansions of the metapterygoid.

The preoperculum (Fig. 110) is slender, little angled, with rather short vertical limb margined with cartilage ventrally. There are seven canal openings, one at each end, two facing ventrad-laterad on the lower limb, and three caudad on the vertical limb, the dorsalmost more laterad than the lower two.

The suborbital series (Fig. 110) consists in a lachrymal and six infraorbitals. The lachrymal has a dorsal, two rostral and one ventral canal opening. The first infraorbital is broad and chiefly laminar and contiguous with the lachrymal; dorsally runs a canal which rostrally has a joint opening with the ventral foramen of the lachrymal canal. The five succeeding infraorbitals are simple canals, partly overlapping at the ends; the first overlies the caudodorsal tip of the preceding infraorbital, and the last is notable for being inclined caudad away from the sphenoid.

The premaxillary (Fig. 111) alveolar processes are slightly longer than the ascending, and carry teeth to near the distal tip, the proximal tip is separated from that of the opposite side premaxilla by a distinct though narrow gap. The articulating process is slightly shorter than the medial process. A long canal penetrates the ascending process, opening on the caudal face by a wide foramen slightly ventral to the tip of the articulating process, between it and the medial process.

The maxilla (Fig. 111) is long, with nearly straight anterior blade margin, and a prominent posterior process near the articulating head.

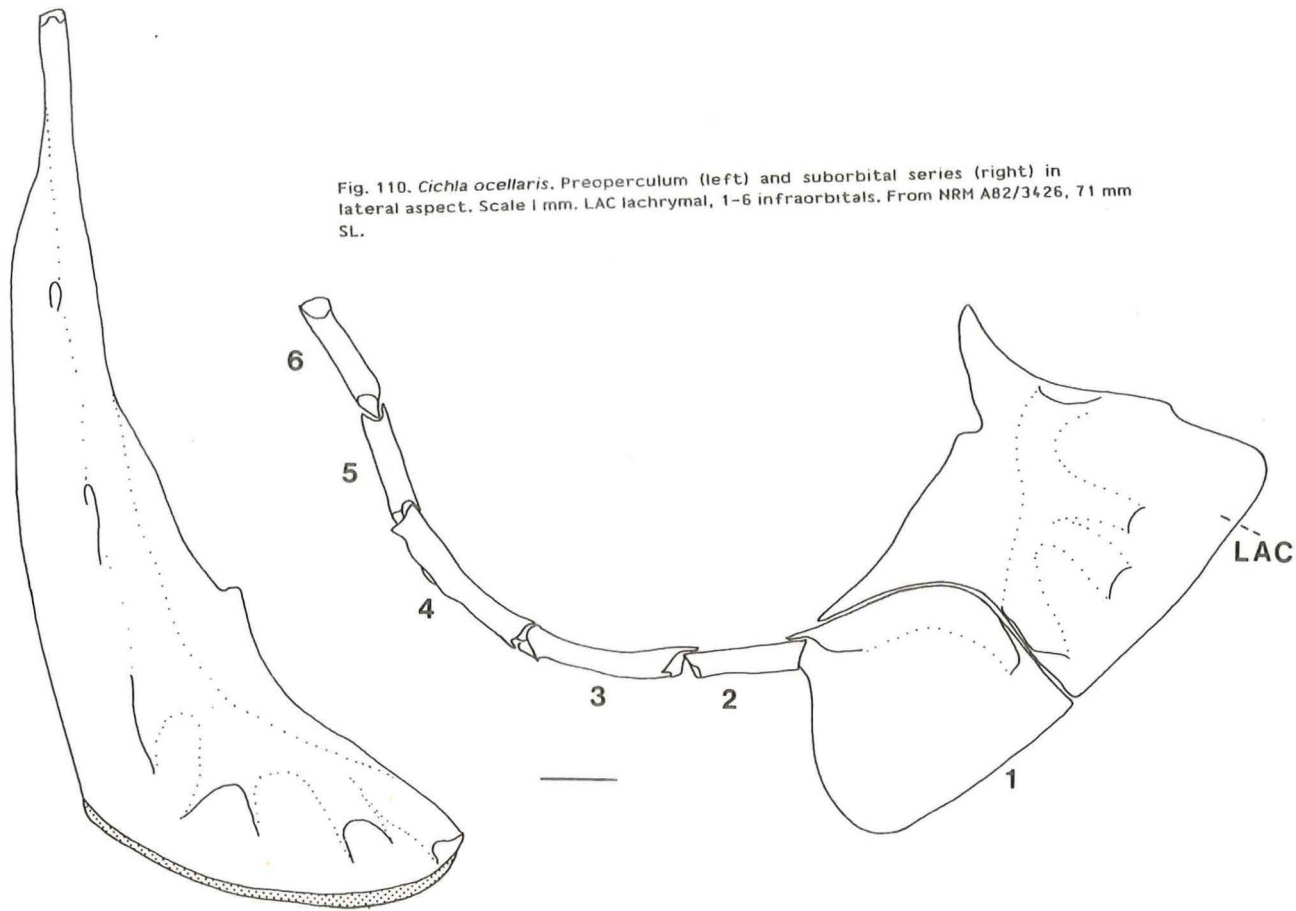
The long dentals (Fig. 112) are united symphysially; the canal-bearing limb has five lateralis foramina. Medially on the anguloarticular is a minute coronomeckelian over the caudal end of the Meckelian cartilage. The retroarticular is recognizable as a separate element. The ascending spine of the anguloarticular is long and prominent, and the ventral process is wide and projects rostrad of the caudalmost dental lateralis foramen.

The dental and the alveolar processes of the premaxilla are extensively toothed. The teeth are small, strongly linguad-curved and depressible, separated from the basal attachment bone stub by an unstained gap. Teeth in about three crowded series on dental, five on premaxilla.

18 + 17 vertebrae, hardly evident ventral apophyses on third vertebra, but opposing ventral parts of 5th and 6th abdominal vertebrae strengthened.

Basapophyses from third vertebra, closed haemal arches behind three last abdominal centra.

Fig. 110. *Cichla ocellaris*. Preoperculum (left) and suborbital series (right) in lateral aspect. Scale 1 mm. LAC lachrymal, 1-6 infraorbitals. From NRM A82/3426, 71 mm SL.



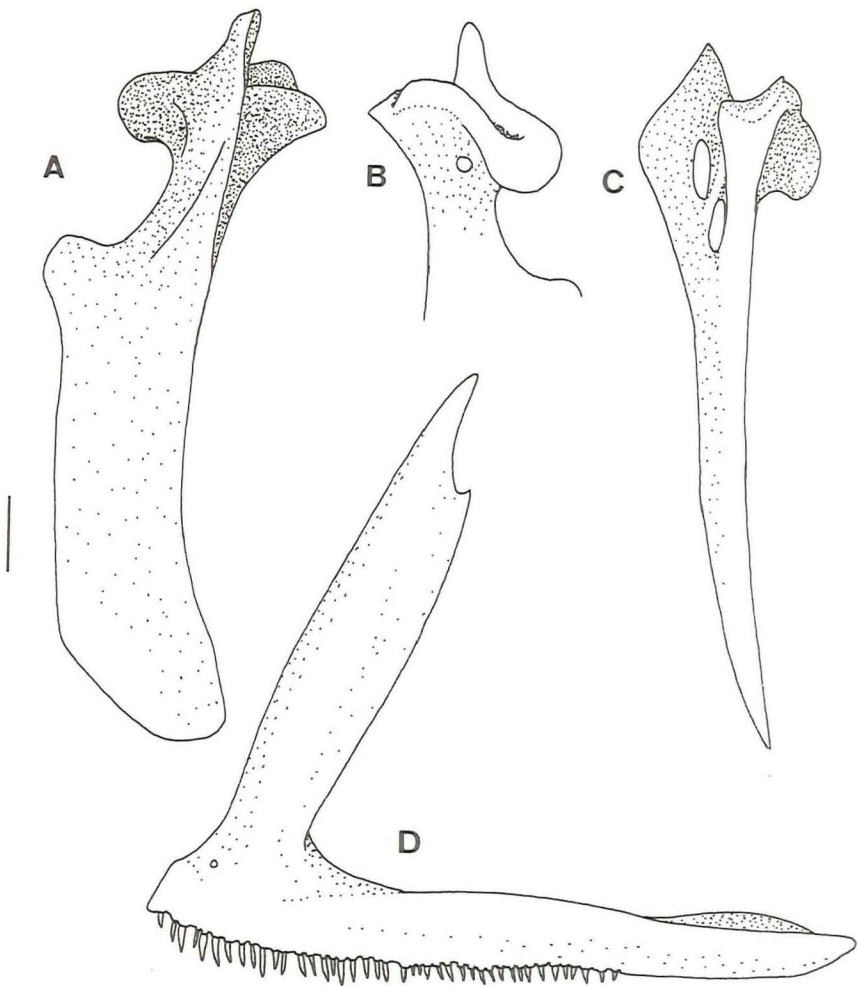


Fig. 111. *Cichla ocellaris*. Upper jaw elements. A, right side maxilla in lateral aspect; B, right side maxillary head in medial aspect; C, right side maxilla in rostral aspect; D, left side premaxilla in rostral aspect. Scale 1 mm. From NRM A82/3426, 71 mm.

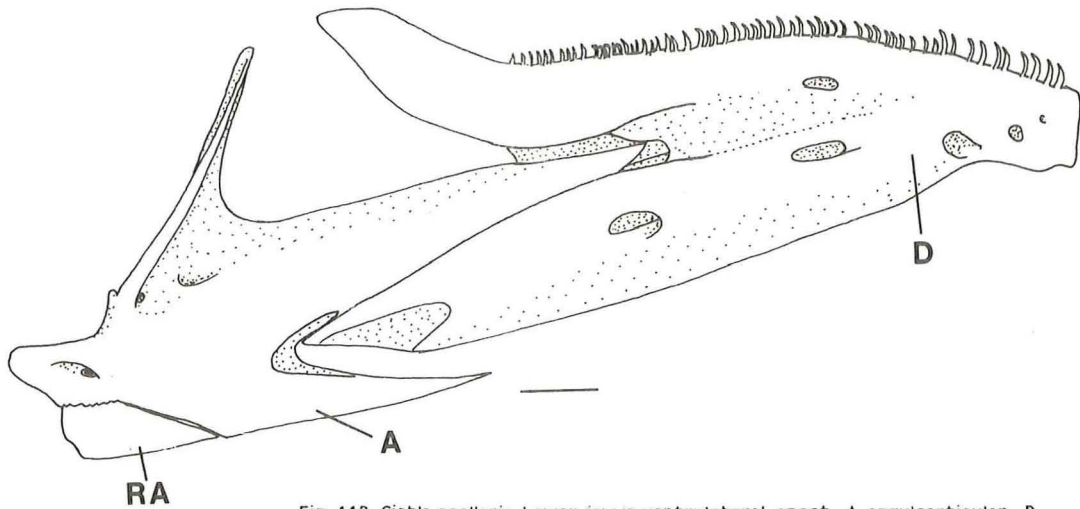


Fig. 112. *Cichla ocellaris*. Lower jaw in ventrolateral spect. A anguloarticular, D dental, RA retroarticular. Scale 1 mm. From NRM A82/3426, 71 mm SL.

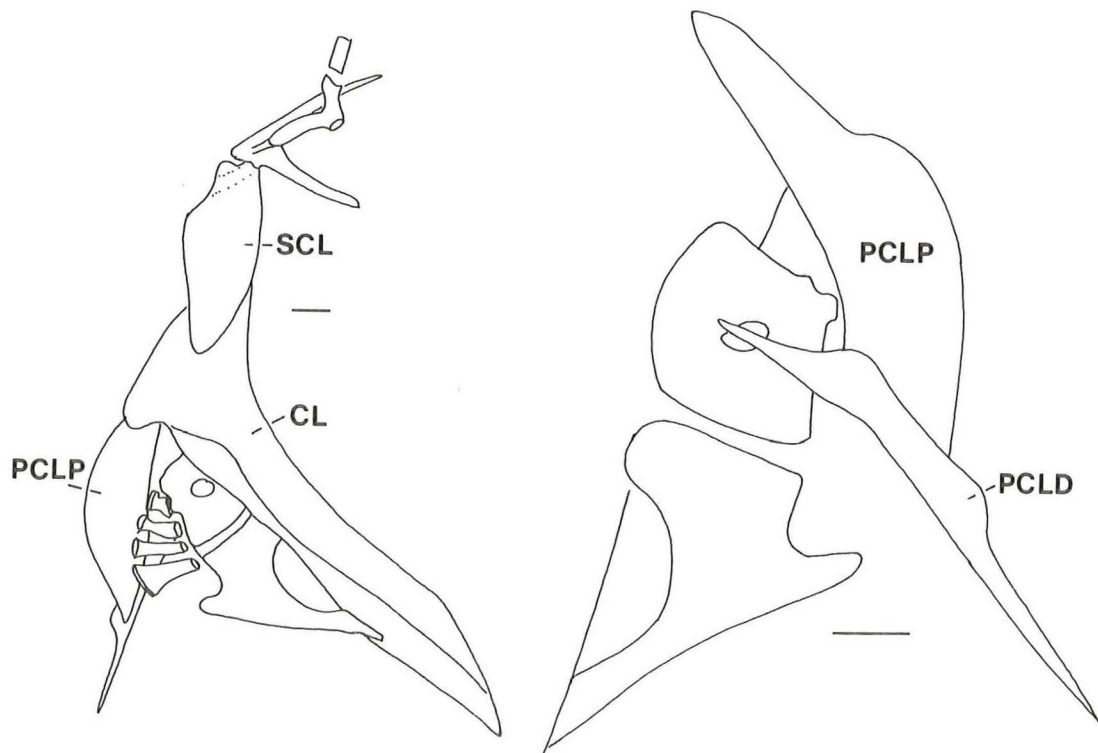


Fig. 113. *Cichla ocellaris*. Right side pectoral girdle in lateral aspect (left) and part of same in medial aspect (right). Scales 1 mm. CL cleithrum, SCL supraclavicle, PCLD distal postcleithrum, PCLP proximal postcleithrum. From NRM A82/3426, 71 mm SL.

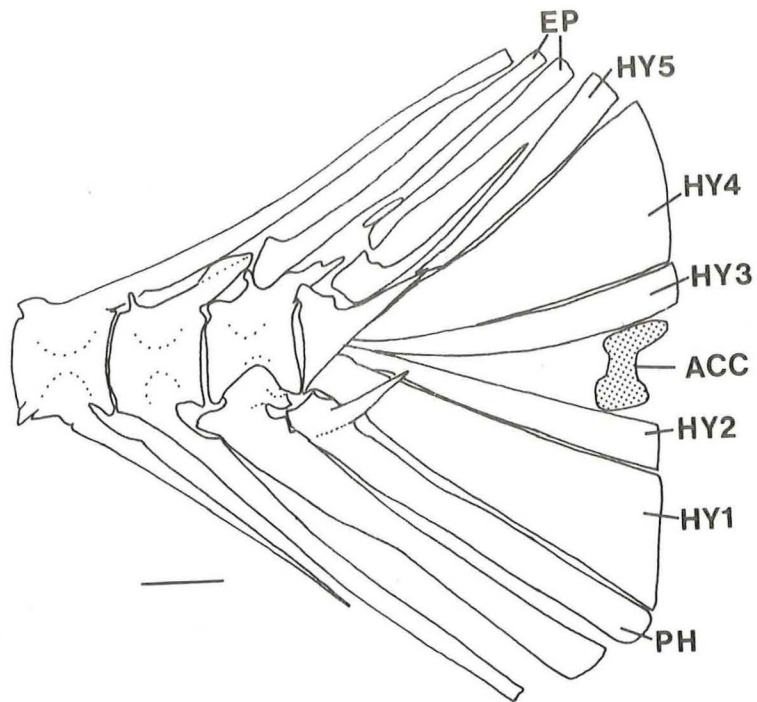


Fig. 114. *Cichla ocellaris*. Caudal skeleton. Scale 1 mm. ACC median interhypural cartilage, EP epurals, HY1-5 hypurals, PH parhypural. From NRM A82/3426, 71 mm SL.

The posttemporal lacks a caudad directed distinct canal opening, but is not closed next to the posttemporal opening of the proximal extrascapular canal. The distal postcleithrum has a prominent rostrad directed spine-like process (Fig. 113).

The caudal skeleton (Fig. 114) is probably atypical in this specimen, in which the neural spine of the fourth caudal vertebra forms part of the ray support, and that of the third is reduced. The first epural articulates with the second vertebra. A prominent parhypural spine. Rostral to the proximal tip of the second epural is a splint of bone, that may be abnormal. All hypurals (3 epaxial, 2 hypaxial) are separate; between the 2nd and 3rd is a piece of cartilage free from the remaining cartilage, viz. ventral and dorsal plates and ends of epurals and hypurals, and a strand slightly distal along the caudal skeleton. Nine procurrent and eight principal rays in each lobe.

Discussion

The genus *Cichla* takes a central position in cichlid systematics, not only for being 'type' of the family, but because of its strikingly perch-like outward appearance (Plate XV, fig. 2), especially the dorsal-fin, colour, and continuous lateral line, and also some internal features reminding both of lower percoids and African rather than other South American cichlids.

Although Regan (1906b) considered Acara (= *Aequidens*, *sensu lato*) the most primitive South American cichlid genus, he illustrated the phyletic position of *Cichla* as a lineage separated at the base from the rest. Reasons were not stated. In 1920, he proposed a difference in the composition of the basicranial pharyngeal apophysis as a basis for dividing African cichlids into two groups, and remarked, in the passing, that 'all the American Cichlidae (except *Cichla*, which resembles *Haplochromis*) have the pharyngeal apophysis formed as in *Tilapia*'. The *Haplochromis* type apophysis is formed by the parasphenoid medially, and the basioccipital laterally; the *Tilapia* type apophysis is formed by the parasphenoid alone (but cf. revision in Greenwood 1978).

The pharyngeal apophysis of cichlid fishes has been of some importance to intrafamilial grouping attempts (eg. Hoedeman 1947), but a survey of the African species showed a variety leading Greenwood (1978) to conclude that its value is doubtful. The South-American cichlids that I examined tend to resemble rather the *Tylochromis* type, distinguished by Greenwood, in which the prootic is excluded from the formation of the apophysis, as in *Tylochromis*, *Eetroplus*, and *Paretroplus*. In *Cichla*, like in other South American cichlids examined, the basioccipital forms some support for the parasphenoidal apophysis, but it seems to be excluded from the articulating surface. Notable for *Cichla* is, however, the very feebly developed apophysis, and the strong admedian ligament ledges of the basioccipital.

Machado (1971, 1973) did a detailed study of *Cichla* taxonomy and osteology, but he looked only for species differences and had no comments on the phylogenetic value of the numerous characters that he studied. A set of characters in different systems were studied and analysed by Stiassny (1982), who arrived at the conclusions that *Cichla* is an advanced form probably related most closely to *Crenicichla*.

The only generic character emphasized by Machado (1973) is the J-shaped (Travassos & Pinto 1958a) preoperculum, but it is seen in several other cichlids, and I doubt that there is a natural break of phylogenetic significance between L- and J-shaped preopercles.

Stiassny (1982) attempted to clarify the phyletic position of *Cichla*, and presented some muscle and skeletal features judged to be apomorphic. She maintained that the lower pharyngeal jaws diverging posteriorly with a large denticular area, origin of the *m. pharyngocleithralis internus* on the lateral face of the cleithrum (also in *Crenicichla*), an elongate and strongly rostrad directed urohyal spine, a unique pars dorsomedialis of the *m. sternohyoideus* between the cleithrum and urohyal, increased number of microgillrakers, arrangement of ligaments and muscle-attachments associated with the maxilla, a cartilage plate between hypurals 2 and 3, a rostrad directed spine on the distal postcleithrum (also in *Crenicichla* and *Serranoides*), and an increased number of abdominal vertebrae (also in *Crenicichla*, *Serranoides* and *Rhamphochromis*) are apomorphic features of *Cichla*, and notes only in passing some lower percoid, non-cichlid features. She ends with suggesting a close relationship to *Crenicichla*.

I have not reexamined the muscle-systems, but do have comments on the other characters. A great majority of the character states studied in *Cichla* (see especially Machado 1973, Regan 1906b, for data additional to those given in the above description) appear to be plesiomorphic. As an autapomorphy I can suggest only the form and position of the symplectic. It seems then somewhat wishful thinking to suggest, as Stiassny does, that the branchiocranial anatomy of *Cichla* insofar as it resembles lower percoids, would be a character reversal instance. Admittedly, *Cichla* may very well be adapted for swallowing large prey, by the elastic branchiocranium and the movable teeth, but it need not be derived relative to other cichlids in those respects.

The jaws of *Cichla* are rather long, yet appear unspecialized. The ascending processes of the premaxilla are relatively short and not much protractile, compared to advanced South American piscivorous cichlids. The premaxilla is notable, however, for not having a large foramen medially on the lateral face of the ascending process. The maxilla is long and straight, but far from the length of advanced piscivorous cichlids like *Caquetaia*. The lower jaw is rather shallow and flat, but quite long. The anguloarticular is notable for the long ventromedial process, similar to that in geophagines. The teeth are completely movable, also the pharyngeal teeth, a condition found also in *Crenicichla*, but, as should be noted, also in *Perca*, and many other teleosts (type 4 teeth in Fink 1981b).

A putative autapomorphic character of *Cichla* is in the shape of the symplectic. In all other cichlids (and fishes) that I have seen, the symplectic ends truncated in the cartilage field lateral to the suspensorial hinge of the interhyal. Machado (1973) described the symplectic with the same form, hence my specimen would not likely be abnormal.

The number of microgillrakers is not increased, and they are not of the modal cichlid type, but of a special, primitive form. The axial accessory cartilage of *Cichla* is found also in some geophagines, and rudimentary in *Crenicichla* and *Aequidens*. Some kind of bud or minor process is commonly present proximally on the distal postcleithrum in South American cichlids, and is *Cichla*-like in some Percichthyids (Arratia, 1982), *Serranus* (Stiassny 1982) and *Stizostedion* (pers. obs.). This would also seem to be a plesiomorphic, at least hardly a convincing apomorphic feature. The abdominal vertebral number (totals = 19+16, 18+17; Regan 1906b, Machado 1973, *supra*) would seem to be ancestral, as pointed out above. A long forwards pointed urohyal spine characterizes also centropomids (Greenwood 1976, Fig. 21), and *Polyprion* (Percichthyidae?; Arratia 1982, Fig. 38).

Considering then, the lateralis system, the infraorbitals, the posteriorly separate (not 'diverging') lower pharyngeal jaw elements, lateral position of the second pharyngobranchial, long epibranchials, the gill-raker number and shapes, slender pharyngobranchial 3 with small dorsal articulation facet, the dorsal-fin shape, continuous lateral line, scaly fins, triradiate caudal-fin lateral line, many procurrent caudal-fin rays, the basioccipital ligament processes, and other plesiomorphic features as listed by Stiassny (1982); perhaps also the depressible teeth, *Cichla* would seem to illustrate the idea that a large generalized piscivore taking large prey is most likely plesiomorphic form to survive relatively unchanged in a high-diversity region like tropical South America. *Cichla* may also have the most primitive karyotype of Neotropical cichlids (Thompson 1979). The problem may be rather asserting the relationships of *Cichla* with any of the lower percoid families. Within the Cichlidae, evidence is conflicting, and outgroup comparisons are needed to see if any of the strong resemblances to *Crenicichla* (Stiassny 1982) or geophagines (p. 309) or African cichlids may contain some decisive apomorphic character.

It may be worth noting that there is a positive correlation in large size, few species in a group, predatory behaviour, and relative ancestry among South American fishes in general. The two nandid species are predators, though of smaller size, isolated members of a family with representatives otherwise in Africa and Asia. The osteoglossids, *Osteoglossum* with two, and *Arapaima* with one species, are large predatory fishes of a relict group. Erythrinids are large predatory characoids that may be the most primitive members of the Characoidea.

Selection pressure appears to affect chiefly non-predators of small to moderate size. Clearly, a fish taking prey of a quarter its own size or more, as *Cichla* and

Hoplias may do, have little food and energy problem in South America, and can stay relatively unmodified. Fish taking prey much smaller than their mouths on the other hand, cannot afford to be generalists in a diverse community, but must elaborate on optimum trophic structures to efficiently utilize food available to them. Preferably, they should reduce size to utilize a larger class of suitable food items and specialize mouth parts and dentition. As small size likely affects dispersal capability, there is here a, partial at least, explanation for the diversity of advanced minute forms in South America.

The large piscivores, like *Cichla* are certainly highly specialized as predators, but may have been so long before the present diversity of the tropical South American fish fauna started to develop.

CICHLASOMA

Plesiops (Cichlasoma) Swainson, 1839. *Nat. Hist. Fish.* 2, p. 230 (type by monotypy *L. punctatus* Linnaeus pt. = *Labrus bimaculatus* Linnaeus as restricted)

Plesiops (Cichlaurus) Swainson, 1839. *Nat. Hist. Fish.* 2, p. 173 (variant spelling of *Plesiops (Cichlasoma)*).

Cichlosoma Regan, 1905. *Ann. Mag. nat. Hist.* (7) 16, p. 61 (unjustified emendation of *Cichlasoma*).

Cichlasoma amazonarum Kullander, 1983. *Revision Cichlasoma*, p. 115, Pl. V, fig. 2 (Peru, depto Loreto, R. Ampiyacu system, little upstreams of Pebas, Sacarita del Tuyé, right bank tributary of the R. Ampiyacu, floating meadow near mouth).

Cichlasoma araguaiense Kullander, 1983. *Revision Cichlasoma*, p. 252, Pl. XIV, fig. 1 (Brasil, est. Mato Grosso, R. Araguaia system, small Igarapé tributary to Igarapé Sangadina, tributary to the R. das Mortes, 1 km from Xavantina).

Labrus bimaculatus Linnaeus, 1758. *Syst. Nat. ed. 10, 1*, p. 285 (M. Mediterraneo).

Acara Gronovii Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 361 (Flüsse in Surinam).

Sparus filamentosus Gray, 1854. *Catal. Fish. Gronow*, p. 60 (Surinami).

Cichlasoma boliviense Kullander, 1983. *Revision Cichlasoma*, p. 165, Pl. VIII, fig. 2 (Bolivia, depto Santa Cruz, R. Guaporé system, R. Uruguaito, tributary of the R. Quizer, 13 km S San Xavier).

Acara dimerus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 351 (Cujabá-Fluss).

Acara marginatus Heckel, 1840. *Annln Wien Mus. Natges.* 2, p. 350 (der Nähe von Cujabá).

?*Heros centralis* Holmberg, 1891. *Revta Argent. Hist. nat.* 1, p. 183 (República Argentina, Provincia de Santiago del Estero).

Cichlasoma orientale Kullander, 1983. *Revision Cichlasoma*, p. 177, Pl. IX, fig. 1 (Brasil, est. Ceará, R. Curu system, Pentecoste, reservoir).

Cichlasoma orinocense Kullander, 1983. *Revision Cichlasoma*, p. 106, Pl. IV, fig. 2 (Colombia, depto Meta, R. Meta system, Laguna Mozambique, at shoreline on N side of lake).

Cichlasoma paranaense Kullander, 1983. *Revision Cichlasoma*, p. 241, Pl. XIII, fig. 1 (Brasil, Est. Mato Grosso do Sul, R. Paraná superior system, mun. Tres Lagoas, varzea on the left bank of the R. Sucuriú, at Fazenda Santa Luzia, near Urubupungá dam).

Acara portalegrensis Hensel, 1870. *Arch. Natges.* 36, p. 52 (bei Porto Alegre in stagnirenden Gewässern).

Cichlasoma pusillum Kullander, 1983. *Revision Cichlasoma*, p. 221, Pl. XII, fig. 1 (Paraguay, depto Alto Paraná, R. Alto Paraná system, Puerto Palma).

Cichlasoma sanctifranciscense Kullander, 1983. *Revision Cichlasoma*, p. 227, Pl. XII, fig. 2 (Brasil, Est. Bahia, R. São Francisco system, Lagoa Viana).

Chromis Taenia Bennett, 1831. *Proc. Comm. Sci. Corr. zool. Soc. Lond.* 1, p. 112 (Apud Trinidad).

See Part I.

CLAVIFORAMINACARA n. gen.

Type-species: *Acara maronii* Steindachner.

Acara Maronii Steindachner, 1882. *Denkschr. k. Akad. Wiss. Wien Math.-natw. Cl.* 43, p. 141, Pl. II, fig. 4 (Maroni-Fluss in Guiana).

Character states meriting generic separation of *C. maronii* have been listed in Part I (p. 280). The characteristic head squamation and first epibranchial are shown in Fig. 115. It is a deep-bodied, strongly compressed species with steep front. The coloration is diagnostic, plain yellowish to greyish with contrasting dark markings: a dark brown stripe from nape through eye to junction of sub- and interoperculum; a black blotch on and above upper lateral line margined by narrow light vertical bars, continued fainter down the side. Fins without markings.

The generic name is feminine, and refers to the keyhole-like flank marking. Although a distinct form, no doubts have been expressed previously about the assignation of *C. maronii* to the genus *Aequidens*. The species is a biparental substrate brooder.

COERULEACARA n. gen.

Type-species: *Cychlasoma pulchrum* Gill.

Cichlosoma (Aequidens) biseriatum Regan, 1913. *Ann. Mag. nat. Hist.* (8) 12, p. 471 (Rio Condoto).

Acara coeruleopunctata Kner & Steindachner, 1863, in Kner. *Sber. k. bayer. Akad. Wiss. Münch.* 2, p. 222 (Rio Chagres im Staate Panama, Nordseite).

Acara coeruleo-punctata var. *latifrons* Steindachner, 1879. *Denkschr. k. Akad. Wiss. Wien Math.-natw. Cl.* 39, p. 27 (grossen, seeartig ausgebreiteten Ciene-ga, welche der Magdalenen-Strom mit einem seiner ostlich gelegenen Hauptarme kurz vor seiner Mündung in das Meer bildet).

Cychlasoma pulchrum Gill, 1858. *Ann. Lyc. nat. Hist. N.Y.* 6, p. 382 (/Western portion of Trinidad/).

Chromis rivulata Gunther, 1859. *Proc. zool. Soc. Lond.* 27, p. 418 (Andes of Western Ecuador).

Acara aequinoctialis Regan, 1905. *Ann. Mag. nat. Hist.* (7) 15, p. 337 (W. Ecuador).

Aequidens azurifer Fowler, 1911. *Proc. Acad. nat. Sci. Philad.* 63, p. 515, Fig. 7 (Affluent of the Chimbo River, near Bucay, Province of Guayas, Ecuador).

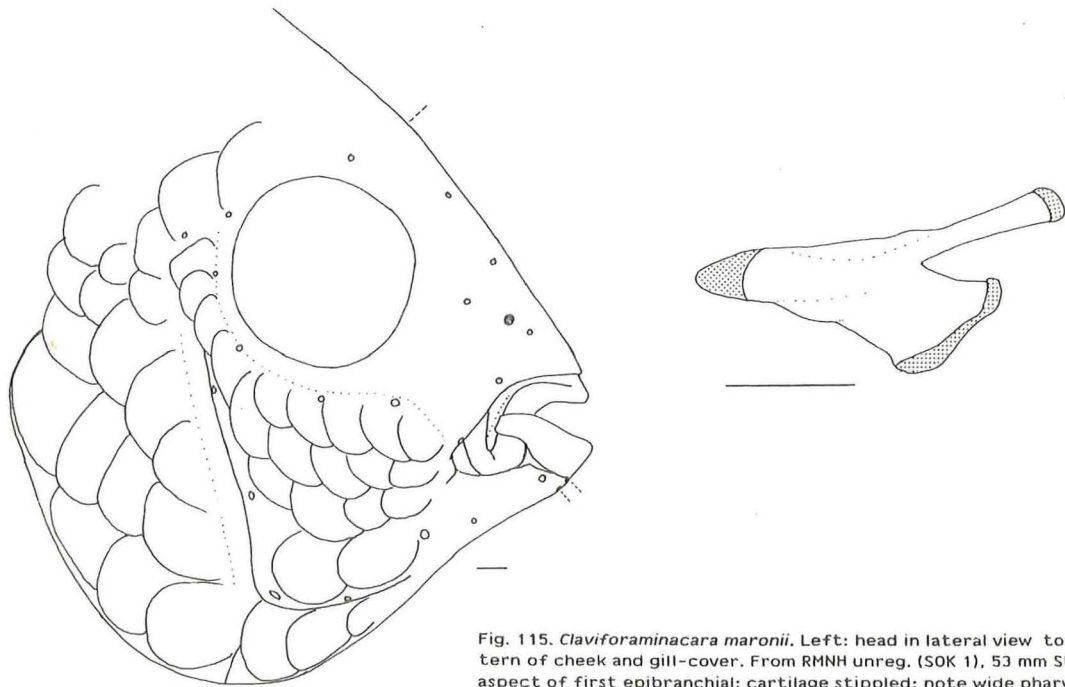


Fig. 115. *Claviforaminacara maronii*. Left: head in lateral view to show scale pattern of cheek and gill-cover. From RMNH unreg. (SOK 1), 53 mm SL. Right: laterorostral aspect of first epibranchial; cartilage stippled; note wide pharyngobranchiad 1 arm. From NRM unreg., Alizarin 4, 43 mm SL. Scales 1 mm.

Acara sapayensis Regan, 1905. *Ann. Mag. nat. Hist.* (7) 15, p. 340 (R. Sapayo).

Coeruleacara has been treated in Part I (p. 277; *pulcher* group), and is recognized on a medially expanded basibranchial 2. There is uncertainty about the validity of the species *C. coeruleopunctata* and *C. latifrons* relative to *C. pulchra* in the literature. I have seen *C. pulchra* only from Trinidad, and do not know the others well, but recognize them provisionally. There is an undescribed species similar to *C. pulchra* in the western Venezuelan Orinoco system.

There may be more Pacific slope forms species than there are names for, but I have not studied them, and the synonymy of *C. rivulata* is provisional.

A form endemic to the R. Huacamayo in eastern Peru, possibly belongs here, but may be a distinct genus. It is a mouth-brooder and has gill-rakers enlarged somewhat like geophagines. The problem with this fish is that it agrees better in morphology with Pacific slope than with Caribbean coast *Coeruleacara*. Further work on these fishes will be interesting.

The gender of *Coeruleacara* is feminine; the name refers to the rich iridescent blue lines and spots, especially on the head in species of the Caribbean group at least.

CORYPHACARA n. gen.

Type-species: *Heros temporalis* Günther.

Heros coryphaenoides Heckel, 1840. *Annin wien Mus. Natges.* 2, p. 373 (Rio-negro...bei Marabitanas).

Heros niger Heckel, 1840. *Annin wien. Mus. Natges.* 2, p. 375 (Rio-negro).

Centrarchus niger Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 159, Pl. 12 (Rio Negro).

Cichlasoma arnoldi Ahl, 1936. *Sber. Ges. naturf. Freunde Berl.* 1936, p. 138 (Amazonas).

Chuco axelrodi Axelrod, 1971. *Trop. Fish Hobby.* 20 (1), p. 15/, fig. (Venezuela).

Chuco axelrodi Fernandez-Yepey, 1971. *Trop. Fish Hobby.* 20 (4) p. 15, figs. p. 16 (Aguaro River, Venezuela).

Heros temporalis Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 286 (-).

Acara (Heros) crassa Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.natw. Cl.* 71, p. 88, Pl. V (Amazonenstrom bei Teffé, Tonantins, Cudajas, Coary, Villa bella und Obidos, im See Hyuanuary und Saraca, so wie im Rio Hyutay).

Heros Goeldii Boulenger, 1897. *Ann. Mag. nat. Hist.* (6) 20, p. 298 (Upper Cunani River, French Guiana, south of the Oyapok River).

Cichlasoma Hellabrunni Ladiges, 1942. *Zool. Anz. Leipz.* 140, p. 199. Fig. 1 (Oberlauf, des Amazonenstromes?).

This group needs further study, but appears closest to *Hoplarchus*, having the lateral line on the dorsal lobe of the caudal-fin running between rays D3 and D4, and the same spots close to the hind margin of the orbit. The pale spots along the back, and the caudal spot are also shared; young have a suborbital stripe, lost in adults. Only *C. coryphaenoides* has a dark stripe back from the mouth across the cheek. The cheek is not naked ventrally, but in *C. coryphaenoides* there is at least anteriorly a naked line back from the labial margin of the preorbital. In *C. temporalis*, scales adjacent to the naked line are closely approximated, so that the cheek appears completely scaled. The hind border of the preoperculum is not notched. Two supranurals. Vertebrae 14+14. Parhypural spine present. Two tooth-plates on fourth ceratobranchial. The scales are larger than in *Hoplarchus* (about 30 (28-34); two series between lateral lines), but the fin squamation is wider. Large *C. coryphaenoides* may have the pectoral-fin base scaled. Young have long pointed snouts; adults have the forehead strongly raised, producing a dolphin-like head shape which is more marked in the slenderer *C. coryphaenoides* than in *C. temporalis*. Teeth slender, conical,

23-27/20-25 in labiad series, forwards size increase; inner teeth in narrow band, much smaller than outer. Gill-rakers short, 6-9 externally on first ceratobranchial. The upper lip fold is continuous in *C. coryphaenoides*, interrupted in *C. temporalis*. Anal-fin spines 6 in *C. coryphaenoides*, 7 or 8 in *C. temporalis*.

The colour pattern of the flanks is distinctive. *C. coryphaenoides* is uniform dark with a black vertical blotch above the posterior half of the upper lateral line. *C. temporalis* commonly features a mottled dark-light pattern, but may also have a narrow horizontal band along the side, with a vertical spot rising from it to slightly above the upper lateral line.

Coryphacara coryphaenoides appears to be restricted to the Orinoco, (Aguaro, Guarrojo) Negro, Trombetas and Branco. *Coryphacara temporalis* is widespread along the Ucayali-Solimões-Amazonas, and collected also in the Oyapock, Tocantins, Cunani, and Xingu.

The generic name is feminine and refers to the *Coryphaena*-like head shape of adults. The group is treated, as 'Section 4', in Part I (p. 273).

CRENICARA

Crenicara Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71*, p. 99 (type by monotypy *C. elegans* Steindachner). - Neuter.

Dicrossus Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71*, p. 102 (type by monotypy *D. maculatus* Steindachner). - Masculine.

Crenicara Regan, 1905. *Proc. zool. Soc. Lond.* 1905, p. 152 (unjustified emendation of *Crenicara*). - Feminine.

Crenicara filamentosa Ladiges, 1958. *Aquar. Terrar. Z.* 11, p. 204, fig. p. 204 (möglicherweise vom Amazonas).

Dicrossus maculatus Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71*, p. 102 (Lago maximo und José Assu sowie in Nebenarmen des Amazonenstromes bei Tonantins, im Rio Hyavary und im Rio Tajapurú).

Crenicara praetoriusi Ahl, 1936. *Mitt. zool. Mus. Berl.* 21, p. 265 (Igarapê-Irurã-Mapiry).

Acara punctulata Günther, 1863. *Ann. Mag. nat. Hist.* (3) 12, p. 441 (Essequibo).

Crenicara elegans Steindachner, 1875. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 71*, p. 99, Pl. I, fig. 1 (Amazonenstromen bei Gurupa, Cudajas und Curupira).

Aequidens madeirae Fowler, 1913. *Proc. Acad. nat. Sci. Philad.* 65, p. 576, Fig. 25 (Igarapê de Candelaria, tributary of the Madeira River, approximately two miles distant in Lat. S. 8° 45', W. Long., 63° 54', Brazil).

Aequidens hercules Allen, 1942, in Eigenmann & Allen. *Fish. West. South Amer.*, p. 394, Pl. XXII, fig. 7 (Creek, Rio Morona).

External characters of *C. filamentosum* have been described in some detail (Kullander 1978). It is an elongate fish with long slender caudal peduncle, large eye, narrow terminal mouth, interrupted lip folds, narrow lachrymal, squ. long. (25-) 26, fins naked except caudal-fin base, no dorsal or ventral caudal-fin lateral lines; D. XIV-XVI.5.i-8.i, spines rising to fifth, then decreasing in length to 10th; A. III.5.i-7; short pectoral-fin; first pelvic-fin ray longest; 3-5 short ceratobranchial rakers.

Osteological data indicate a geophagine with very strong oral jaw dentition and some reductions correlated with small size.

Vertebrae 13+13 or 13+14; 1-2 last abdominal vertebrae with hemal arches; 1 supra-neural; parhypural spine; six procurent caudal-fin rays in each lobe; no vertebral hypapophyses; lower pectoral radials coalesced; no median interhypural cartilage.

Head depressed; no frontal crest; low short supraoccipital crest; four dental, five preopercular, four lachrymal lateralis foramina; infraorbitals 2-5 contiguous or separate in various combinations in different specimens; infraorbital 6 present. Preopercular hind margin, posttemporal and supraclieithrum strongly serrated. Jaws strongly

toothed, rostral teeth enlarged and procumbent, entire rim of alveolar process of premaxilla toothed. Ascending anguloarticular process wide, ending truncate. Rostral foramen on ascending premaxillary processes. Gill-rakers short, non-denticulate; no microgillrakers, rakers on lower pharyngeal tooth-plate, fourth ceratobranchial teeth or interarcual cartilage. Small lobe on first epibranchial; third pharyngobranchial large, wide, with well-developed neurocraniad apophysis, parasphenoidal pharyngobranchial apophysis weak; fourth upper tooth-plate small; lower pharyngeal tooth-plate short and wide. Base of fifth branchiostegal ray medial to anterior ceratohyal. Urohyal spine caudad directed. *Crenicara punctulatum* has 14+14 vertebrae.

The genus is distinct in the reduced dental lateralis foramen number, evidently brought about by loss of the rostral foramen due to a rostroventral shift of the anterior lower jaw teeth, also an apomorphic condition. Bright red pelvic-fins of breeding females also appear unique, at least among South American cichlids.

Crenicara has been associated with *Batrachops* and *Crenicichla* (Regan 1905a) for reason of the serrate preoperculum, a character state then not known in other cichlids. The epibranchial lobe is not evident externally, but coalesced pectoral radials and abdominal hemal canal suggest rather a geophagine group. The colour pattern and shape of the smaller species reminds greatly of *Biotoecus*, but that genus needs deeper study.

Crenicara encompasses six species in two groups. *C. punctulatum* and the undescribed Bolivian form are larger (to c. 100 mm SL) and more high-backed than the rest (to c. 40 mm SL).

Crenicara filamentosum is found in the Orinoco and upper and middle R. Negro; males have lyrate caudal-fin.

Crenicara maculatum is collected in the upper R. Amazonas in Brazil (Solimões material reported by Steindachner (1875) and Guaporéan material reported by Haseman (1911c) may be misidentified or mislabelled). Males have a broad lanceolate caudal-fin.

Undescribed *filamentosum*-like forms are a small species with minute spots over the body in the middle R. Negro, and one with three horizontal series of side-blotches in the upper R. Tapajós.

Crenicara punctulatum is taken along the Essequibo, Huallaga, Ucayali, Javari, Madeira, Solimões, Peruvian and Brazilian R. Amazonas.

Similar to *C. punctulatum* is an undescribed species in the Bolivian Amazonía, which has the axial flank spots much deeper.

Crenicara filamentosum was recently re-described (Kullander 1978); Steindachner (1875) has detailed descriptions of *C. punctulatum* (also figured) and *C. maculatum*.

Ohm (1978, 1980a, b, c) has documented protogynous hermaphroditism in *C. punctulatum*; such is more or less well verified in other cichlids (Polder 1971; Ebermann 1961; Koslowski 1981; pers. obs.), as well as in labroids and other fishes.

CRENICICHLA

Crenicichla Heckel, 1840. *Annl. wien. Mus. Natges.* 2, p. 416 (type by subsequent designation by Eigenmann & Bray (1894), *C. macrophthalmia* Heckel). - Feminine.

Crenicichla acutirostris Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 307 (River Cupai (800 miles from the sea)).

Crenicichla alta Eigenmann, 1912. *Mem. Carneg. Mus.* 5, p. 516, Pl. LXVIII, fig. 3 (Guick Island).

Crenicichla pterogramma Fowler, 1914. *Proc. Acad. nat. Sci. Philad.* 66, p. 281, Fig. 20 (Rupununi River, British Guiana).

Crenicichla anthurus Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 252, pl. X, fig. 1 (Ambyiacu).

- Crenicichla biocellata* R. von Ihering, 1914. *Revta Mus. paul.* 9, p. 333 (Rio Doce, Est. do Espírito Santo).
- Perca brasiliensis* Bloch, 1792. *Natges. ausländ. Fische* 6, p. 84, Pl. CCCX, fig. 2 (Flüssen Brasiliens).
- Crenicichla britskii* Kullander, 1982. *Revue suisse Zool.* 89, p. 642, Fig. 7 (Brasil, Estado de São Paulo, mun. Promissão, R. Tietê system, km 143 on BR-153, above road in small brook).
- Crenicichla cametana* Steindachner, 1911. *Anz. k. Akad. Wiss. Wien Math.-natw. Kl.* 48, p. 369 (Tocantins bei Cameta).
- Crenicichla Johanna*; var. *carsevennensis* Pellegrin, 1905. *Bull. Soc. zool. Fr.* 30, p. 168 (Entre les rivières Carsevenne et Cachipour (contesté franco-brésilien)).
- Crenicichla cincta* Regan, 1905. *Proc. zool. Soc. Lond.* 1905, p. 166 (nom. nov. pro *C. brasiliensis* Var. *fasciata* Pellegrin).
- Crenicichla brasiliensis* Var. *fasciata* Pellegrin, 1904. *Mém. Soc. zool. Fr.* 16, p. 383, fig. 42,3 (Marajo (Brésil)).
- Cyca conibos* Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 18, Pl. 10, fig. 3 (l'Ucayale).
- Crenicichla dorsozellata* Haseman 1911. *Ann. Carneg. Mus.* 7, p. 355, Pl. LXIII (Campos, R. Parahyba).
- Crenicichla frenata* Gill, 1858. *Ann. Lyc. nat. Hist. N.Y.* 6, p. 386 (Western portion of the Island of Trinidad/).
- Crenicichla Geayi* Pellegrin, 1903. *Bull. Mus. Hist. nat.* 9, p. 123 (Vénézuéla).
- Crenicichla haroldoi* Luengo & Britski, 1974. *Acta biol. Venez.* 8, p. 554, Fig. 1 (rio Paraná frente a Jupia, Mato Grosso).
- Crenicichla iguassuensis* Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 352, Pl. LXI (Porto União da Victoria, Rio Iguassú).
- Crenicichla jaguarensis* Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 351, Pl. LX (Jaguara, Rio Grande of the Paraná, Minas).
- Crenicichla johanna* Heckel, 1840. *Annin wien. Mus. Natges.* 2, p. 425 (Rio-Guaporê).
- ?*Cychla fasciata* Jardine, 1843. *Nat. Libr. Ichthyol.* 5, 141, Pl. 4 (-).
- Crenicichla obtusirostris* Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 305 (River Capin).
- Crenicichla jupiaensis* Britski & Luengo, 1968. *Paps avuls. Zool. S. Paulo* 21, p. 171, Fig. 1 (Rio Paraná, no Salto de Urubupungã, entre os Estados de Mato Grosso e São Paulo).
- Cychia labrina* Spix, 1831, in de Martius, *Sel. Gen. Sp. Pisc. Bras.* p. 99, Pl. LXII, fig. 1 (as *Cichla labrina*) (marí Brasiliae).
- Cyca lacustris* Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 19, Pl. 8, fig. 3 (Dique, ou etang près de Bahia).

- Crenicichla lenticulata* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 419 (Rio-negro, bei Marabitanas).
 ?*Crenicichla adspersa* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 421 (Rio-Guaporè).
- Crenicichla lepidota* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 429 (Rio-Guaporè).
 ?*Crenicichla saxatilis* (Var. *semicincta*) Steindachner, 1892. *Denkschr. k. Akad. Wiss. Wien Math.-natw. Cl.* 59, p. 376 (Bolivia, Provinz Yuracares, im oberen Chaparè bei Puerto de San Mateo).
- Crenicichla lucius* Cope, 1870. *Proc. Amer. philos. Soc. Philad.* 11, p. 570 (tributaries of the Upper Maranon, in Equador).
- Crenicichla lugubris* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 422 (Rio-negro).
 ?*Crenicichla funebris* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 424 (Matogrosso am Rio-Guaporè).
 ?*Cychna? rutilans* Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 142, Pl. 5 (Rio Branco).
Crenicichla johanna var. β . *strigata* Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 306 (River Capin; River Cupai (800 miles from the sea)).
- Crenicichla macrophthalmia* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 427 (Rio-negro).
Crenicichla santaremensis Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 354, Pl. LXII, fig. 1 (lagoon along the margin of the Amazon, three miles above Santarem).
- Crenicichla brasiliensis* Var. *marmorata* Pellegrin, 1904. *Mém. Soc. zool. Fr.* 16, p. 383, Fig. 42,4 (?).
- Crenicichla mucuryna* R. von Ihering, 1914. *Revta Mus. paul.* 9, p. 335 (Theophilo Ottoni, rio Todos os Santos, affl. do Mucury, Est. de Minas Geraes).
- Crenicichla* (*Batrachops*) *multidens* Steindachner, 1915. *Sber. k. Akad. Wiss. Wien Math.-natw. Kl.* 124, p. 567, Pl. I, fig. 1 (La PLata).
- Cycla multifasciata* Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 18, Pl. 10, fig. 2 (un des affluents de l'Ucayale).
- Crenicichla multispinosa* Pellegrin, 1903. *Bull. Mus. Hist. nat.* 9, p. 124 (Guyane française).
- Crenicichla nanus* Regan, 1913. *Ann. Mag. nat. Hist. (8)* 11, p. 502 (British Guiana).
- Acharnes Niederleinii* Holmberg, 1891. *Revta Arg. Hist. nat.* 1, p. 181 (Rio Pequirí, en Misiones, y en otros inmediatos).
- Crenicichla notophthalmus* Regan, 1913. *Ann. Mag. nat. Hist. (8)* 11, p. 502 (the Amazon at Manaos).
- Crenicichla ornata* Regan, 1905. *Proc. zool. Soc. Lond.* 1905, p. 167, Pl. XV, fig. 2 (Rio Negro).
- Crenicichla polysticta* Hensel, 1870. *Arch. Natges.* 36, p. 58 (Rio Cadea des Urwaldes von Rio Grande do Sul).
Crenicichla punctata Hensel, 1870. *Arch. Natges.* 36, p. 57 (aus dem Guahyba bei Porto Alegre...Bachen des Urwaldes; Waldbachen von...Sta. Cruz).

- Crenicichla proteus* Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 252 (Ambyiacu River).
- Crenicichla proteus* Var. *Y* (*argynnis*) Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 253 (Ambyiacu River).
- Batrachops nemopterus* Fowler, 1940. *Proc. Acad. nat. Sci. Philad.* 91: 283, Fig. 64 (Ucayali River basin, Contamana, Peru).
- Sparus saxatilis* Linnaeus, 1758. *Syst. Nat. ed. 10, 1*, p. 278 (Surinam).
- Sparus biocellatus* Walbaum, 1792. *Artedi Gen. Pisc. Ichth.* 3, p. 298 (Surinam).
- Scarus pavoninus* Gray, 1854. *Cat. Fish Gronow*, p. 63 (Surinami).
- ?*Crenicichla saxatilis* Var. *albopunctata* Pellegrin, 1904. *Mém. Soc. zool. Fr.* 16, p. 374 (Surinam; Guyane anglaise; Guyane française).
- Batrachops scottii* Eigenmann, 1907. *Proc. Wash. Acad. Sci.* 8, p. 455, Pl. XXIII, fig. 8 (Buenos Aires).
- Crenicichla lacustris* var. *semifasciata* Devincenzi 1939. *Anles Mus. Hist. nat. Montevideo* (2) 4 (13): 34, Fig. 11 (Rio Uruguay (Paysandú)).
- Crenicichla ternetzi* Norman, 1926. *Ann. Mag. nat. Hist.* (9) 18, p. 97 (Oyapock River at "Sant" Cafesoca, French Guiana).
- Crenicichla Vaillanti* Pellegrin, 1903. *Bull. Mus. Hist. nat.* 9, p. 124 (La Mana (Guyane française); Essequibo (Guyane anglaise)).
- Crenicichla vittata* Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 417 (Flusse Cuyabà; Flusse Paraguay).
- Crenicichla wallacii* Regan, 1905. *Proc. zool Soc. Lond.* 1905, p. 163, Pl. XIV, fig. 2 (R. Essequibo).

There is uncertainty about many of the species listed above as valid, yet *Crenicichla* is one of the most speciose groups of South American cichlids. There remain to be described a large number of species, making a likely total of over 50. As there is considerable morphological interspecific variation and as several species groups can be distinguished, extensive splitting is, however, anticipated.

Species of undoubted validity are *acutirostris*, *brasiliensis*, *britskii*, *cametana*, *cincta*, *frenata*, *geayi*, *haroldoi*, *iguassuensis* (but the type-series a composite), *jaguarensis*, *johanna*, *jupiaensis*, *labrina*, *lacustris*, *lenticulata*, *lepidota*, *lugubris*, *macrophthalma*, *marmorata*, *multispinosa*, *niederleini*, *ornata*, *proteus*, *saxatilis*, *ternetzi*, *vittata*, and *wallacii*. *Crenicichla alta* is problematic, as the type-series of *C. vaillanti* includes two species, one of which is Eigenmann's; but *C. vaillanti* may come to be suppressed in favor of the better known name. *Crenicichla anthurus* may be the same as *C. lucius*, but the types of the latter are lost. *Crenicichla biocellata* von Inering (homonym of *Sparus biocellatus* Walbaum; but that name never used after Walbaum), *C. dorsocellata*, *C. mucuryna*, *C. multiensis*, *C. polysticta* (and *C. punctata*), *C. scottii*, and *C. semifasciata*, are *C. lacustris*-like species, all of which cannot reasonably be valid, with doubtful differentiating characteristics and partly from the same places. *Crenicichla carsevennensis* may be within *C. johanna* variation, but little material is available of the cycloid-scaled *Crenicichla*. Castelnau's *C. conibos* and *C. multifasciata* are based on field sketches; most authors refer them to *Cichla* - the genus is hardly recognizable from the figures, and they may be composites of *Cichla* and *Crenicichla* specimens, although tending more to the latter genus. *Crenicichla nanus* and *C. notophthalmus*, like *C. wallacii*, are dwarf forms, of which there are several species in which dorsal-fin ocelli (diagnostic of *C. notophthalmus*) are obviously a female characteristic - a revision must precede further attempts at evaluating their status.

Few species are well-known from external characters (recent descriptions in Kullan-

der 1982c, 1981d, Britski & Luengo 1968), and osteological work has been limited and non-comparative (Travassos & Pinto 1957, 1958a, V. B. Ribeiro (1970b), Vandewalle 1971, Regan 1905a).

Diagnostic generic character states listed by Regan (1905a), eg. denticulate preopercular margin, inner teeth depressible (fixed in *Batrachops*), projecting lower jaw (jaws equal in *Crenicara*) are not shared by all species or not apomorphic.

All species are elongate and relatively small-scaled (squ. long. 33 to c. 130); with symmetrical, rounded, short pectoral-fin; roundish caudal-fin; naked pelvic-fin; some species with scaly pectoral-fin base; soft dorsal- and anal-fin bases with a few scales in very large specimens; separate flank lateral line, no dorsal or ventral lateral line sequences on caudal-fin; long dorsal-fin (usually about 20-24 spines); discontinuous American type lower lip fold; second pelvic-fin ray longer than or subequal in length to the first; three anal-fin spines.

Coloration varies among species. There is usually a caudal-fin ocellus; often also ocelli in dorsal-fin or anteriorly on the side.

Most species are rather large, some reaching over 300 mm, others only 50 mm total length. Most have long snouts with projecting lower jaw, a few have subequal jaws. Sexual dimorphism is recorded for several species; there is also considerable ontogenetic and individual variation in morphology and coloration, making species-level work difficult without large series.

The type-species, *C. macropthalma* (Plate XV, fig. 4), has extraordinarily large eyes and extensively ctenoid squamation.

The geographical distribution of the genus is similar to, but more extensive than that of *Cichlasoma*, including also the Marowijne, Oyapock, Negro, upper Orinoco, coastal rivers from the La Plata northwards, even two Patagonian localities. All species are relatively restricted in distribution, however, with, eg. R. São Francisco, R. Paraná superior, R. Oyapock, Trinidad, and R. Negro endemics.

Much remains to be learned about particular species. Proposed groupings therefore, are rather provisional. Regan (1913a), judging from his key, separated *C. johanna* from the rest on account of its cycloid scales, and the rostral position of the nostril, but the extent of cycloid squamation is very variable within the genus, and the nostril is in a similar position in some other species. A further division into small-scaled and large-scaled species is confirmed by my data. Most species have 50-70 squ. long. scales; *C. ternetzi* and *C. vittata* 80-90, *C. multispinosa* c. 90-100, the extremely small-scaled species well over 100. Dorsal-fin and vertebral counts are correlated. Curiously there is no form with ranges between 70 and 80 even though intraspecific variation in *Crenicichla* species may span over as much as ten scales. Scale counts alone, however, do not suggest clear natural groups, although there is an interesting correlation with lip shape and size (small-scaled species larger).

Blunt snouted, small-scaled species, but also including *Batrachops*, have the upper lip fold continuous through a moderately fleshy medial fold which usually fits convexly with the concave postlabial fold. The lower lip fold extends two thirds the distance to the lower jaw tip. (Characteristic species *C. johanna*, *C. cincta*, *C. lenticulata*, *C. ornata*, *Batrachops* spp.).

Species with moderately pointed snout, in the lower scale count range and *C. vittata*, have the upper lip fold interrupted medially, the symphysis fleshy or not; the postlabial fold is truncate or convex anteriorly; the lower lip fold extends to near the lower jaw tip.

Crenicichla multispinosa and *C. ternetzi* with acutely pointed snouts, have the upper lip fold interrupted medially, the symphysis with a fleshy convex fold extending slightly backwards and fitting the concave postlabial fold. The lower lip fold extends to near the lower jaw tip.

The *Crenicichla lepidota* group that I recognized (1982c) appears valid with inclusion of *saxatilis*-like species. The *lacustris* group (Kullander 1981c, 1982c) needs revision insofar as characters listed are not unique, and *C. cametana* with fixed inner teeth and somewhat *Batrachops*-like head strains the limits even of the genus.

The following notes are a reply to Stiassny's (1982) association of *Crenicichla* with *Cichla*, which appears unfounded.

Osteology

Descriptive notes. Vandewalle (1971) described and figured the osteology, especially the cranium, and myology of what he calls *Crenicichla multispinosa*. (Upon comparison with intact *C. multispinosa*, I do not feel certain about the species determination.) Travassos & Pinto figured and described jaw bones (1957) and opercular bones (1958a) of *C. jaguarensis*. Stiassny (1982) studied some aspects of cranial morphology in connection with an evaluation of character states in *Cichla*. For a more complete view, I have taken notes on an alizarin specimen of a *C. saxatilis* group species (NRM unreg., Alizarin 33, 57 mm) and an alizarin-alcian blue specimen of *C. proteus* (NRM SOK/3431, Alizarin 69, 58 mm):

Most striking about the *Crenicichla* head is the wide separation of orbit and vertical parts of the suspensorium, and the extensive precommissural cranium. In these respects *Crenicichla* resembles lower periods such as percids and centropomids. However, these features are effects related to the lengthening of the head, in *Crenicichla*, as well as in *Cichla*. Related features are probably the lateral prominent, long horizontal autosphenoid ridge, the caudally displaced *mm. levatores externi* and *interni* (Stiassny 1982), and lack of a 'hyomandibulad snell' (a lateral extension of the ventral floor of the rostral hyomandibulad articulation socket; Stiassny 1982), although the latter feature may be plesiomorphic.

Crenicichla also have a much depressed head, showing in low frontoparietal crest, absence of frontal median crest, and very slightly elevated braincase. Associatedly, the opposed pterosphenoid and prootic pedicles anterior to the lateral commissure are connected by a short ligament (united on Stiassny's figure, not shown at all by Vandewalle), instead of a long as in *Cichlasoma*; the pterosphenoid pedicle is prominent, as pointed out by Stiassny, but less developed than in, eg. *Nannacara*. The palatopterygoid series (Fig. 116) is strikingly narrow, featuring some likely apomorphic characters. The palatine has only a short ventrad caudal projection, the ectopterygoid is long and wide, covering the dorsal portion of the entopterygoid, which does not contact the reduced metapterygoid. As pointed out by Vandewalle, the dorsal tip of the ectopterygoid contacts, ligamentously in my specimens, the vomer head laterally. The supraoccipital, well removed from the coronalis foramen, extends caudad by a spinous process bearing narrow dorsal and caudal lamina.

The suborbital series (Fig. 117) has a slender lachrymal, somewhat like in *Astronotus*, in my specimens (Vandewalle's fish has an approximately equal-sized squarish lachrymal), with a foramen in each corner. It is succeeded caudad by five tubular infraorbitals, the last strongly curved.

The anguloarticular has a short primordial process (lateral, not medial to the ectopterygoid as in Vandewalle's Fig. 14), a long lateralis canal and an elongate wide ventral process, with also a horizontally elongated retroarticular. The dental has five lateralis canal foramina, two near the anterior end, one near the rostral tip of the anguloarticular, and one close to that facing the anterior angular foramen. The nasal has posterior and anterior foramina, but the skin openings differ from the modal cichlid in that the anterior skin pore lies far anterior to the rostral nasal canal, connected to it by a canal in the flesh of the postlabial fold; the posterior opening is anterolaterally extended, and the skin pore lies over the anterior end of the foramen, i.e. near the middle of the nasal (on one side in one of my specimens, the posterior and anterior ends of the foramen are completely separated by bone cover). On the frontal the long marginal canal opens to the nasal, with another foramen caudolaterally connected to a skin perforation; the transverse canals open dorsally through a circular coronal foramen, that is not raised and lies medial to the posterior part of the orbit and cliff3.

There are six preopercular lateralis foramina, and the preoperculum is conspicuously wide over the corner section: serrated along the vertical edge of the laminar posterior edge. The interoperculum has a conspicuous notch in the dorsal edge (Fig. 118). The nearly triangular shape of the operculum, with almost horizontal dorsal edge appears characteristic of the genus. Except for the preoperculum, none of the opercular or pectoral girdle bones are serrated.

The pharyngeal apophysis and articular surface is formed by parasphenoid alone; notably the apophysis is not chiefly horizontal, but the articular surfaces slope laterally on a very slight ventral ridge of the parasphenoid, the upper pharyngeals

are correspondingly oriented. The basioccipital lacks particular ligament facets, but Baudelot's ligament attaches to the lateral ledges.

A rostral foramen is lacking from the premaxilla; the medial processes reach nearly to the middle of the orbits and are slightly longer than the alveolar. Jaw teeth are differentiated in a labial series of stronger, pointed fixed teeth, and a narrow lingual band of smaller, completely depressible teeth. The teeth are implanted on stubs of attachment bone and there are teeth encapsuled in the bone.

The branchial skeleton offers three noteworthy features. First, the first pharyngobranchial is well-formed, slender with widened epibranchial end, but entirely cartilagenous (a 'tendon' on Vandewalle's fish). Second, an interarcual cartilage is lacking (as also reported for *C. alta* by Travers 1981). Third, there is a series of minute gill-rakers along the lateral edge of the lower pharyngeal tooth-plate. Aside from a long slender glossohyal (Vandewalle, Fig. 18), a series of tooth-plates (7 with 5-8 teeth) along the dorsal margin of the fourth ceratobranchial (a single long tooth-plate medially on Vandewalle's fish) and a somewhat dorsoventrally compressed third pharyngobranchial with slightly mediad directed articulation facet, the aspect is similar to that of *Cichlasoma*, with short epibranchials, the fourth upper tooth-plate united to the third pharyngobranchial, the second pharyngobranchial rostral to the third, suturally united lower pharyngeal jaw elements (slightly diverging anteriorly). The lower pharyngeal jaw is not particularly rostrad elongated, but the arms are relatively long, terminating in narrow horns. The external first ceratobranchial rakers are like in *Cichla*, but considerably shorter, all other rakers are bud-like but heavily toothed; only two external first epibranchial and no hypobranchial (but 1-2 on the succeeding hypobranchials). The epibranchial 2 cartilage articulating with pharyngobranchial 2 is slightly laterad extended. The lower pharyngeal teeth are of modal form, conical anteriorly, caudally compressed, with posterior point, all fixed; emerging teeth in sockets.

Microgillrakers on the external surface of the three posterior gill-arches. First ceratobranchial gill-raker counts in *Crenicichla* average 10 (7-12).

The very slender urohyal has a short dorsad or dorsad-rostrad pointing process anteriorly.

The distal postcleithrum in *C. proteus* has a long rostrad directed spinous process, but also a projection ventral to it (Fig. 118).

The caudal skeleton in *C. proteus* has two epurals and five hypurals and there is no parhypural spine; caudal-fin rays vii, 8, 8, vi. There is a small piece of blue-stained cartilage distally between the second and third hypurals.

Supraneurals are lacking, and the first dorsal-fin pterygiophore inserts between the first two neural spines. Examination of radiographs of numerous *Crenicichla* specimens presents no example of a first pterygiophore articulating with two instead of one spine (cf. Vandewalle, Fig. 16C).

Discussion. Stiassny (1982) emphasized four characters that would associate *Cichla* and *Crenicichla*, viz. 1, a large sheet-like *m. pharyngocleithralis internus* originating from the lateral (instead of the medial) face of the cleithrum; 2, an elongate, rostrally directed urohyal spine; 3, an antrorse pointed process on the distal postcleithrum on which inserts a muscle sheet from the first pleural rib; 4, an increased number of abdominal, and high total number of vertebrae.

Character states 2-4 are not identical in the genera; a urohyal process, sometimes spine-like, occurs in various percoids; the postcleithral process in neither unique, and of different form; high abdominal vertebral number may be ancestral (*p.* 00). Remains the *m. pharyngocleithralis internus*, on which I do not have sufficient data from outgroups.

Crenicichla are much more specialized than *Cichla*. There are some lower percoid resemblances in the elongation of the skull, but these are shape-related, and apparently there is intrafamilial variation in the length of the premissural skull and in the suborbital-suspensorial distance also in labrids (Rognes 1973, Figs. 2-5, 11-15), making an evaluation difficult.

The branchial skeleton is as in the other cichlids, except *Cichla*, with socket-teeth, short epibranchials, united lower pharyngeals, pharyngobranchial 2 anterior to pharyngobranchial 3, etc. The oblique parasphenoidal articulation facets and

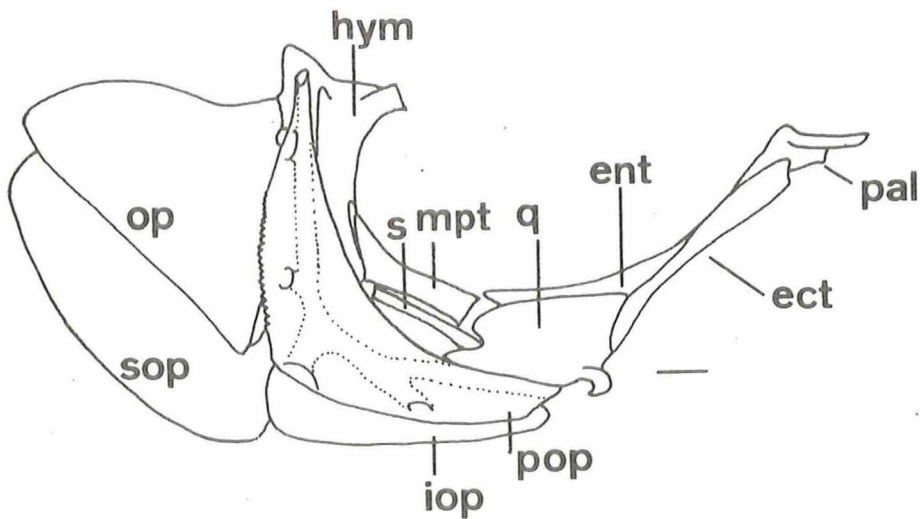


Fig. 116. *Crenicichla* sp. Lateral aspect of right side suspensorium and opercular series. Ect, ectopterygoid; ent, entopterygoid; hym, hyomandibula; iop, interoperculum; mpt, metapterygoid; op, operculum; pal, palatine; pop, preoperculum; q, quadrate; s, symplectic; sop, suboperculum. Scale 1 mm. From NRM unreg., Alizarin 33, 57 mm.

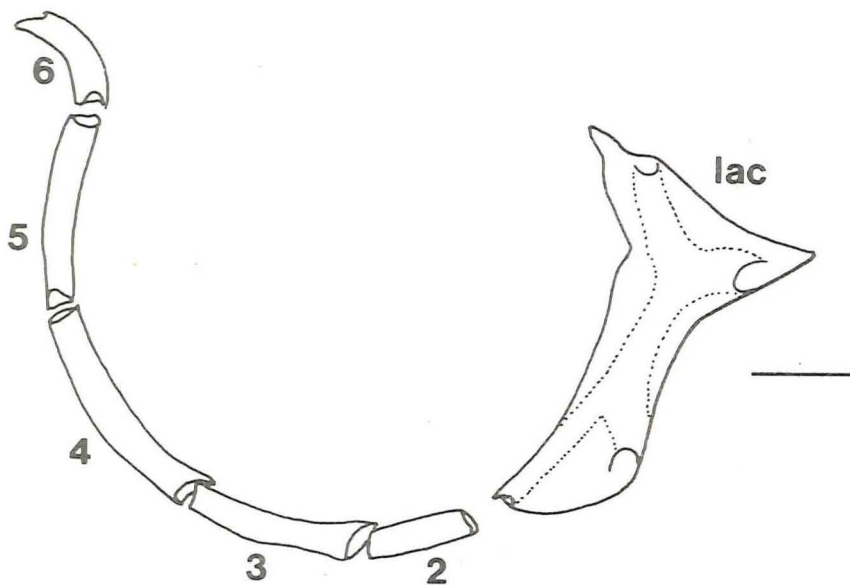


Fig. 117. *Crenicichla* sp. Lateral aspect of right side suborbital series. Infraorbitals numbered; lac = lachrymal Scale 1 mm. From NRM unreg., Alizarin 33, 57 mm.

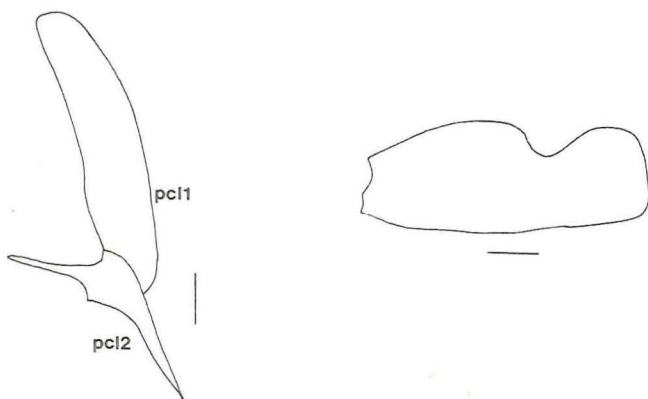


Fig. 118. Left: *Crenicichla proteus*; Right side postcleithra in medial view; pcl1, proximal postcleithrum, pcl2, distal postcleithrum; scale 1 mm; from NRM SOK/3431, Alizarin 69, 58 mm SL. 118. Right: *Crenicichla* sp. Outline of right side interoperculum in medial view; scale 1 mm; From NRM unreg., Alizarin 33, 57 mm SL.

mediad-dorsad directed pharyngobranchial 3 apophyseal articulation facet, cartilagenous first pharyngobranchial, and absence of an interarcual cartilage are, however, apomorphic for *Crenicichla*, only the missing interarcual cartilage found in other cichlids. The narrow posterior pterygoids and quadrate, and the palatine-ectopterygoid-vomer connections appear autapomorphic.

The absence of supraneurals is probably associated with the caudad directed supraoccipital process; both are apomorphic. Interestingly, also in *Gymnogeophagus* absence of supraneurals is associated with presence of a spine, but this one on the first pterygiophore.

Ancestral characters include the suborbital series arrangement, with separate infraorbitals 3 and 4 and serrated preoperculum, but several species have secondarily lost the preopercular serrations.

The deep notch in the dorsal border of the interoperculum is another autapomorphy, although a shallow concavity in about the same region is not uncommon in other cichlids. The nasal skin pores separate *Crenicichla* and *Batrachops* from all other cichlids.

Missing infraorbital 1, but with American type lips, and six preopercular lateralis pores, it would seem that *Crenicichla* appears to be more closely related to other cichlids than to *Cichla*, *Astronotus*, the chaetobranchines, *Retroculus*, and most African cichlids.

GALLOCHROMIS n. gen.

Type-species: *Geophagus steindachneri* Eigenmann & Hildebrand.

Geophagus (Satanoperca) crassilabris Steindachner, 1876. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl. 74*, p. 65, Pl. VII (einem Bache des Isthmus von Panama, wahrscheinlich in der Nähe von Candelaria).

Geophagus pellegrini Regan, 1912. *Ann. Mag. nat. Hist. (8)* 9, p. 505 (Tado, Rio San Juan, Choco, S.W. Colombia).

Geophagus steindachneri Eigenmann & Hildebrand, 1910, in Eigenmann. *Repts Princeton Univ. Exped. Patagonia Zool.* 3, p. 478 (Magdalena Basin).

Geophagus honda Regan, 1912. *Ann. Mag. nat. Hist. (8)* 9, p. 506 (Honda, Colombia).

Geophagus Magdalena (Magdalanae) Brind, 1943. *All-Pets Mag.* 14, p. 42 (lake at El Banco, Columbia).

Named with particular reference to the red top of the prominent nuchal hump of *G. steindachneri* males, at least the hump is, however, not unique to these fishes. Nuchal protuberances are common among large American cichlids, and characterize also the African *Cyphotilapia* Regan, *Cyrtocara* Boulenger, s. str., *Steatocranus* Boulenger, s. str., and a few other species. The hump was discussed by Pellegrin (1904), but its nature is not yet understood. The hump of *Margaritacara* and some *Gymnogeophagus* species, resembles that of *Gallochromis*, but has no signal colour. The gender of *Gallochromis* is feminine.

My experience with this group is limited to *G. steindachneri*, a Magdalena-Cauca-Maracaibo basin species reaching c. 150 mm SL. Nomenclatural problems were discussed in Gosse & Kullander (1981). Taphorn & Lilyestrom (1979) have a re-description based on Maracaibo basin material.

Gallochromis pellegrini, in the San Juan and Atrato basins, differs in lacking fin-dotting (Gosse 1976).

Gallochromis crassilabris in the Tuira, Bayano and Canal Zone area in Panama, is distinguished (Eigenmann 1922, Gosse 1976:) in having generally one less dorsal-fin spine and vertebra than *G. pellegrini*. Those species otherwise have thick lips, like *Gymnogeophagus labiatus*.

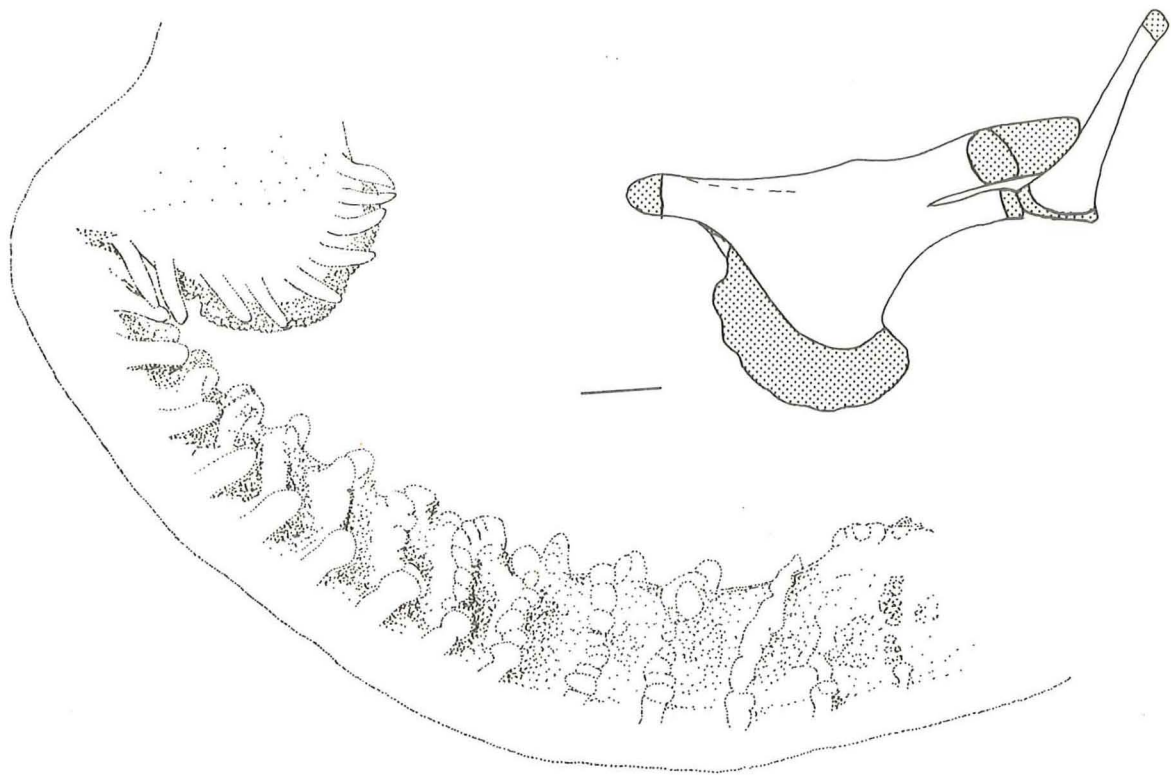


Fig. 119. *Gallochromis steindachneri*. First gill-arch in lateral aspect (gills not shown) to the left. To the right, first epibranchial, first pharyngobranchial and interarcual cartilage in rostralateral view; cartilage and connective tissue pad stippled. Scale 1 mm. From NRM unreg., 71 mm SL.

The lips are thick also in *G. steindachneri* compared to most geophagines, and emphasize the apomorphic prognathy of the upper jaw; both lip folds are interrupted.

Opercular bones are smooth. The jaw dentition is as in *Margaritacara*, i.e. the upper jaw with an outer series of strong and about two inner series of small teeth, two-thirds of the jaw toothed; lower jaw similar, but with three inner series, more than half of jaw toothed.

Vertebrae 14+14 (15+15 in *G. pellegrini*, 14+13 and 14+15 in *G. crassilabris* examined by Gosse 1976). Scales moderately large, squ. long. 27; cheek nearly completely scaly rostrad. Basal caudal-fin and narrowly, interradially, posterior spinous and most of soft dorsal-fin scaly, other fins naked. Pectoral-fin short, not reaching to above anal-fin base. Caudal-fin hind edge emarginate; moderately long lateral lines between caudal-fin rays V4 and V5, and D3 and D4. Dorsal-fin spines subequal in length except shorter anterior. Single supraneural. Four procurent caudal-fin rays; parhypural spine present.

Lower pharyngeal tooth-plate with gill-rakers; fourth ceratobranchial with four small tooth-plates; first pharyngobranchial widened ventrally; first epibranchial ventral extension depth half length of epibranchial. Lobe with 8 conical rakers near and reaching beyond edge; first ceratobranchial with 12-15 rakers, most on skin fold over gill-filaments, the upper connected to median swellings, the ventral to median soft ridges (Fig. 119); no microgillrakers. Interarcual cartilage slightly elongated.

Gallochromis steindachneri, at least, has no suborbital stripe, but a diffuse midbasal caudal spot and on the maxillary tip an orange dot thought to play some role in spawning procedures.

Unlike other geophagine mouth-brooders which commonly, according to aquarium observations, are biparental and tend the eggs on a substrate, and some of which like *Aequidens* and *Acarabobo flavilabris* cover the eggs with sand, *G. steindachneri* spawns rapidly and the female takes up the eggs at once. The male takes no part in the brood-care.

Gallochromis is in most respects like *Margaritacara*. It differs in the distribution of ceratobranchial 1 rakers, in which it resembles *Satanoperca*, but the internal rakers are on the arch, not on the filament skin fold; absence of microgillrakers; upper jaw prognathy; naked anal-fin. A slightly longer interarcual cartilage, more gill-rakers, long caudal-fin lateral lines and emarginate caudal-fin are ancestral character states.

Gosse (1976) was not aware of type-material of *G. Magdalena*, USNM 120299, male, and 120207, female. These are specimens kept in aquaria, but they agree with wild *G. steindachneri*.

GEOPHAGUS

Geophagus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 383 (type by subsequent designation by Eigenmann & Bray (1894), *Geophagus altifrons* Heckel). - Masculine.

Geophagus altifrons Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 385 (Barra do Rio-negro).

Geophagus camopiensis Pellegrin, 1903. *Bull. Mus. Hist. nat.* 9, p. 123 (Riv. Camopi (Guyane française)).

Geophagus harreri Gosse, 1976. *Mém. Acad. r. Sci. Outre-Mer (N.S.)* 19 (3), p. 88, Fig. 21 (rivière Ouaiqui à Saut Bali (Affluent du Tampok, bassin du Maroni), Guyane française)).

Geophagus megasema Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 388 (einer grossen Lache Juquia genannt, bei Mattogrosso am Fluss Guaporè).

Chromys proxima Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 14, Pl. 7, fig. 1 (un lac près de l'Ucayale, dans la mission de Sarayacu, au Pérou).

Perca surinamensis Bloch, 1791, *Natges. ausländ. Fische* 5 p. 112, Pl. CCLXX-VII, fig. 2 (Surinam).

A recent revision of the larger geophagines (Gosse 1976) distinguished three major groups:

Geophagus. Ten species, with single supraneural, lacking antrorse spine on the first dorsal-fin pterygiophore.

Biotodoma. Two species, with two supraneurals, lacking antrorse spine on first dorsal-fin pterygiophore.

Gymnogeophagus. Four species, without supraneural, but an antrorse spine on first dorsal-fin pterygiophore.

I have had occasion to work chiefly with the species of the genus *Geophagus sensu* Gosse and have arrived at a very different result regarding generic characters and species richness. Some preliminary findings, chiefly the recognition of one more *Gymnogeophagus* species, have already been communicated (Kullander 1981d). The following is new:

Although I give Gosse right in considering a higher supraneural number as plesiomorphic in contrast to a lower, the one (in *Geophagus*) or two (in *Biotodoma*) supraneurals counted by Gosse do not hold as generic characters, as one supraneural is a widespread condition, and as two supraneurals is, as stated, a plesiomorphic trait. Gosse's character states are therefore key character states useful in determination work, but cannot be claimed to have a phylogenetic basis, except, perhaps, for the pterygiophore spine of *Gymnogeophagus*.

What I have observed then, is that the number of species in the three genera is much greater than Gosse thought. I recognize eight species among his *G. surinamensis*, and four species in his *G. jurupari*. All of them are more different from each other than *Cichlasoma* species.

Most important is, however, that these fishes feature a much greater number of interesting character states than those listed above, suggesting that *Geophagus sensu* Gosse consists of four distinct lineages. These are herewith separated into the genera *Gallochromis* (p. 382), *Satanoperca* (p. 403), *Margaritacara* (p. 394), and *Geophagus*.

Geophagus is different from all other geophagine cichlids in having the swim-bladder continued above the anal-fin and accompanied by pleural (not epi-pleural as in *Apistogramma*) ribs to the 6th to 12th vertebra, and in having the rostral half of the cheek naked.

The genus is advanced over *Satanoperca* in having a reduced interarcual cartilage and smooth supraclithrum. Greatest overall similarity is shown to *Retroculus*, especially in the opisthopolyspondyly, but *Geophagus* lack a separate first infraorbital.

Geophagus species are moderately elongate to high-backed, compressed, with relatively long caudal peduncle, deep preorbital and small mouth. The larger species reach 230 mm SL. All have a large midlateral blotch, but no caudal spot; a suborbital stripe is variously developed. The scales are small, squ. long. 32-34, 18-22 circumpendicular scale series; anterior half of cheek naked. Predorsal, chest and prepelvic scales small. Long lateral lines; also on densely scaly dorsal (between rays D3 and D4) and ventral (between rays V4 and V5) caudal-fin lobes. Dorsal-fin basally with interradial scales on posterior spinous and anterior half of soft fin; anal-fin also scaly, or naked. Pectoral- and pelvic-fins naked.

Sixteen principal, five to seven procurrent caudal-fin rays; hind margin of caudal-fin concave. A. III.7-8. D. XV-XIX.10-13, spines equal or subequal in length from fifth, sixth or seventh. Pectoral-fin long, to above anal-fin base. Pelvic-fin with first ray longest.

Vertebral column with more caudal than abdominal vertebrae (14-15+16-19 = 30-33), 1-2 abdominal with hemal arch; pleural ribs over 6-12 anterior caudal hemal spines (enclosing swim-bladder extensions). Long simple hypapophysis on third vertebra; parhypurapophysis present; cartilage present between hypurals 2 and 3. Single supraneural.

Simple lacrymal, with four lateralis foramina, deep; infraorbitals io2, io3-4, io5, io6; five dental, six preopercular lateralis foramina.

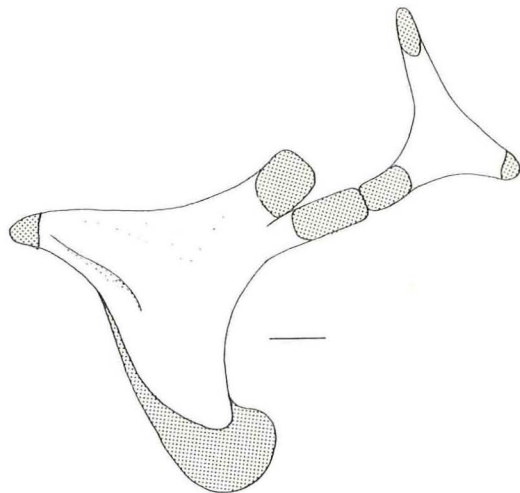
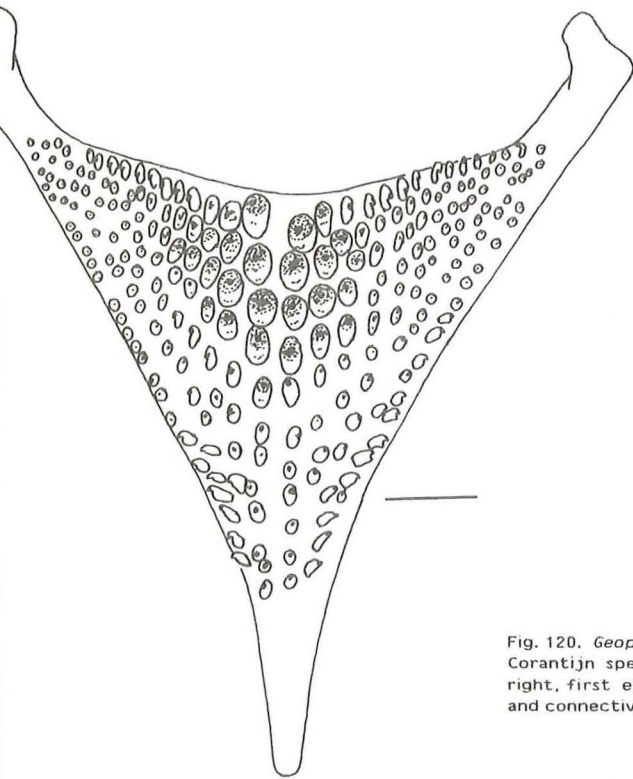
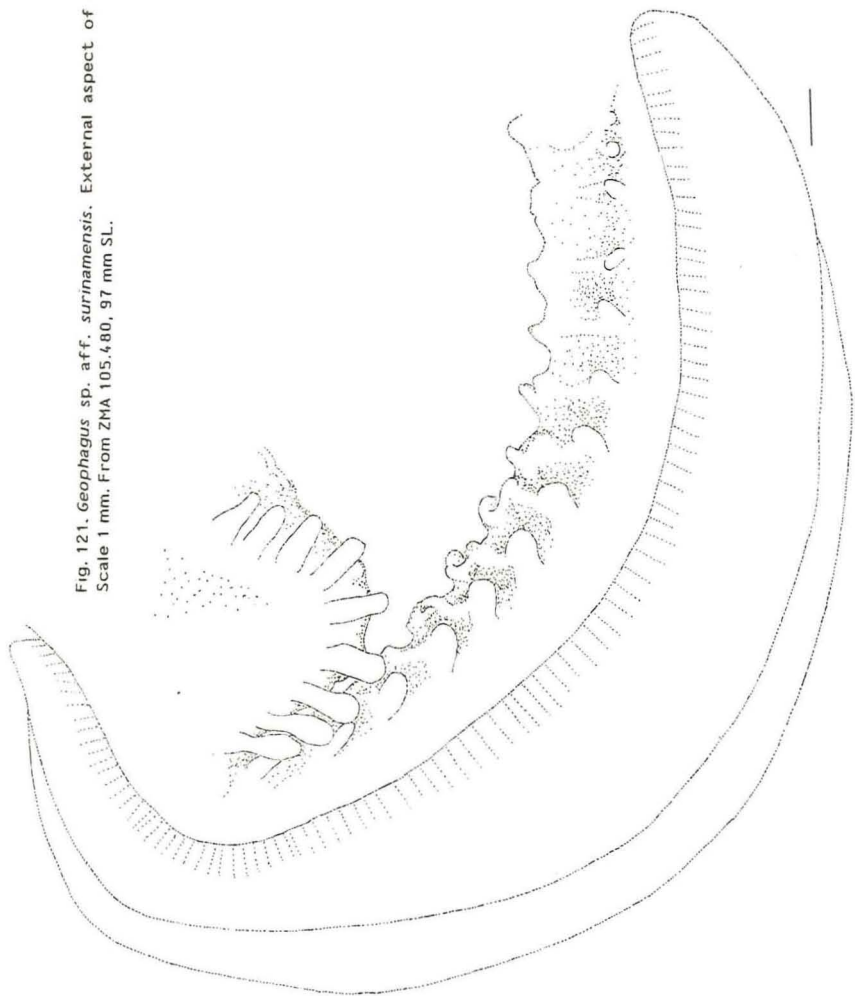


Fig. 120. *Geophagus*. To the left, lower pharyngeal tooth-plate of undescribed Corantijn species in occlusal view; scale 1 mm; from ZMA 106.193, 82 mm SL. To the right, first epibranchial and pharyngobranchial of *Geophagus harreri*; cartilage and connective tissue pad stippled; scale 1 mm; from IRSNB unreg. (SOK 61), 88 mm SL.

Fig. 121. *Geophagus* sp. aff. *surinamensis*. External aspect of first gill-arch.
Scale 1 mm. From ZMA 105.480, 97 mm SL.



Microgillrakers absent, or present externally on second to fourth arches. First pharyngobranchial widened ventrally; in *G. harreri* rather triangular (Fig. 120). Minute interarcual cartilage. Five to six tooth-plates on fourth ceratobranchial; only three in *G. harreri*. No rakers on fifth ceratobranchial. Epibranchial lobe as deep as length of first epibranchial; about eight to ten long fingerlike rakers near, and reaching beyond edge. Ceratobranchial rakers (9-14 externally on first arch) attaching over bone, not on skin fold below, mediad connected to transverse folds (Fig. 121). Lower pharyngeal tooth-plate relatively broad, with strong teeth (Fig. 120).

Lip folds moderately wide, interrupted anteriorly. Jaws equal anteriorly. Most of alveolar process of premaxilla toothed; outer series teeth distinctly larger than those of two to four shorter inner series in a band well separated from the outer series. Anterior half of each dental with an outer series, anteriorly somewhat forwards curved, and an inner band of smaller teeth anteriorly in two to four, posteriorly one series.

This is a speciose group with geographically well-restricted species. *Geophagus surinamensis* is endemic to the Marowijne and Suriname R. systems; *G. altifrons* known only from the R. Negro and upper R. Orinoco; *G. camopiensis* endemic to the Oyapock system; *G. harreri* to the Marowijne; *G. megasema* to Bolivian Amazonia. The Ucayali-Solimões-Amazonas form may be *G. proximus*, but too little material is available for a decision. Undescribed species are an upper Xingu, a Caura, a Parnaíba, a Suriname R., and an Essequibo-Corantijn species.

The most distinct is *G. harreri*, rather elongate, with more reduced jaw dentition, naked predorsal midline, embedded ventral head scales, and a colour pattern resembling that of nominate *Guianacara* species. The remainder conform to descriptions of *G. surinamensis* in literature, differentiated by colour pattern details, shape variation, different degree of fin squamation, width of gills, etc.

Species called *G. surinamensis* in the aquarium hobby are larvophilous (Peters & Berns 1982) or ovophilous (Minde 1982) mouthbrooders.

GUIANACARA n. gen.

Type-species: *Acara geayi* Pellegrin.

Acara Geayi Pellegrin, 1902. *Bull. Mus. Hist. nat.* 8, p. 417 (Riviere Camopi (Guyane française)).

Guianacara is a group of moderate-sized (to c. 70 mm SL) geophagines without first epibranchial lobe. It is known hitherto from only one species, *G. geayi* but actually comprising at least four species, referable to two subgenera:

Guianacara n. subgen. Two supraneurals; anterior dorsal-fin lappets produced in adults; a prominent dark stripe across middle of side (may be reduced to a dorsal spot in adults).

Oelemaria n. subgen. Type-species *Guianacara oelemariensis* n. sp.; diagnosis as for subgenus; holotype IRSNB unreg. (SOK 36), 81.0 mm SL. Suriname, distr. Marowijne, Marowijne R. system, small right bank tributary to the upper Oelemari R. 14 November 1966. Leg. J.-P. Gosse (Mission Suriname 1966, Sta. 163). Single supraneural; no produced dorsal-fin lappets at any size; large dark blotch posteriorly on the side.

Oelemaria is advanced with regard to supraneural and dorsal-fin shape; Nominate *Guianacara* have an apomorphic colour-pattern. The gender of both names is feminine.

Scales moderately small, sq. long. 25, rarely 24 or 26, smaller preventrally; cheek completely scaled, with 4-6 scale series. Fins naked except caudal-fin with basal concave scale-layer. Up to five canals in lateral line branches between caudal-fin rays D3 and D4, and V4 and V5. Caudal-fin hind edge truncate or subtruncate, often with marginal filaments. D. XV.10 (rarely 14 or 16 spines, 9, 11, or 12 rays). Dorsal-fin spines increase in length to fifth, behind shorter to about tenth from

which subequal, last three again longer; anterior lappets correspondingly produced in *Guianacara* s. str. A. III.8 (rarely 7 or 9 rays). Pelvic-fin with first ray longest. Pectoral-fin to above anal-fin origin.

No microgillrakers; 1-2 epibranchial, 5-7 ceratobranchial short rakers externally on first arch; no fifth ceratobranchial rakers; 3-4 tooth-plates on fourth ceratobranchial; first pharyngobranchial expanded ventrally; minute interarcual cartilage. Lower pharyngeal tooth-plate strong, wide, with enlarged posteromedian teeth. Third pharyngobranchial wide, with well developed dorsal apophysis.

Mouth small, jaws equal anteriorly, anterior jaw teeth subprocumbent, outer series of jaw teeth well separated from inner 2-3 (upper jaw) or 3-5 (lower jaw) series; half or less of distal portion of alveolar process of premaxilla naked. Lips moderately thick, folds interrupted. Upper jaw with long ascending processes with rostral foramen, alveolar process short. Fifth branchiostegal ray base medial to anterior ceratohyal. Preoperculum occasionally serrated. Supraoccipital crest low; well elevated median frontal crests.

Vertebrae 13+14 (occasionally 13+13); well developed parhypural spine; 4-5, occasionally 3, procurrent rays in each caudal-fin lobe; no interhypural median cartilage; moderate paired hypapophysis on third vertebra.

Five dental, six preopercular lateralis foramina; infraorbitals io2, io3+4, io5, io6.

Guianacara would appear to be intermediate between other cichlids and geophagines and would seem to be referable to the latter chiefly by plesiomorphic characters. There are resemblances to *Gymnogeophagus*, *Papiliochromis*, and *Crenicara*, but no definitive synapomorphy.

Species recognized besides the Oelemari R. endemic *G. oelemariensis*, include *G. geayi* in the Oyapock system, one undescribed in the Marowijne, Suriname and Saramacca rivers, and one undescribed in the Corantijn R. system. Material from the upper R. Trombetas, the Essequibo, Caura, and upper R. Branco is in bad condition or juveniles, and could not be decisively identified to species.

Adult nominate *Guianacara* are light, with a dark stripe curved from nape through eye to sub-/interopercular junction; and a ventrad pointed contrasting stripe across the middle of the side from back down to the lower sides; a caudal spot is lacking, but soft unpaired fins are variously spotted and the anterior soft dorsal-fin is blackish. The flank pattern is remarkable although a similar vertical contrasting bar, but not ventrad pointed, is shown by *Symphysodon discus*, *Caquetaia myersi*, and the Central American *Neetroplus nematopus* Günther, and *Centrarchus sajica* (Bussing).

The colour pattern of nominate *Guianacara* is as in young and medium-sized *Geophagus harreri* but for especially a spot below the dorsal-fin base end in the latter. As the pattern is very contrasting and unusual, some kind of mimicry is suggested. *Geophagus harreri* and the Marowijne *Guianacara* are commonly collected together. Large *G. harreri* tend to be more uniformly, dull-coloured.

GYMNOGEOPHAGUS

Gymnogeophagus A. Ribeiro, 1918. *Revta Mus. paul.* 10, p. 790 (type by monotypy *G. cyanopterus* A. Ribeiro). - Masculine.

Geophagus australe Eigenmann, 1907. *Proc. Wash. Acad. Sci.* 8, p. 454. Pl. XXIII. fig. 7 (Buenos Aires).

Geophagus Balzanii Perugia, 1891. *Ann. Mus. civ. Stor. nat. Genova.* (2) 10, p. 623 (Villa Maria (Matto Grosso), Rio Paraguay a 15° Lat.).

Geophagus duodecimspinosus Boulenger, 1895. *Proc. zool. Soc. Lond.* 1895, p. 524 (Paraguay).

Gymnogeophagus cyanopterus A. Ribeiro, 1918. *Revta Mus. paul.* 10, p. 790 (Itaqui - R. Grande do Sul).

Geophagus gymnogenys Hensel, 1870. Arch. Natges. 36, p. 61 (Gebirgsbächen des Urwaldes von Rio Grande do Sul).

Geophagus camurus Cope, 1894. Proc. Amer. philos. Soc. 33, p. 104, Pl. IX, fig. 17 (Jacuhy river).

Geophagus labiatus Hensel, 1870. Arch. Natges. 36, p. 64 (Rio Santa Maria des Urwaldes von Rio Grande do Sul).

Geophagus bucephalus Hensel, 1870. Arch. Natges. 36, p. 63 (Rio Cadea und seinen Zuflüssen).

Geophagus pygmaeus Hensel, 1870. Arch. Natges. 36, p. 68 (in Guahyba bei Porto Alegre).

Geophagus scymnophilus Hensel, 1870. Arch. Natges. 36, p. 65 (-).

Geophagus rhabdotus Hensel, 1870. Arch. Natges. 36, p. 60 (Rio Cadea).

Geophagus brachyurus Cope, 1894. Proc. Amer. philos. Soc. 33, p. 105, Pl. IX, fig. 18 (Jacuhy river).

This group is being revised by Roberto Reis, and I have done little about it since I re-validated *Gg. labiatus* and reported on an Alto Parana form which, it seems, is an undescribed species (Kullander 1981d). I have re-examined Hensel's and Cope's types, resulting in a new synonymy for *Gg. labiatus*, *Gg. gymnogenys* and *Gg. rhabdotus*. Cope's material had been mixed up, explaining Gosse's (1976) identification of *Gg. camurus* as *Gg. rhabdotus*.

It is a very heterogeneous group in many respects. The diagnostic antrorse spine on the first pterygiophore of the dorsal-fin (Gosse 1976), would seem to be an outstanding apomorphy, but the same spine is found in *Ptychochromis* and there is no morphological homogeneity otherwise in the group (see descriptions and figures in Gosse 1976). *Gymnogeophagus balzanii* and *Gg. labiatus* are mouth-brooders, *Gg. rhabdotus* is a substrate brooder.

The type-species, *Gg. balzanii* has dorsal- and anal-fins scaly; 2-3 tooth-plates on fourth ceratobranchial; a long ventral lobe lateral line on caudal-fin but none on the dorsal lobe; second pelvic-fin ray longer than the first; five infraorbitals; widely grooved supraoccipital crest edge; moderately elevated median frontal crest; very little elongated interarcual cartilage; no microgillrakers; jaw dentition similar to *Geophagus*; slender first epibranchial; plate-like first epibranchial with well separated medial arms; short wide lobe with about 6 marginal short rakers (as in *Biotodoma*); 9-12 ceratobranchial relatively small rakers; relatively large scales (squ. long. 26-28) and about equal number of dorsal-fin spines and rays, D. XII-XIV.12-15 (Gosse 1976), vertebrae 14+14 modally (Gosse 1976); no gill-rakers on lower pharyngeal tooth-plate.

HEROS

Heros Heckel, 1840. Annln wien. Mus. Natges. 2, p. 362 (type by subsequent designation by Jordan & Gilbert (1893), *H. severus* Heckel). - Masculine.

Heros severus Heckel, 1840. Annln wien. Mus. Natges. 2, p. 362 (Marabitanas im Rio-negro).

Heros coryphaeus Heckel, 1840. Annln wien. Mus. Natges. 2, p. 364 (Rio-Guaporè...Morasten um Matogrosso).

Heros efasciatus Heckel, 1840. Annln wien. Mus. Natges. 2, p. 372 (Rio-negro).

Heros modestus Heckel, 1840. Annln wien. Mus. Natges. 2, p. 366 (Rio Guaporè).

Heros spurius Heckel, 1840. Annln wien. Mus. Natges. 2, p. 368 (Rio-Guaporè...Sümpfen).

Uarus centrarchoides Cope, 1872. Proc. Acad. nat. Sci. Philad. 23, p. 253, Pl. XI, fig. 2 (Ambyiacu River).

Centrarchus notatus Jardine, 1843. Nat. Libr. Ichthyol. 5, p. 160, Pl. 13 (-).

Chromys appendiculata Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 15, Pl. 7, fig. 3 (as *Chromis appendiculata*) (l'Ucayale (Pérou)).

Chromys?? fasciata Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 17, Pl. 9, fig. 2 (l'Araguay).

Cichlasoma severum var. *perpunctatum* A. Ribeiro, 1918. *Comissão Linhas telegr. estrat. Matto Grosso Amazonas Publ.* (46), p. 187, Pl. XVI (Manãos).

Heros, which is also discussed in Part I, p. 271, is currently regarded as monotypic, but no thorough analysis has yet been made of larger samples from all over the range of the species. There is considerable intraspecific variation in coloration, much evidently ontogenetic. Variation among adults remains to be studied but includes probably sex differences and variation depending on sexual activity. The long synonym list reflects colour variation and neglect of earlier work on the species. Günther (1862), as first reviser, selected the name *spurius* before *severus*; but later authors have generally preferred *severus* as senior synonym.

The geographical distribution includes the Amazonas basin including the Guaporé, Negro and Branco, the Tocantins, the Essequibo (Rupununi, Potaro), Oyapock, Orinoco system and the upper Paraguay. Examination of Steindachner's (1874) *Acara spuria* from the R. Paraíba near Juiz de Fora supports doubts about the locality data.

Body deep, compressed, with narrow nape and flattened posterior chest, orbit well removed from frontal outline.

Young (c. 20 mm) more elongate and with upper lip fold discontinuous symmetrically. 8 dark vertical bars across side, posteriormost over posterior edge of caudal peduncle and caudal-fin base, anteriormost above operculum, continued over chest to pelvic-spine; second bar from posteriormost connecting light-margined black blotch on dorsal-fin base with similar but fainter blotch on anal-fin base. Strong suborbital stripe continued fainter above orbit to nape midline. Adults with bars less contrasting but usually intensified hypaxially; dorsal-fin with dark dots, head stripes faded.

All scales are ctenoid except ventrally on gill-cover and cheek, latter without naked ventral zone. Scales relatively small, sq. long. 27-30. 20 circumpeduncular scale series. Two scale series between lateral lines. Scales smaller gradually toward nape and chest; posterior prepelvic scales about half size of anterior flank scales. Pectoral axilla and base of pectoral-fin scaly. Posterior spinous anal- and dorsal-fin bases, most of soft dorsal-fin and all of soft anal-fin base narrowly scaled; anal-fin squamation wider than dorsal-fin squamation; interradial scales in one or two series. One-third of caudal-fin scaly marginally; accessory caudal-fin lateral lines on membranes D2-D3, and V4-V5, not extending beyond rest of caudal-fin squamation.

Caudal-fin with three procurent rays in each lobe. Anal-fin with 7-8 spines, 12-14 rays, long; caudal peduncle much reduced in length.

Vertebrae 13+15, 14+14; basapophyses on first on two first postabdominal vertebrae; anterior three caudal vertebrae with median plane laminar expansions making contact serially. Swimbladder diverticulae to fourth hemal spine. Parhypural spine moderately developed. Hypapophyses on third and fourth vertebrae well-developed. First three vertebrae strongly compressed compared to succeeding; first supraneural with strong anterior distal spine.

Anterior jaw teeth pointed, little recurved, with a small cusp subapically on the lingual side. Marginal outer teeth small and unicuspid, strong symphyseal size increase accompanied by development of second cusp. Inner, small teeth in anterior half of each hemijaw, simple. Lower lip fold wide, thick, continuous; upper lip fold broad and continuous.

First epibranchial short and wide, featuring a distinct projection medially on the anterior edge; interarcual cartilage clump-like; first pharyngobranchial slightly expanded ventrally; rakers short, 3+1+9-10; 4-5 small tooth-plates on fourth ceratobranchial; second pharyngobranchial toothed; third pharyngobranchial slightly compressed dorsoventrally, with slightly elongate dorsal articulation facet; second basibranchial with a rostroventral directed lateral process fitting concavity in caudal border of first hypobranchial. Pharyngeal apophyses of skull moderately raised; median ledges of basioccipital well-developed; Baudelot's ligament inserting anteriorly.

Median frontal crests high; coronalis canal long, opening dorso-rostrad; supraoccipital crest high, not reaching rostrad to coronalis opening. Other lateralis foramina, and infraorbital series as in *Cichlasoma*.

Regan considered *H. severus* close to *Symphysodon*, and there is some claim for that in the coloration, swim-bladder extension, vertebrae, mouth shape, but there are also profound differences between the genera (cf. *Symphysodon*, p. 407).

Vandewalle (1971) has a brief description of the osteology and myology of *H. severus*, with emphasis on the cranium.

HOPLARCHUS

Hoplarchus Kaup, 1860. *Arch. Natges.* 26, p. 128 (type by subsequent designation by Eigenmann (1910a), *Hoplarchus pentacanthus* Kaup). - Masculine.

Heros psittacus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 369 (Rio-negro, nördlich von Marabitanas am Fusse des Berges Cocui).

Hoplarchus pentacanthus Kaup, 1860. *Arch. Natges.* 26, p. 129, Pl. VI, fig. 1 (? Südamerika).

Centrarchus cycnia Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 157, Pl. 11 (Rio Negro).

Regan's (1905e) account of this R. Negro + upper Orinoco species is an abstract of preceding descriptions, as he did not have preserved material available. This shortcoming may explain the inclusion of *Pomotis fasciatus* Jardine in the synonymy. That species is described as having 8 anal-fin spines and appears, from the description and drawing, to be rather an *Uaru* species, and is here tentatively identified as *U. amphiacanthoides*.

These are large, moderately deep, compressed fishes, reaching at least 205 mm SL. Nape and interorbital narrowly rounded over midline; orbit well removed from forehead contour. Snout somewhat beak-like with steep dorsal contour; mouth narrow, upper jaw slightly projecting; premaxillary ascending processes not reaching to orbit. Preoperculum with deep notch in vertical margin just dorsal to angle, and angle slightly expanded caudad.

The scales are small (squ. long. nearly 50), ctenoid on sides and thoracally, distinctly gradually smaller dorsad above upper lateral line; cycloid and very small along predorsal midline and anterior to extrascapulars; prepelvic scales minute, the largest, near pelvic-fins about half size of flank scales, much smaller rostrad; gill-cover and cheek scales small, though of varying size; cheek naked ventral to line continuing labiad margin of lachrymal caudoventrad; circumpeduncular scale series 24; four horizontal scale series between lateral line ends; caudal-fin narrowly scaled, marginally along basal third of fin, centrally less; lower lateral line continued by two tubed scales between caudal-fin rays V1 and V2, and by long tube sequences between rays V4 and V5 and D3 and D4 reaching beyond adjacent fin squamation; very narrow layer of packed scales on base of most of anal-fin and anterior two-thirds of soft dorsal-fin.

Fins of modal type; caudal-fin subtruncate-roundish; anal-fin with five spines (six-spined specimen reported by A. Ribeiro 1918d). Caudal-fin with three procurrent rays in each lobe. A strong pointed parhypural spine. Vertebrae 12+15, 2 supraneurals. Swimbladder restricted to abdominal cavity and no caudal ribs. Moderately developed hypapophyses on fourth vertebra. Distal postcleithrum with a short blunt rostradorsal process. The skull is more compressed than in *Cichlasoma*, otherwise grossly similar. Lateralis canal foramina about as in *Cichlasoma*, only positions slightly different due to other head proportions.

The upper lip fold is widely interrupted mesially; the lower lip fold is continuous, but nearly interrupted by a frenum symphysially. The teeth are fixed, simple, pointed, apically recurved, those of labiad series much stronger than those of inner band of teeth. Upper jaw dentition lining anterior two-thirds of each jaw half.

Interarcual cartilage clumplike. First pharyngobranchial slender, little widened ventrally. First epibranchial short, slightly wide. Upper pharyngeal jaw similar to

that of *Cichlasoma*, neurocraniad apophysis little longer than wide. Baudelot's ligament attached to very low admedian basioccipital ledges. No tooth-plates on fourth epibranchial. Gill-rakers well-denticulated, 2+1+6-7 externally on first arch.

Juveniles similar to adults but more elongate, with naked fins and no notch in the preopercular margin.

The coloration is very different from that of *Cichlasoma*. Juveniles have a distinct suborbital stripe. They also have distinct dark spot close behind the orbit, possibly homologous with the cheek spot in *Cichlasoma*. In adults the cheek spot is, however, stripe-like and lies over the median infraorbitals.

Juveniles with distinct vertical bars, one on caudal peduncle, three over caudal-fin base, one above vent and one immediately posterior to the head; the five anterior bars carry each a darker blotch along the middle of the side. The bars are less evident in adults, which, however, have a blotch also in the caudal peduncle bar. Adults have the back light brownish with light areas along the dorsal-fin base.

The caudal spot is midbasal in juveniles, in adults positioned in the lower half of the dorsal lobe adjacent to the caudal peduncle, without light ring around, squarish in shape.

Adults are characterized by a dark stripe along the ventral margin of the cheek squamation; a dark spot on the suspensorial process of the preoperculum, another close to the posterodorsal edge of the orbit, and another, in series with lateral blotches, dorsally on operculum. No light preorbital stripe. Soft unpaired fins and spinous dorsal-fin light with dark dots.

Considered close to *C. severum* and ancestral to *Uaru* by Regan (1905e), I feel positive only about relationship to *Coryphacara* (q.v., and Part I).

Regan's diagnosis is rather useless ('Body ovate. Scales of the lateral line larger than those above and below it. Dorsal XV 12-13. Anal V 8-10.'). Attention may be given instead to the shape of the preoperculum which is apparently unique to a neotropical cichlid, and was also emphasized by Heckel (1840).

The naked ventral cheek is a character state reminiscent of that in *Cichla*, chaetobranchines and *Astronotus*, in which, however, the cheek squamation is divided entirely or anteriorly by a naked line continuing the labial margin of the lachrymal caudad. But as in the genera mentioned, and also *Satanoperca daemon* and a similar *Satanoperca* species, the naked line is marked by a dark stripe not found in any other cichlids.

'*Cichlasoma*' *microlepis* Dahl (1960), is based on two specimens from the R. Baudó, departamento Chocó, on the Pacific slope of Colombia. Dahl's figure and description suggests some resemblance to *H. psittacus*, as well as to Pacific slope *Nandopsis* species. Scales in a 'lateral series' are given as 50 and 52 in the description, and emphasized as species diagnostic; but on the figure is shown only about 32 squ. long. scales. In some people's handwriting, 5 and 3 are nearly indistinguishable, but a check of Dahl's examination notes on other fish, deposited at NRM, shows his handwriting to be clear and easily read.

KROBIA n. gen.

Type-species: *Aequidens itanyi* Puyo.

Acara guianensis Regan, 1905. *Ann. Mag. nat. Hist.* (7) 15, p. 340 (Guiana).

Nannacara hoehnei Ribeiro, 1918. *Comissão Linhas telegr. estrat. Matto Grosso Amazonas Publ.* (46), p. 14, Pl. VII, fig. /1/ (rio Branco, afluente do Araguaya, e n uma lagôa do Coxipó da Ponte, em Matto-Grosso).

Aequidens itanyi Puyo, 1943. *Bull. Soc. Hist. nat. Toulouse* 78, p. 146, Fig. 4 (crique du haut Itany).

Aequidens potaroënsis Eigenmann, 1912. *Mem. Carneg. Mus.* 5, p. 490, Pl. LXVI, fig. 2 (Amatuk).

Krobia is a surinamese name applied on smaller cichlids. As a generic name for what is called the 'Aequidens' *guianensis* group in Part I (p. 280), its gender is feminine.

Krobia guianensis is a mis-known species insofar as it is, except for the holotype, identified as *Aequidens vittatus* in the literature on Guianan fishes (Eigenmann 1912; Lowe-McConnell 1969; Keenleyside & Bietz 1981), whereas *vittatus* is actually a Paraguayan-Bolivian species (*Pharyngotocacara vittata*). It reaches c. 130 mm SL and is common in Surinam and Guyana from the lower Marowijne west to the Demerara (a single record from the Mazaruni by Lowe-McConnell 1969).

Krobia itanyi is endemic to the Marowijne system upstream of *K. guianensis* localities and easily distinguished from the latter in that the lateral band ends at the end of the upper lateral line instead of at the dorsal-fin base.

An undescribed species in the Oyapock system is more obscure, with washed-out coloration compared to the two above.

Krobia hoehnei was described from the Araguaia and Coxipó da Ponte. I doubt the correctness of the Paraguayan locality. Since, the species has been collected only in the Xingu. It is smaller and more round-bodied than Guianan forms, and lacks dorsal-fin scales.

Krobia potaroensis in the Potaro and nearby Essequibo has the lateral band running to the caudal-fin base. There is a similar, undescribed species in Surinam, apparently restricted to the Paloemeu R. system.

The colour pattern differences indicate that two lineages are involved, but other characters, especially the diagnostic slender pharyngobranchial 1 shape, suggest common ancestry. See further Part I, p. 280.

MARGARITACARA n. gen.

Type-species: *Chromis brasiliensis* Quoy & Gaimard.

Chromis brasiliensis Quoy & Gaimard, 1824, in Freycinet. *Voy. autour monde*. Zool., p. 286 (baie de Rio de Janeiro).

Geophagus brasiliensis Kner, 1855. *Reise Novara. Fische*, p. 266, Pl. X, fig. 3 (Rio Janeiro).

Chromys unimaculata Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 13, Pl. 7, fig. 2 (eaux douces des environs de Rio-de-Janeiro).

Acara gymnopoma Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 278 (-).

Acara minuta Hensel, 1870. *Arch. Natges.* 36, p. 53 (kleinen Tümpeln bei Porto Alegre).

Geophagus brasiliensis iporangensis Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 364, Pl. LXXI (Iporanga...a mountain stream of the Rio Ribeira da Iguapé).

Geophagus brasiliensis itapicuruensis Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 365, Pl. LXXII (Queimadas, Rio Itapicuru).

Chromys obscura Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 14, Pl. 6, fig. 3 (rio Paraguassu (province de Bahia)).

Chromys unipunctata Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 13, Pl. 8, fig. 2 (rio Paraguassu, dans la province de Bahia).

In this group uniquely among geophagines, the caudal-fin may be rounded, and richly adorned by alternating light and dark spots. Adult *M. brasiliensis* are covered by pearly spots suggesting the name of the group (gender feminine).

Gill-rakers on the fifth ceratobranchial; four fourth ceratobranchial tooth-plates, small interarcual cartilage; very short first epibranchial lobe, and widened epibranchial end of first pharyngobranchial (Fig. 122); microgillrakers externally on three posterior arches; no median interhypural cartilage; simple hypurapophysis on third vertebra; smooth opercular and pectoral girdle bones; four infraorbitals; end of rostral branchiostegal ray medial to anterior ceratohyal; relatively large scales (sq).

long. 26-27); scaly soft dorsal- and anal-fin bases (interradial scales only) in large *M. brasiliensis* at least; a large midlateral spot and not well-exposed midbasal caudal spot; a strong medial nuchal elevation in adult males; interrupted lip folds; single supraneural; 5-8+1+8-10 weak gill-rakers externally on first gill-arch (Fig. 122); infrequently one or two canals on caudal-fin between rays D3 and D4, and V4 and V5; vertebrae 14+14, naked cheek ventral to line continuing adlabial lachrymal margin caudad; much reduced frontoparietal crest; low median frontal crest not raising coronal foramen, and almost no laterad projecting frontal ledge along orbit; jaw dentition as in *Gallochromis*; jaws equal anteriorly.

Margaritacara brasiliensis reaches at least 226 mm SL according to my records, and is the largest species. It is certified from the Rio de Janeiro area. North of it, there is *M. itapicuruensis* in the Itapicuru with emphasized, vertically extended midlateral spot. I have not seen fresh Paraguassu material, but Castelnau's two species may represent a distinct form. In the R. de Contas is a species almost uniform, with faint midlateral spot and indicated lateral band. *Margaritacara iporangensis* is known only from the type series of which I only examined the holotype. It may be distinct by the wide thick lower lip. *Margaritacara* species other than *M. brasiliensis* have truncate caudal-fin. All were considered the same species by Gosse (1976).

I have not been able to separate southern Brazilian *Margaritacara* from *M. brasiliensis* from Rio; but clearly there is a lot of basic work to do on species level taxonomy in *Margaritacara*.

Species called *Geophagus brasiliensis* in the literature are biparental substrate brooders.

MESONAUTA

Mesonauta Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 300 (type by monotypy *Heros insignis* Heckel). - Masculine.

Heros festivus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 376 (Fluss Guaporè und dessen nahe gelegenen Moraste).

Heros insignis Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 379 (Waldache bei Marabitanas am Rio-negro).

Chromys?? acora Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 17, Pl. 9, fig. 1 (lacs de l'Araguay).

The genus is discussed also in Part I, p. 272.

The body shape is unique; compressed, but with rather broad forehead-nape, and level dorsal contour; the chest is deep; the head is conspicuously narrowed rostrad in lateral aspect and ends with a small terminal mouth at the tip of a long snout. Juveniles already at c. 10 mm similar to adults in shape. The outer branch of the first, strong, pelvic-fin ray is much elongated, reaching the middle of the caudal-fin in adults; whereas the rest of the fin is short, extending only slightly behind the anal-fin origin. The caudal-fin has a slightly convex posterior margin; three procurrent rays in each lobe. Pectoral-fin short, rounded, with third or fourth ray longest. Anal-fin spines 8 (modally) or 9.

All scales ctenoid, save some of cheek and gill-cover. Squ. long. 24-25. Circumpeduncular scale series 20; three series of scales on cheek; two horizontal scale series between lateral lines. Nape and chest scales not much smaller than flank scales, former stochastic, latter in median series larger, about half size of anterior flank scales. Pectoral- and pelvic-fins naked. Posterior spinous dorsal- and anal-fins, most of soft dorsal- and all of soft anal-fin, narrowly scaly basally; anal-fin squamation wider than dorsal-fin squamation. Up to about half of caudal fin scaled; long tube sequences on caudal-fin membranes D2-D3, V4-V5, and one associated with ray V1.

The head is slender and compressed, with low supraoccipital crest; the median frontal crest is only feebly raised and the coronal foramen not elevated; likewise the frontoparietal crest is very narrow. A prominent antrorse spine distally on the first supraneural, the second blunt-tipped. Anterior two hemal spines little widened; no

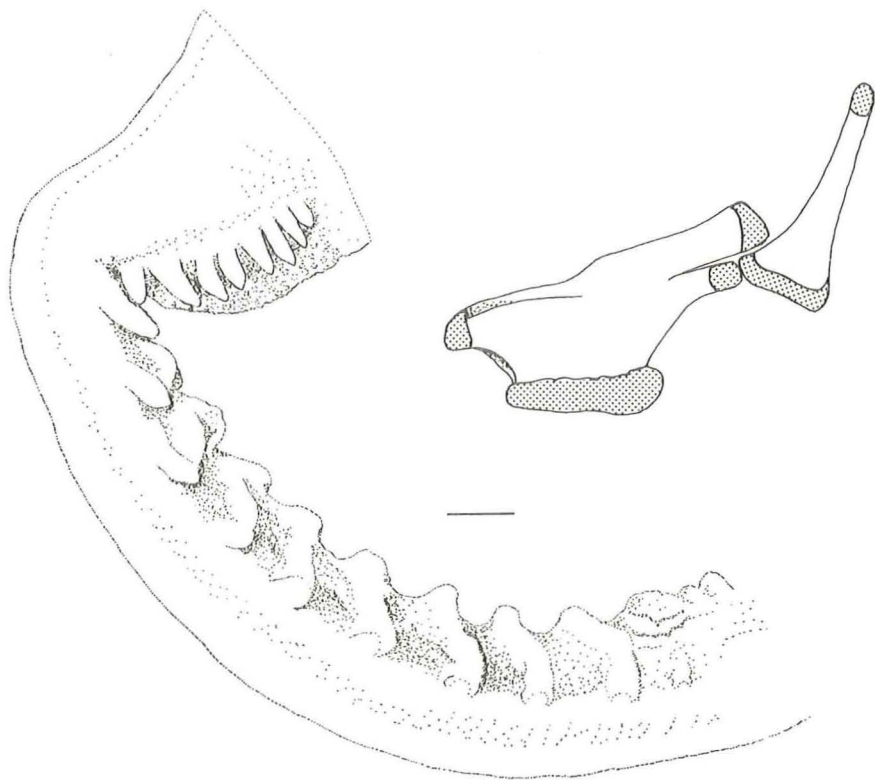


Fig. 122. *Margaritacara* sp. cf. *brasiliensis*. External aspect of first gill-arch to the left. First epibranchial and pharyngobranchial in rostralateral aspect to the right, cartilage and connective tissue pad stippled. Scale 1 mm. From NRM A82/3453, 85 mm SL.

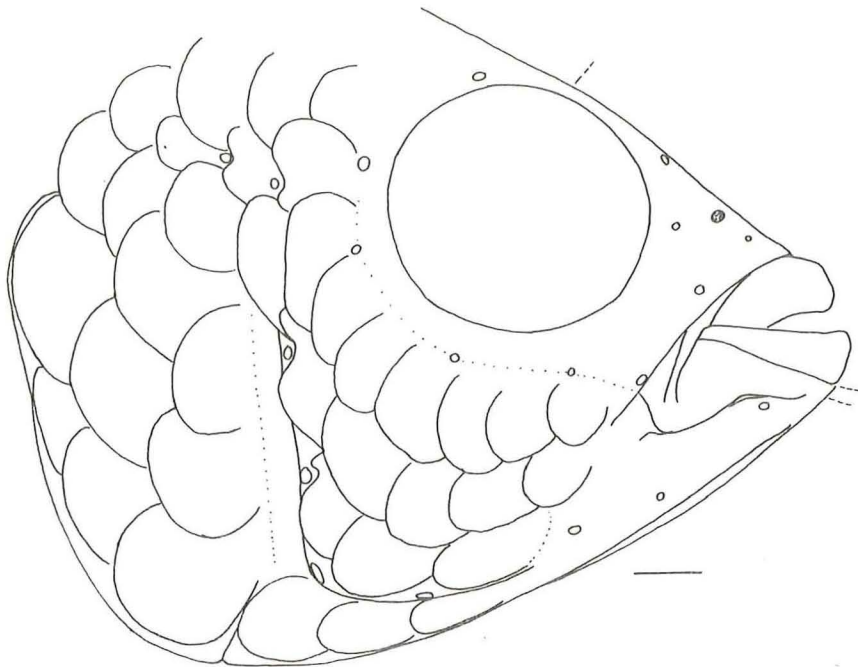


Fig. 123. *Nannacara anomala*. Lateral view of head to show scale pattern of cheek and gill-cover. Scale 1 mm. From IRSNB unreg. (SOK 23), 33 mm SL.

parhypural spine. Vertebrae 12+14-15 or 13+14. No process on distal postcleithrum. Moderately developed hypapophysis on third vertebra.

Lateralis pores about as in *Cichlasoma*.

Branchial skeleton similar to *Cichlasoma*. First epibranchial short and stout; interarcual cartilage minute. Two small tooth-plates on fourth ceratobranchial. Rakers short, denticulate, 2+1+6-7 externally on first arch. Pharyngobranchial neurocranial apophysis short and broad, little elevated. Baudelot's ligament attaching to moderately developed basioccipital ledges.

Jaw teeth mostly unicuspid, conical; in labiad series, distinct size increase forwards, and development of a minor second cusp on linguad edge, also these larger teeth somewhat labiad-inclined; inner teeth small, in narrow band anteriorly in jaws.

A suborbital stripe is lacking of all sizes. The caudal spot is formed already at c. 10 mm, then little more intense than ventral lobe pigment of the caudal-fin base. At slightly larger sizes the spot is brightly ocellated, black with whitish margin, as in adults, and the most prominent marking occupying the space between lateral line level and dorsal fin edge.

A dark stripe runs from the mouth, interrupted by the eye to the anterior dorsal-fin soft rays, along which it may be continued; the stripe is often reduced to spots on the flanks. The body is otherwise adorned by irregular vertical bars, usually more or less confluent and forming a mottled ground pattern.

Regan considered *Mesonauta* close to *Cichlasoma bimaculatum* and *C. autochthon* (= *Australacara faceta*), considering especially, I gather, the relatively large scales.

Mesonauta is widely distributed, collected in the Orinoco, Negro, Branco, Essequibo, Ucayali-Solimões-Amazonas, Tocantins, Mamoré, upper Paraguay drainages. Revision of the group may show it to consist of geographical species.

NANNACARA

Nannacara Regan, 1905. *Ann. Mag. nat. Hist.* (7) 15, p. 344 (type by monotypy *N. anomala* Regan). - Feminine.

Nannacara anomala Regan, 1905. *Ann. Mag. nat. Hist.* (7) 15, p. 344 (R. Essequibo).

Nannacara taenia Regan, 1912. *Ann. Mag. nat. Hist.* (8) 9, p. 505 (the Amazon at Manaos).

Subject of a note in Part I (p. 281), this genus, notable chiefly for its reduced lateralis system, needs little further comment.

These are small fishes, reaching 56 mm SL (males) or 39 mm SL (females). Continuous lip folds; uniserial predorsal squamation; cycloid predorsal and prepelvic scales; two cheek scale series, one preopercular scale series (Fig. 123); mostly only pored scales in lateral lines; commonly a membrane connecting caudal peduncle and proximal part of the last anal- and dorsal-fin ray; fifth pectoral-fin ray longest; elongately rounded caudal-fin; well-toothed jaws (entire rim of premaxillary alveolar process); long dorsal-fin (D. XVI.8 modal); short caudal peduncle; no parhypurapophysis; 5-6 external ceratobranchial rakers; two infraorbitals with wide ventral lamellae; truncate supraoccipital crest tip; no fourth ceratobranchial teeth, interarcual cartilage, vertebral hypapophysis, or microgillrakers; a rostral premaxillary foramen; epipleural ribs on 2-3 anterior caudal vertebrae; complex last abdominal vertebra with hemal canal; are character states which besides the small size partly point to *Adistogramma*, otherwise distinguish the genus from other cichlasomines; those italicized unique among cichlids, like the 14 caudal-fin rays. There is some similarity to *Acarabobo* and *Claviforaminacara* in the cheek + preopercular squamation, but the detailed arrangement is not identical (Figs. 100, 115, 123)

Nannacara anomala is widely distributed in Guiana and Suriname, from the lower Marowijne west to the Essequibo; a Caripito record (Schultz 1949) needs checking. There is a similar species with one vertical bar less in the Approuague and Oyapock R. systems.

Acara syspilus Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 255, Pl. XI, fig. 3 (Ambyiacu River).

Acara vittatus Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 346 (Sümpfen um Cujabá, der Hauptstadt in der Provinz Matagrosso).

Aequidens paraguayensis Eigenmann & Kennedy, 1903. *Proc. Acad. nat. Sci. Philad.* 55, p. 534 (Asuncion).

Acara zamorensis Regan, 1905. *Ann. Mag. nat. Hist.* (7) 15, p. 339 (Rio Zamora).

This is a group of moderately large (70-90 mm), little elongated species somewhat similar to *Krobia* and *Coeruleacara* in colour pattern, and called the '*Aequidens*' *syspilus* group in Part I.

The first epibranchial is long and slender, but also somewhat curved, and the first pharyngobranchial is slightly widened epibranchiad. In a cleared and stained *P. syspilus*, there is a small interarcual cartilage clump on the left side, but not on the right side. Two or three small tooth-plates on fourth ceratobranchial; microbranchios-pines absent or (in *P. syspilus*) on outside of second to fourth arches. 0-1 epibranchial, 5-7 ceratobranchial rakers externally on first arch.

Modal vertebral numbers 13+13 and 13+12; 2 supraneurals. Similar in cranial osteology to *Cichlasoma*, only more elongate, with relatively lower supraoccipital crest. Paired short hypapophyses on third vertebra.

The fins are naked, except the caudal-fin base. The caudal-fin has one or two median tubed scales and rather long dorsal and ventral lobe lateral line branches, the dorsal (up to four scales) running between rays D1 and D2, the ventral (up to seven scales) between rays V4 and V5.

Preoperculum naked; cheek scales in three series. The predorsal scales are large and in three series, the median of eight, rarely seven scales, the posteriormost scale often with a deep incision in the posterior edge. The cycloid prepelvic scales are similarly large, in three series. Scale pattern otherwise as in *Cichlasoma*; squ.-long. 24-26, rarely 23 or 27.

The caudal-fin hind edge is truncate or slightly emarginate, often with short prolongation of marginal rays. Anal-fin with 3 spines, modally 7 or 8 rays.

Ground colour light (yellowish); a dark more or less blotchy band from the orbit caudad to or towards posterior part of soft dorsal-fin; continued forwards around nape across anterior predorsal scales (except in one species); caudal base spot chiefly in dorsal lobe but close to lower lateral line level, not or indistinctly ocellated; seven vertical bars, two anterior mostly as spots close to dorsal-fin base; caudal-fin with scattered dark dots or, rarely, immaculate; dark stripe down from eye across cheek commonly restricted to a spot, in varying position, in adults.

Characteristically the dorsal contour is more arched than the ventral, and the mouth appears in a low position, but body and mouth shapes vary.

Pharyngotocacara is defended on the basis of the unique colour pattern, the predorsal scale pattern, and position of the dorsal branch of the caudal-fin lateral line.

Pharyngotocacara mariae (Peters & Berns 1982), *P. vittata* (Timms & Keenleyside) and the Madre de Dios species (pers. obs.) are biparental mouthbrooders and a preserved female of an undescribed form has larvae in the mouth. Like *Krobia* and *Coeruleacara*, studied species spawn on loose leaves (see especially Vierke 1983). The generic name is suggested by the mouthbrooding, and is feminine.

There is a superficial similarity to some *Krobia* species in the lateral band course, but in *Pharyngotocacara* the band modally runs toward the bases of the posterior dorsal-fin rays, not to the end of the fin, and in *Krobia* the band does not continue rostrad across the nape; an oblique lateral band is found also in *Mesonauta*, *Acaronia*, *Chaetobranchius* and *Chaetobranchopsis*.

Although a large group, the outer morphology and colour pattern is very similar in all species. *Pharyngotocacara mariae* is endemic to the upper R. Meta; *P. vittata* is widespread in the Mamoré, Paraguay and adjacent Paraná; *P. syspilus* common along the Ucayali- Peruvian R. Amazonas. The remainder are known from only one or

Nannacara taenia is based on a female aquarium specimen, apparently with incorrect locality data; at the time *N. anomala* was known only from adult males.

PAPILIOCHROMIS

Papiliochromis Kullander, 1977. *Zool. Scr.* 6, p. 253 (type by original designation *Apistogramma ramirezi* Myers & Harry, 1948).

Crenicara altispinosa Haseman, 1911. *Ann. Carneg. Mus.* 7, p. 344, Pl. LVIII (along a sand-bank in the Rio Marmoré, below the mouth of the Rio Guaporé).

Apistogramma ramirezi Myers & Harry, 1948, in Anon. *Aquarium, Philad.* 17, p. 77 (evidently from one of the tributaries of the Rio Apuré or Rio Meta in the states of Guárico, Portuguesa, or Apuré).

Robins & Bailey (1982) suggested that 'Microgeophagus', as used by Axelrod (1971b) would be an older available name for this group. They apparently did so because the gender of *Papiliochromis* is feminine and that would weaken their (Bailey et al. 1980) arguments in a proposal to the International Commission on Zoological Nomenclature to rule that all names ending in *-chromis* be considered masculine, following an error in Robins et al. (1980). Close reading of Axelrod (1971b) suggest that 'Microgeophagus' as used there is not available, and may at best fall in the category of conditionally proposed names.

Papiliochromis ramirezi (to 34 mm SL) was recently re-described (Kullander 1980c) from Colombian llanos material; since I have seen also Venezuelan llanos material.

A larger species (to 59 mm), with higher counts, is *P. altispinosa* in the Guaporé and Mamoré systems, of which notes and photos can be found in Kullander (1981a).

In shape, colour pattern and osteological characters the genus approaches *Biotodoma*, *Guianacara*, *Margaritacara*, and *rhabdotus*-like *Gymnogeophagus*.

The branchial skeleton of *P. ramirezi* is relatively compact; remarkable are the laterally strongly compressed medioposterior bicuspid lower pharyngeal teeth; few microrillrakers externally on the three posterior gill-arches; minute interarcual cartilage; ventrally expanded first pharyngobranchial; short wide lobe with 3-4 marginal rakers; 5-7 minute rakers along first ceratobranchial externally; two ceratobranchial 4 tooth-plates, and lack of fifth ceratobranchial rakers. The third vertebra bears paired hypapophyses. The parhypurapophis is moderately developed; a median interhypural cartilage plate appears lacking (no alcian blue stained material available); no ribs on caudal vertebrae; four procurrent rays in each caudal-fin lobe. The rostrodorso-dorsal distal postcleithral process is very small. A rostral foramen on premaxillary ascending process. Cephalic lateralis system modal, including five dental foramina, infraorbital io2, io3+4, io5, io6. See Kullander (1980c, 1981a) for additional data. The lower lip fold is continuous in *P. ramirezi* only.

Lack of fifth ceratobranchial gill-rakers, a small epibranchial lobe with marginal gill-rakers, narrow lachrymal, 25-27 vertebrae, and a single supraneural were considered diagnostic of *P. ramirezi* (and the genus, then monotypic) in Kullander (1980c). None of these states alone presents a strong case for the group. Contrasted to *Biotodoma*, apomorphies would be represented by the single supraneural, absence of median interhypural cartilage and strongly compressed pharyngeal teeth.

PHARYNGOTOCACARA n. gen.

Type-species: *Acara vittatus* Heckel.

Aequidens mariae Eigenmann, 1922. *Boln Soc. colomb. Cienc. nat.* 9, p. 197 (Barrigón; Cmaral, Llanos; Caño Caricera; Rio Negro, Villcio; Oriente de Bogotá; Q. Gramalote, Villcia); 1922. *Mem. Carneg. Mus.* 9, p. 240, Pl. XXX, fig. 1 (Barrigón).

two localities, one species in the Paraguay, one in the Madre de Dios in Peru, one in the Belém area, the rest in Peru and Ecuador, to a total of 16 species.

PTEROPHYLLUM

Pterophyllum Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 334 (type by monotypy *Platax scalaris* Cuvier). - Neuter.

Plataxoides Castelnau, 1855. *Anim. nouv. rares. Poissons*, p. 21 (type by monotypy *P. dumerilii* Castelnau). - Masculine.

Pterophyllum altum Pellegrin, 1903. *Bull. Mus. Hist. nat.* 9, p. 125 (Atabapo (Orénoque)).

Plataxoides leopoldi Gosse, 1963. *Bull. Inst. r. Sci. nat. Belg.* 39 (35), p. 4, Pl. I, fig. 1 (Furo du village de Cuia (rive gauche du Solimões à environ 90 km en amont de Manacapuru)).

Zeus scalaris Lichtenstein, 1823. *Verz. Doubl. Mus. Berl.* p. 114 (Or. Brasil).

?*Platax?* *scalaris* Cuvier, 1831, in Cuvier & Valenciennes. *Hist. nat. Poiss.* 7, p. 237 (-).

?*Plataxoides Dumerilii* Castelnau, 1855. *Anim. nouv. rares. Poissons.* 21, pl. 11, fig. 3 (Para).

?*Pterophyllum eimekei* Ahl, 1928. *Zool. Anz. Leipz.* 76, p. 252, Fig. 1 (Mündung des Rio Negro in den Amazonas).

Species taxonomy in this group is extremely confused. None of the later revisers (Ahl 1928, L.P. Schultz 1953, 1954, 1967, Burgess 1976) did much but count fin-rays and scales and contributed nothing to an understanding of the basic morphology of these fishes. A major failure of all revisions has been the neglect to define *Pt. scalare*. As this species was described in but two lines, with data partly probably incorrect and otherwise certainly not excluding any *Pterophyllum*, and as the type is lost without having been re-examined by any later author, there is no ground for any later determination of the species. Indeed, some identifications refer to *Pt. scalare* (Cuvier), but the type of it has not been consulted by later revisers either.

Furthermore, Schultz (1967) refers to the colour pattern of the holotype of *Pt. dumerilii* from the specimen and Castelnau's (1855) plate, when recognizing the species. This is puzzling as the nearly scaleless holotype agrees with the plate in absence of coloration on sides and head. The *dumerilii* holotype does not have the wide nape and straight predorsal outline of *Pt. leopoldi*; hence these cannot be synonyms. As *Pt. leopoldi* is a rare species, it is not likely a synonym of *Pt. scalare* and hence listed here as valid.

Pterophyllum altum is a valid species in the upper R. Negro and R. Orinoco, with the character states presented by Schultz (1967). There are at least two more species, identified on Peruvian and lower R. Negro material respectively, but I am uncertain about the characters on material from the rest of Amazonia, Guyana and the Oyapock, most in very bad condition.

Pterophyllum is similar to *Mesonauta*. It differs in the unique colour pattern, principally silvery, with black vertical stripes, one from nape through eye onto chest, two across the side strong, bars between these faint or reduced to spots dorsally; caudal spot not ocellated, ventrad extended; also in the much deeper and more compressed body and much produced anterior soft dorsal- and anal-fins. The caudal-fin is truncate with marginal rays filamentously produced, like the first pelvic-fin ray. The scales are small (squ. long. 33-48), strongly ctenoid. A series of ctenoid scales anteriorly on ventral limb of preoperculum.

Vertebrae 12-14+14-18 = 27-31 (Schultz 1967); *Pt. scalare* auctt. has the hypapophysis on the third vertebra with a strong caudal, caudad directed spinous process; 2 supraneurals; swimbladder diverticula reaching to 7th hemal spine, ribs on 2-3 anterior caudal vertebrae. Two extrascapulars, well-developed parhypural spine.

The skull is deep, with well developed frontal, frontoparietal and supraoccipital crests; but features many differences from the superficially similarly shaped *Symphysodon*. The lower jaw is long and slender; both jaws are well toothed with simple teeth. The parasphenoidal pharyngobranchial apophysis is transverse, not pillar-like; microgillrakers externally on second to fourth arches; second pharyngobranchial well-toothed; about 6+1+12+4, most rather strong, well-denticulate rakers externally on first arch, small interarcual cartilage, 4-5 tooth-plates on fourth ceratobranchial.

Lateral lines on caudal-fin short, between rays D3 and D4, D1 and V1, and V4 and V5, but fin scaly only basally; dorsal- and anal-fins extensively scaly.

D. XI-XIV.18-31; A. V-VII.19-32 (Schultz 1967, Burgess 1976; limital counts rare).

This may be the most plesiomorphic group among those with swim-bladder extension. The shape of the vertebral hypapophysis, the produced dorsal- and anal-fin, perhaps also the coloration defines the group; relationship with *Mesonauta* is suggested by the postabdominal ribs, and the long and thickened first pelvic-fin ray.

Paepke (1979) has monographed the genus from an aquaristic view-point, but including aspects of history, taxonomy, anatomy, distribution and behaviour. Vandewalle (1971) has some osteological and myological data; Koltzer (1953) described the abdominal anatomy.

RETROCOLUS

Retroculus Eigenmann & Bray, 1894. *Ann. N.Y. Acad. Sci.* 7, p. 614 (type by monotypy *R. boulengeri* Eigenmann & Bray). - Masculine.

Chromys lapidifera Castelnau, 1855. *Anim. nouv. rares. Poissons.* 16, pl. 12, fig. 1 (as *Chromys lapidifer*) (la grande cascade de l'Araguay (Caxoeira grande)).

Retroculus boulengeri Eigenmann & Bray, 1894. *Ann. N. Y. Acad. Sci.* 7, p. 614 (Brazil).

Retroculus septentrionalis Gosse, 1971. *Bull. inst. r. Sci. nat. Belg.* 47 (43), p. 11, Pl. V (Guyane française dans le fleuve Oyapock à Saut-Alikoto (en amont du village de Camopi)).

Retroculus xinguensis Gosse, 1971. *Bull. inst. r. Sci. nat. Belg.* 47 (43), p. 7, Pl. IV (Brésil dans le Rio Xingu aux Caxoeira von Martius (à la limite Nord de l'Etat du Matto Grosso)).

Generic characters listed by Gosse (1971) include: prognathous upper jaw; first (epi)branchial lobe with gill-rakers along the base; absence of microgillrakers; first gill-arch internally with some small spines on tuberosities forming the tip of each gill-rakers; second and third gill-arch with similar spines on both sides on gill-raker tips; fourth gill-arch with those spines only on the external side; two supraneurals. The genus would be similar to *Geophagus*, but with gill-rakers along the base of the lobe, and to *Acanichthys*, but with deeper lachrymal, no microgillrakers, and two instead of one supraneural.

Retroculus species are large (to c. 190 mm SL) specialized rheophilous cichlids with narrowly triangular facial outline, low mouth, thick lips, broad pelvic-fin, superiorly placed eyes, and embedded, small, or absent ventral scales anteriorly on body and head. Most extreme in these regards is *R. septentrionalis*, in the Oyapock basin, which I consider the most derived form. *Retroculus xinguensis* is collected in the middle Xingu, and *R. lapidifer* in the middle R. Araguaia.

In *Retroculus xinguensis* at least, the epibranchial lobe is chiefly a soft, tuberculate pad; the osseous laminar expansion is very narrow. Long fingerlike external epibranchial rakers are placed along the hind margin of the epibranchial skin, (strictly not on the lobe base). External first ceratobranchial rakers are long, narrow tooth-less structures, covered by skin that continues across the arch as budded ridges; remarkable are additional, soft, projections along the edge of the skin fold on the lower portion of the arch. Other rakers, except inner fourth ceratobranchial, as described by Gosse, with apical teeth. No microgillrakers, or

fifth ceratobranchial rakers, but three tooth-plates on fourth ceratobranchial. The roof and sides of the posterior part of the oral chamber is covered by numerous, often budded papillae.

The jaw dentition is as in *Geophagus*, but with inner teeth in *R. septentrionalis* and *R. lapidifer* reduced in number and to an anterior patch; in *R. septentrionalis* anterior teeth also blunt-tipped. Upper jaw prognathous.

Two supraneurals; low supraoccipital crest; no ribs on caudal vertebrae; 7-8 procurrent caudal-fin rays. Premaxillary ascending processes very long; no parhypural spine; posterior margin of hypural plate notably curved.

Counts slightly lower in *R. septentrionalis*; in the others vertebrae 15+17-19; D. XVI-XVII.10-12; A. III.6-7; squ. long. 36-40; external first gill-arch with 9-11 epibranchial and 10-13 ceratobranchial rakers; *R. septentrionalis* with abdominal vertebral number reduced, 13-14+17-18 according to Gosse.

The lateral line is in two sections, the posterior continued onto the base of the caudal-fin, which is densely scaly to near the hind edge except along most of middle membranes. There are no canals on dorsal and ventral lobes, but well-preserved specimens show short lines of pored scales between rays D2 and D3, V4 and V5.

The pectoral-fin is scaly basally; the anal-fin base covered by a scaly sheath and short series of interradial scales; the dorsal-fin has a scaly sheath basally and long series of interradial scales also on posteriormost membranes. The pelvic-fin is naked.

The pelvic-fin is broad and much thickened along the outer half; the third ray is the longest and extensively branched. Pectoral-fin short, extension as pelvic-fin. Caudal-fin emarginate, with rounded lobes.

Retroculus are plesiomorphic cichlids for reason of the African type lips, both lip folds, however, discontinuous anteriorly; five dental, seven preopercular lateralis foramina; lachrymal with four foramina, margined by a narrow first infraorbital with joint rostral foramen with a lachrymal foramen as in *Cichla*, five separate infraorbitals behind.

Aside from the lobe, which is rather atypical, and a general resemblance to *Geophagus*, there is nothing that definitely ties *Retroculus* to geophagines. Similarities to African cichlids are apparent (also p. 307), but not precise. *Tylochromis* aside from the opercular spot also has a similar richly folded gill-arch skin, but the inner ceratobranchial rakers are similar to the external ceratobranchial rakers, slender, non-denticulate, the fourth ceratobranchial is edentulous, the first epibranchial is slender, and the prominent pharyngeal pad derives from the second epibranchial. No association of *Tylochromis* with any particular South-American genus is suggested by data available at present.

Gosse (1971) has good figures of all three species. The neotype-locality of *Retroculus lapidifer* was incidentally figured on the cover of Lowe-McConnell (1978; island in center).

SATANOPERCA

Satanoperca Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 312 (type by subsequent designation by Eigenmann (1910a), *Geophagus acuticeps* Heckel). - Feminine.

Geophagus acuticeps Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 394 (Barra do Rio-negro).

Geophagus Daemon Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 389 (Rio-negro).

Geophagus Jurupari Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 392 (an der Mündung des Rio-negro in den Amazonenstrom).

Geophagus mapiritensis Fernández Yépez, 1950. *Mem. Soc. Cienc. nat. La Salle* 10, p. 117, fig. p. 117 (Rio Mapirito al Sur de Maturín, Venezuela).

Geophagus leucostictus Müller & Troschel, 1849, in Schomburgk. *Reisen Brit. Guiana* 3, p. 625 (See Amucu; Sümpfen der Savanne).

Satanoperca macrolepis Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 314 (De-

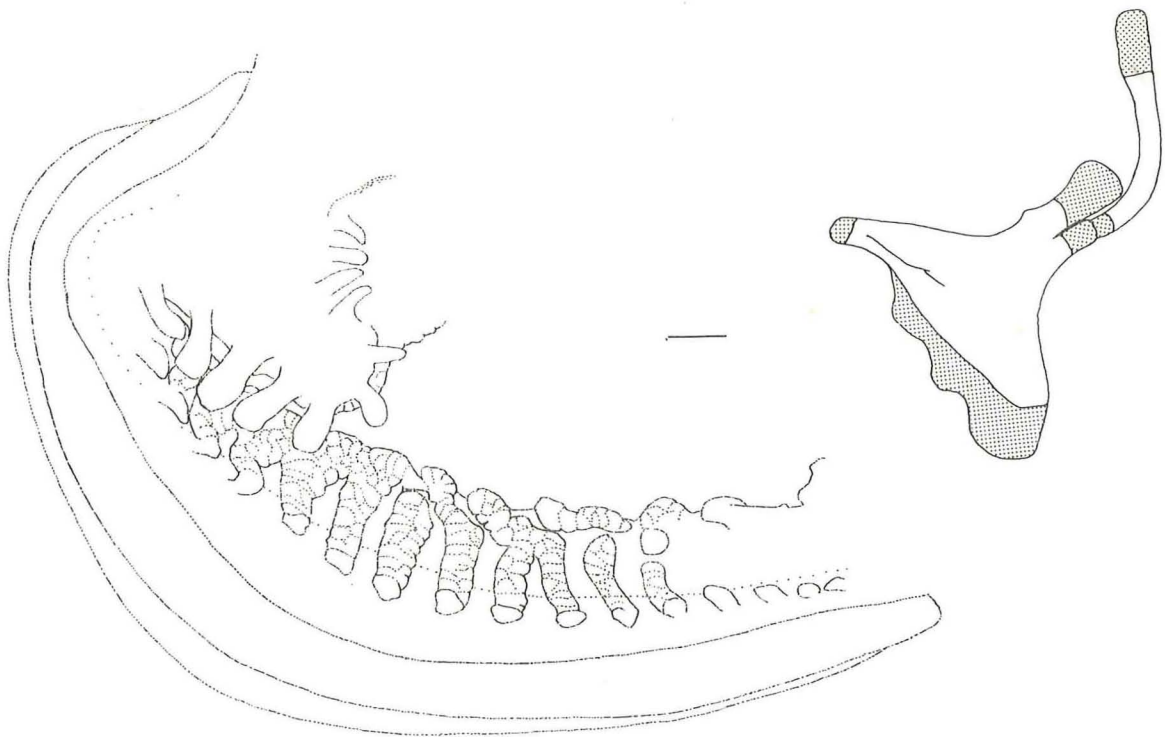


Fig. 124. *Satanoperca leucosticta*. External aspect of first gill-arch (left) and laterorostral aspect of first epi- and pharyngobranchial (right; epiphyseal cartilage and ventral connective tissue pad stippled). Scale 1 mm. From ZMA 105.818, 74 mm SL.

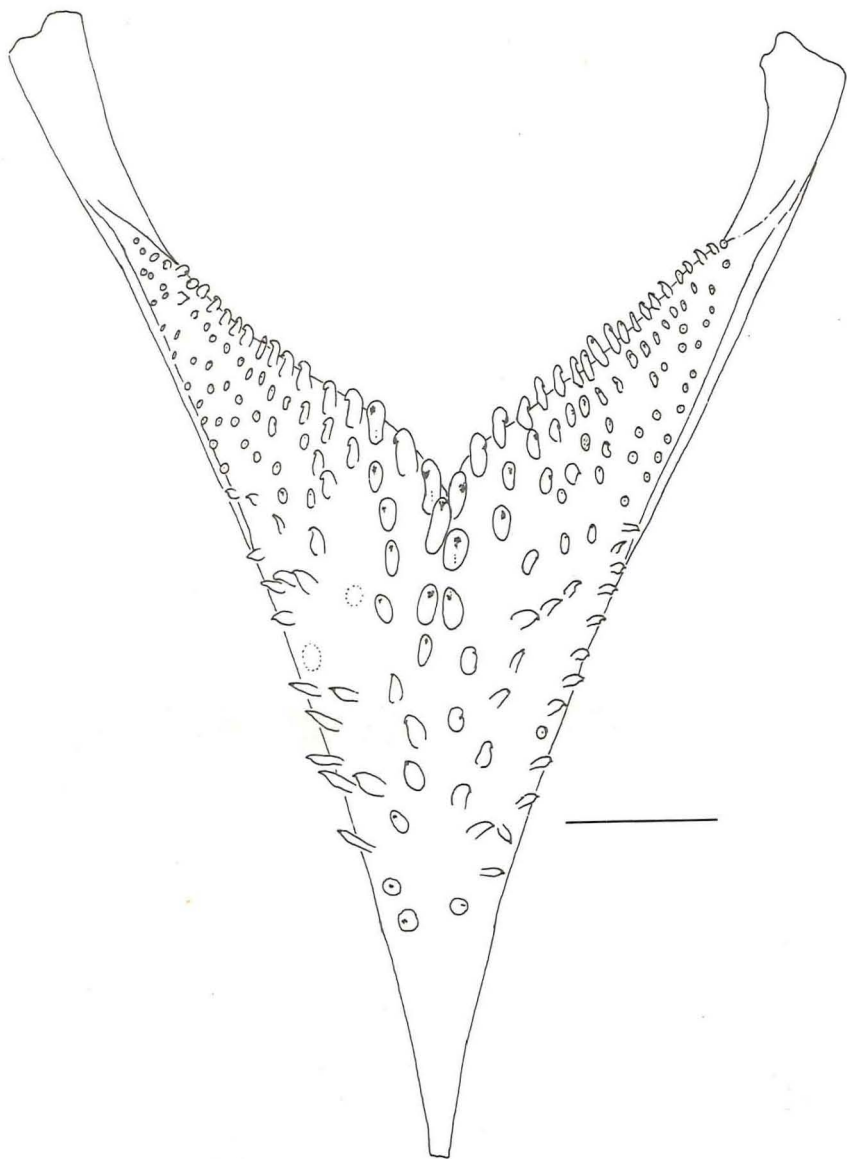


Fig. 125. *Satanoperca* sp. aff. *daemon*. Occlusal view of lower pharyngeal tooth-plate. Scale 1 mm. From IRSNB unreg. (SOK 63), 72 mm SL.

merara; British Guiana).

Geophagus Pappaterra Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 396 (Rio-Guaporè).

This group, included in *Geophagus* by Gosse (1976) and most authors after Günther, is very different from *Geophagus s. str.*, even in the appearance of the epibranchial lobe, and no closer relationship with *Geophagus s. str.* is suggested. Furthermore, there are apparently three well-differentiated phyletic lineages within the genus, here provisionally regarded as species groups, with the following principal characteristics:

Satanoperca acuticeps, uniquely among larger geophagines has a large forwards (instead of ventrad/rostrad) protrusible mouth; both lip folds are continuous. Upper jaw teeth run in one (young) or two (adults) series; lower jaw with short anterior series and an inner anterior patch of teeth. Vertebrae 14+14. Three distinct flank spots and caudal ocellus in line just above lateral line level.

Satanoperca daemon and an undescribed species in the R. Negro and R. Trombetas, both called *G. daemon* by Gosse (1976), have low, rostroventrad protrusible mouth and the lower lip fold discontinuous; upper jaw dentition uniserial, along anterior two-thirds of alveolar process of premaxilla; lower jaw with short anterior series and a few anterior inner teeth. Vertebrae 16+14 or 16+15. Larger than the others (to 230 mm SL) and with generally higher counts. Prominent superior caudal fin ocellus, one or two epaxial flank blotches.

Satanoperca jurupari and remaining species (all *jurupari sensu* Gosse), have mouth, teeth, and lips like the preceding. Vertebrae 15+13-14. Minute superior caudal spot, flank markings obscure or absent.

Moderately elongate with long snout. The supracleithrum is, with few individual exceptions, serrated. The lower jaw is prognathous. Squ. long. 28-30 (26-31); 16-20 circum-peduncular scales series. Cheek completely scaly. Dorsal- and anal-fins naked. Caudal-fin scaly, with moderately long lateral line sequences between rays D3 and D4, V4 and V5. D. XIII-XVI.9-11; spines increasing in length to fifth to seventh to ninth, behind shorter, last again a little longer, or increasing in length to last. A. III.(6)7-9. Caudal-fin truncate. Pectoral-fin subacuminate, to above spinous anal-fin. Pelvic-fin with first ray longest.

Branchial skeleton attenuate. Third pharyngobranchial with long, elongate dorsal apophysis. The fifth ceratobranchial lack rakers, the fourth ceratobranchial is edentulous. The interarcual cartilage and the first pharyngobranchial are long, rod-like. Microgillrakers are found on both sides of the second and third arches, externally on the fourth. The lobe depth equals the epibranchial length; along the margin runs a series of 5-11 distally expanded rakes, medially four to five pointed. Most of the 15-22 external ceratobranchial and also the internal rakers attach to the skin fold below the ceratobranchial, and continue transversely over the arch by tuberculate soft low ridges (Fig. 124). Lower pharyngeal tooth-plate long, slender, with deeply incised hind margin; teeth bi- or tricuspid (Fig. 125).

Vertebrae see above; long hypapophysis on third vertebra. Single supraneural. No ribs on caudal vertebrae. Parhypural spine well-developed. Procurent caudal-fin rays 5-6.

Five dental, six preopercular lateralis foramina; infraorbitals io2, io3-5 with two median foramina, io6. The reduced dentition and ventrally placed ceratobranchial rakers are primary apomorphic character states, other characteristic tend to be plesiomorphic or regularly occurring derived character states.

Satanoperca acuticeps which was confused with both *S. daemon* and *S. jurupari* in Gosse's (1976) description, is collected along the Solimões-Amazonas from Tefè to R. Tapajós.

Satanoperca daemon, with two flank spots, is found in the upper R. Negro, Casiquiare, and upper R. Orinoco. A similar species, with single flank spot, occurs in

the lower R. Negro and R. Trombetas.

The *jurupari* group has a near pan-Amazonian distribution. *Satanoperca leucosticta* is taken in the Essequibo and Corantijn. *Satanoperca pappaterra* is a Guaporéan-Paraguayan species. An undescribed *leucosticta*-like species is known from the Upper R. Orinoco system. All the rest, including *G. mapiiritensis*, are tentatively identified as *S. jurupari*; from the Ucayali, Solimões, Amazonas, Oyapock, Orinoco, Golfo de Paria system, but not sympatric with other species. Members of this group kept by aquarists are biparental larvophilous mouthbrooders (Peters & Berns 1982; Reid & Atz 1958, *G. jurupari* = *S. leucosticta*).

SYMPHYSODON

Symphysodon Heckel, 1840. *Annl. wien. Mus. Natges.* 2, p. 332 (type by monotypy *S. discus* Heckel). - Masculine.

Symphysodon discus var. *aequifasciata* Pellegrin, 1904. *Mém. Soc. zool. Fr.* 16, p. 250 (Teffé (Brésil); Santarem (Brésil)).

Symphysodon aequifasciata axelrodi L.P. Schultz, 1960. *Trop. Fish Hobby.* 8 (10), p. 14, fig. p. 9 (Belem, Brazil, Amazon River).

Symphysodon aequifasciata haraldi L.P. Schultz, 1960. *Trop. Fish Hobby.* 8 (10), p. 11, fig. p. 8 (Benjamin Constant, Brazil in the Amazon).

Symphysodon discus Heckel, 1840. *Annl. wien. Mus. Natges.* 2, p. 333 (bei Barra do Rio-negro im Flusse selbst).

Symphysodon discus willischwartzi Burgess, 1981. *Trop. Fish Hobby.* 29 (7), p. 37, fig. p. 37 (Rio Abacaxis (a tributary of the Rio Madeira), Brazil).

Symphysodon resemble *Heros*, but are more compressed and deep-bodied, with smaller scales and longer vertical fins (D. VIII-X.28-32; A. VI-IX.27-31). Dorsal- and anal-fins are extensively scaly. Inner half of caudal-fin scaly; lateral line on dorsal lobe between rays D2 and D3, and on ventral lobe between rays V4 and V5. The mouth is small, with short jaws, fleshy lips with continuous folds; 2-4 simple teeth on each side of upper jaw close to symphysis, about 5 teeth in a group correspondingly in each lower jaw half. Swimbladder diverticula reach to the 13th hemal spine, and are not associated with ribs. Vertebrae 12-14+17-20 (modal 13 and 18) = 30-33 (Schultz 1960). Two supraneurals, no parhypural spine; three procurrent caudal-fin rays. Four dental, six preopercular lateralis foramina; infraorbitals io2, io3+4, io5, io6; frontoparietal crest wide; median frontal crests high, diverging anteriorly and lifting up coronalis canal. Three extrascapulars, apparently correlated with the high nape.

The branchial skeleton is noteworthy for the absence of microgillrakers, fourth ceratobranchial and second pharyngobranchial teeth, as well as first epibranchial rakers; five or six non-denticulate very small external ceratobranchial rakers.

The extrascapulars, the reduced jaw dentition and absence of pharyngobranchial 2 teeth are autapomorphies of *Symphysodon*.

Symphysodon discus willischwartzi was defended by Burgess on the basis of higher squ. long. count (53-59) than R. Negro-R. Trombetas *S. discus* (45-53). As I find squ. long. 48-60 in R. Negro *S. discus* (including some of Burgess' specimens, and Schultz' fish with 44 (actually 50)), and 55-62 in the paratypes of *S. d. willischwartzi*, it seems evident that there is too much variation in their type-locality area to give emphasis to a slightly higher range in a small Abacaxis sample, especially as no other difference can be found.

Schultz' subspecies are based on life colours and what appears to be individual variation in head squamation (pers. obs., and cf. Hanel 1981). Preserved material cannot be told apart; but the lack of a blue or green field along the anal-fin base in the 'brown discus' (*axelrodi*) as compared to the 'green' (*aequifasciatus*) and 'blue' (*haraldi*), permits recognition of at least two forms, the former in the Brazilian R. Amazonas, the latter in the Solimões and adjacent Peruvian Amazonia. As long as there is no lectotype of *S. aequifasciatus*, and the syntypes come from localities each within the range of two of Schultz' subspecies, it is, however, not

possible to distinguish them nomenclaturally. Only the holotype is known of *S. ae. haraldi*, which in its present state offers no distinguishing features. Commercial aspects on these highly priced/prized aquarium fishes, have probably played some role in the nomenclomania.

Symphysodon is thus regarded tentatively as composed of two species, distinguished primarily by colour pattern: *S. discus* with emphasized vertical stripe across the middle of the side, *S. aequifasciatus* with sides crossed by seven equally intense, but not particularly strong vertical bars.

The genus has received attention as the young apparently require to feed on mucus from the parents' sides (especially Hildemann 1959), but many other cichlids are recorded for similar parent-young interaction (Noakes 1979). The chromosome number (2N = 60) is unique and very high for cichlids (Thompson 1979).

TAENIACARA

Taeniacara Myers, 1935. *Proc. biol. Soc. Wash.* 48, p. 11 (type by original designation *T. candidi* Myers). - Feminine.

Taeniacara candidi Myers, 1935. *Proc. biol. Soc. Wash.* 48, p. 11 (in the Amazon (middle)).

Apistogramma weisei Ahl, 1936. *Mitt. zool. Mus. Berl.* 21, p. 268 (Santarem).

This is probably the most mis-known South American cichlid. It was first described by Myers on aquarium material without certain locality. Myers noted that the lateral line as well as first gill-arch lobe were lacking; consequently he placed *Taeniacara* near *Nannacara*. A few months later, Ahl described the same species as *Apistogramma weisei* from Santarém. Ahl noted the lateral line as hardly visible; and wrote that the middle and preceding dorsal-fin membranes were strongly produced, a characteristic well shown in the illustration in Arnold & Ahl (1936).

I have not seen Myer's type-specimens, but re-examined Ahl's type, which has short dorsal-fin lappets. Neither are produced dorsal-fin lappets shown by other male *T. candidi* that I have examined. Besides there is a small lobe on the first epibranchial easily overlooked on intact fish and comparatively much smaller than in *Apistogramma*. The lateral lines are present, but all or nearly all scales bear only a small central pore.

Taeniacara is characterized by the far-going reduction of the lateralis system, agrees otherwise very well with *Apistogramma*. There are only three dental pores; comparing with *Apistogramma* it appears that the rostral two are combined to one, and the adanguloarticular is closed; the anguloarticular canal is missing, like the middle pterotic and second (clf2) frontal foramen, and the distal extrascapular bone; of infraorbitals remain only a sickle-shaped autogenous bone (Fig. 126), apparently compact, that probably represents io3+4. Hypurapophysis, interarcual cartilage, and vertebral hypapophysis are lacking. The last abdominal vertebra has a hemal arch and the anterior two caudal vertebrae bear epipleural ribs (vertebrae 12+12). One supra-neural.

There is occasionally a rudimentary first ceratobranchial raker. Fifth ceratobranchial rakers are difficult to distinguish, but frequently verifiable and much reduced even compared to *Apistogramma*. The chest is naked rostrally. The reduction of the number of circumpeduncular scale series to 12 (among South American cichlids shared only with an aberrant *Apistogramma* species), and a very wide lateral band as compared to *Apistogramma*, are probably correlated with the extremely attenuate body shape.

The largest wild specimen that I examined is 29.9 mm SL. The species is known only from the lower Tapajós, Monte Alegre, and lower and middle R. Negro.

Taeniacara may be regarded as an extremely reduced *Apistogramma*, but there is no clear relationship to any particular *Apistogramma* lineage. *Taeniacara* parallel *Nannacara* in the loss of the clf2 foramen, but these fishes are otherwise different enough not to be considered closely related.

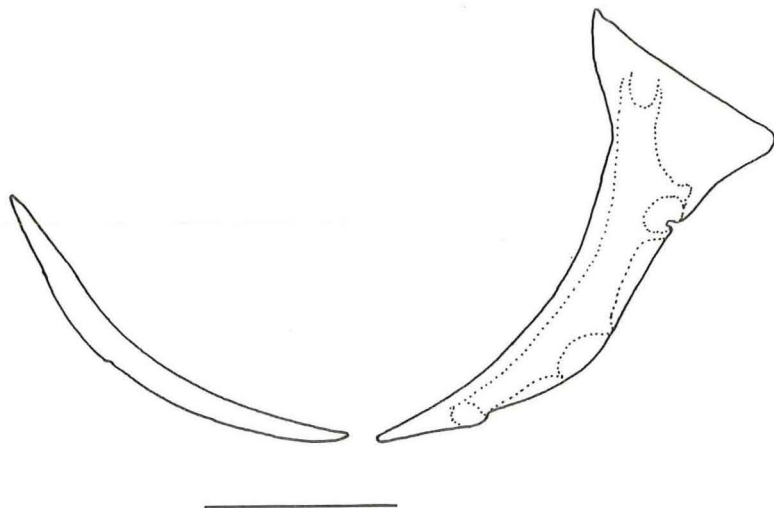


Fig. 126. *Taeniacara candidi*. Suborbital series in lateral aspect, the lachrymal is the right hand bone. Scale 1 mm. From NRM unreg., Alizarin 22, 26 mm SL.

TELEOCICHLA n. gen.

Type-species: *Teleocichla digramma* n. sp.

This is, as far as known, a small group of three species collected at the same occasion in the Cachoeira von Martius in the upper R. Xingu. They are similar to *Crenicichla*, but much modified apparently in response to rheophily: Snout short, downturned; jaws narrow, short, upper slightly projecting before lower; upper lip folded along alveolar process of premaxilla, interrupted near symphysis but continued by a fleshy pad extended and widened caudad to cover premaxilla rostral to postlabial snout skin, separated from upper lip lateral fold caudad by a groove; anterior nasal lateralis canal opening perforating postlabial skin fold well caudal to anterior skin fold margin; total vertebrae 34-35, abdominal (16-17) vertebrae equal in number to or fewer than caudal (17-20) vertebrae; pelvic-fin strong, third ray longest, outer edge thickened.

The generic name is given in allusion to the resemblance to the African cichlid genus *Teleogramma*. The gender is feminine.

Teleocichla digramma, n. sp. is known from seven specimens 39-60 mm (IRSNB 649, 650); it has separate upper and lower lateral lines, four anal-fin spines and wide interorbital (width 3.4-3.6 % of SL). Holotype IRSNB 649, 56.3 mm SL. Br sil, Rio Xing , Cachoeira von Martius. Haut Xing .  tat de Mato Grosso. 29 October 1964. Leg. J.-P. Gosse & L opold III.

Teleocichla gephyrogramma, n. sp. is known from three specimens, 37-46 mm (IRSNB 647, 648), with almost continuous upper and lower lateral lines, three anal-fin spines and wide interorbital (width 3.3-3.7 % of SL). Holotype IRSNB 647, 43.8 mm SL. Collecting data as preceding.

Teleocichla monogramma, n. sp., from the single known specimen, 63 mm, has a continuous lateral line, three anal-fin spines and narrow interorbital (width 2.4 % of SL). Holotype IRSNB 646, 63.2 mm SL. Collecting data as preceding.

No field behaviour observations are available, but comparison with known rheophilic cichlids suggest that most characters separating those three species from *Crenicichla* are specializations correlated with benthic rheophily, although unlike the majority of African rheophilic forms, the *Teleocichla* species seem to be open-bottom dwellers judging from the light overall coloration with a cryptic pattern of dark speckles. Few anatomical data are available, as dissections seemed unadvisable with respect to the few specimens known. However, as in *Crenicichla*, the supraoccipital crest is reduced, supraneurals are lacking, and the *m. pharyngocleithralis internus* is attached to the lateral face of the cleithrum. The scales are small (64-89), the dorsal-fin long (XX-XXI. 9-11), and there are rakers on the lower pharyngeal tooth-plate.

Gill-rakers number (3-6 on first ceratobranchial) and jaw dentition (15-19/14-25 teeth, in 3-5 inner series) are reduced compared to *Crenicichla*, however, and the preopercular edge is smooth.

The shape is more terete than in most *Crenicichla*, with lower gravity center, and suggests a more cobitid-like motion. The downwards directed mouth, with prognath upper jaw indicates bottom feeding, and the thickened upper lip suggests that food is obtained in the bottom substrate.

The scales of ventral regions are reduced in size and deeply embedded in skin; lower cheek and gill-cover scales may be wanting, but also the nape scales are small or wanting anteriorly, the former condition characteristic of bottom fishes, the latter common to rheophilic cichlids but also minute cichlid species.

One species, *T. monogramma*, uniquely among crenicichlines, has an asymmetrical pectoral-fin, with the upper portion long, the third ray the longest, and the lower edge slightly thickened.

The pelvic-fin is inserted close to the head, compared to *Crenicichla*, and is long and pointed, reaching to or almost to the genital papilla. The outer edge from

spine tip to first or second ray branches is thickened; the rays are stout and the fin cannot be much spread. The paired fins are thus as in benthic fishes in general, and the pelvic-fins are probably used as a support for the fish resting on the bottom.

A continuous lateral line is met with in two African rheophilic cichlid genera, *Teleogramma* Boulenger, and *Gobiocichla* Kanazawa, and correlates with the extremely attenuate body shape of these fishes.

There are very few specialized rheophilic cichlids known from South America; in addition to *Teleocichla*, only the three *Retroculus* species, but *Crenicichla jupiaensis* in the Paraná system have characters suggesting it they may be benthic at least, and *Geophagus harreri* also shows rheophilous traits.

Very little collecting has been done in rapids in South America; partly because of the technical problems, but also because rapids are relatively rare and in remote regions, chiefly in the margins of the Guianas and Brazilian highlands. So, I suspect that more rheophilic cichlids will turn up, and that the distribution of the genus *Teleocichla* will be found to be more extensive, perhaps including more species.

UARU

Uaru Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 330 (type by monotypy *U. amphiacanthoides* Heckel). - Masculine.

Uarus Cope, 1872. *Proc. Acad. nat. Sci. Philad.* 23, p. 254 (unjustified emendation of spelling of *Uaru*). - Masculine.

Uaru amphiacanthoides Heckel, 1840. *Annln wien. Mus. Natges.* 2, p. 331 (Rio-negro oberhalb Airao).

Pomotis? fasciatus Jardine, 1843. *Nat. Libr. Ichthyol.* 5, p. 169, Pl. 17 (Rios Padauri and Negro).

Uaru obscurum Günther, 1862. *Catal. Fish. Br. Mus.* 4, p. 302 (River Cupai).

Acara (Heros) imperialis Steindachner, 1879. *Sber. k. Akad. Wiss. Wien Math.-natw. Cl.* 80, p. 161 (Ausstände des Amazonenstromes zunächst der Mündung des Rio negro).

These cichlids are remarkable for the ontogenetic changes in coloration. Juveniles have a contrasting dark/light pattern similar to that of young *Astronotus*. Young are dark with light spots providing a mottled flank pattern. Adults then, are light brownish with a large dark brown blotch, caudad tapering, over most of the side below the upper lateral line above the level of the lower edge of the caudal peduncle, also a dark spot over the dorsal half of the caudal-fin base, one dorsally on the pectoral axilla and one behind the eye.

The largest specimens seen are c. 180 mm SL. The body is relatively deep and compressed. Scales small (squ. long. 47-48), ctenoid except on head, preventrally and predorsally. Soft dorsal- and anal-fins scaly basally; caudal-fin scaly only basally, with short lateral line sequences between rays D2 and D3 and V4 and V5.

The dorsal-fin spines increase in length to the fifth, but are shorter behind the seventh, the last two only slightly longer; a unique condition among cichlasomines. D. XVI.14-15; A. VIII.13-14. Caudal-fin subtruncate.

The genus is distinguished in particular by the jaw dentition. The anterior teeth are gradually greatly enlarged and procumbent, distally compressed linguad-labial, with blunt tip, the lingual edge otherwise with a narrow ledge with two or three small projections (Pellegrin 1904, Figs. 3, 20). Posterior teeth simple, pointed. Dorsal skull crests are well-developed and the lower jaw massive. Vertebrae 14+15, third and fourth with ventrally contiguous long hypurapophyses (Pellegrin 1904, Fig. 8); second pharyngobranchial toothed; fourth ceratobranchial edentulous, microgillrakers externally on second to fourth arches; small interarcual cartilage; lower pharyngeal tooth-plate with rounded convex hind margin; parasphenoidal pharyngobranchial apophysis transversely wide.

Swim-bladder confined to abdominal cavity, but anterior two caudal vertebra, with short pleural ribs. Lip folds interrupted, but upper lip thickened and widened sympathically. Gill-rakers short, conical, non-denticulate, 2+1+6-7 externally on first

arch.

A single species, known from scattered localities along the Solimões-Arzonas from Tonantins to Porto do Moz, is recognizable. It was most recently re-described in a superficial way by Travassos & Pinto (1960).

The type-series of *U. imperialis* consists of four juveniles, 25 mm SL, now completely dried-out, so only generic identification is possible.

Uaru resembles *Hoplarchus* and *Heros* in general, in the stout lower jaw also *Symphysodon*, but the precise relationships remains here an unsolved problem.

The generic name is said to be derived from the local Uarù-urà, apparently a singular variant transliteration of Bararuá. It is masculine following the International Code of Zoological Nomenclature, Art. 30 (b)(ii).

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Titles listed below are either cited in the preceding text (Part II only) or contain information about South American cichlids, or both.

It has not been possible to compile a complete bibliography of South American cichlids, but the list should be up to date (31 December 1982) with regard to taxonomy.

Papers missing should be chiefly in the field of physiology, ethology, and histology, although all important ethnological works are covered.

There are also flaws in the coverage of literature published in South America, but to what extent is difficult to estimate. This literature is either of limited circulation or never entered into literature recording journals. The classical example is Fernández-Yépez' *Evencias* (thanks to Stanley Weitzman, Gordon Howes, and Francisco Mago for copies of those cited).

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